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RESEARCH ARTICLE

High-tech or field techs: Radio-telemetry is a cost-effective method for reducing bias in songbird nest searching

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ABSTRACT

We compared the efficacy of standard nest-searching methods with finding nests via radio-tagged birds to assess how search technique influenced our determination of nest-site characteristics and nest success for Golden-winged Warblers (*Vermivora chrysoptera*). We also evaluated the cost-effectiveness of using radio-tagged birds to find nests. Using standard nest-searching techniques for 3 populations, we found 111 nests in locations with habitat characteristics similar to those described in previous studies: edges between forest and relatively open areas of early successional vegetation or shrubby wetlands, with 43% within 5 m of forest edge. The 83 nests found using telemetry were about half as likely (23%) to be within 5 m of forest edge. We spent little time searching >25 m into forest because published reports state that Golden-winged Warblers do not nest there. However, 14 nests found using telemetry (18%) were >25 m into forest. We modeled nest success using nest-searching method, nest age, and distance to forest edge as explanatory variables. Nest-searching method explained nest success better than nest age alone; we estimated that nests found using telemetry were 10% more likely to fledge young than nests found using standard nest-searching methods. Although radio-telemetry was more expensive than standard nest searching, the cost-effectiveness of both methods differed depending on searcher experience, amount of equipment owned, and bird population density. Our results demonstrate that telemetry can be an effective method for reducing bias in Golden-winged Warbler nest samples, can be cost competitive with standard nest-searching methods in some situations, and is likely to be a useful approach for finding nests of other forest-nesting songbirds.

Keywords: bias, cost effectiveness, Golden-winged Warbler, nest searching, radio-telemetry, *Vermivora chrysoptera*

Alta Tecnología o Técnicas de Campo: La Radio Telemetría es un Método Efectivo en Términos de Costo para Reducir el Sesgo en la Búsqueda de Nidos de Aves Canoras

RESUMEN

Comparamos la eficacia de los métodos estándar de búsqueda de nidos con el hallazgo de nidos a través de aves marcadas con radios y evaluamos como la técnica de búsqueda influencia la caracterización de los sitios de nidificación y la determinación del éxito del nido en *Vermivora chrysoptera*. También evaluamos el costo-beneficio de usar aves marcadas con radios para hallar los nidos. Usando el modo estándar de búsqueda de nidos en tres poblaciones, encontramos 111 nidos en ubicaciones con características de hábitat similares a las descriptas en estudios previos: bordes entre bosque y áreas relativamente abiertas de vegetación en sucesión temprana o humedales arbustivos, con 43% dentro de los 5 m del borde del bosque. Los 83 nidos encontrados usando telemetría tuvieron la mitad de la probabilidad (23%) de estar dentro de los 5 m del borde. Empleamos poco tiempo buscando nidos a >25 m en el bosque, ya que los informes publicados señalan que los individuos de *V. chrysoptera* no nidifican allí. Sin embargo, encontramos 14 nidos (18%) a >25 m dentro del bosque usando telemetría. Modelamos el éxito de nidificación usando el método de búsqueda del nido, la edad del nido y la distancia al borde como variables explicativas. El método de búsqueda del nido explicó el éxito de nidificación mejor que la edad sola; estimamos que los nidos encontrados con telemetría tuvieron 10% más de probabilidad de emplumar polluelos que los nidos encontrados usando el modo estándar de búsqueda. Aunque la radio telemetría fue más costosa que la búsqueda estándar de nidos, el costo-beneficio de ambos métodos difirió dependiendo de la experiencia del buscador, la cantidad de equipamiento propio y la densidad de la población de aves. Nuestros resultados demuestran que la telemetría puede ser un método efectivo para reducir el sesgo en las muestras de nidos de *V. chrysoptera*, puede ser competitivo en términos de costo en relación a los métodos estándar de búsqueda en algunas situaciones, y es probable que sea un enfoque útil para encontrar nidos de otras aves canoras que nidifican en el bosque.

Palabras clave: búsqueda de nidos, costo-beneficio, radio telemetría, sesgo, *Vermivora chrysoptera*

INTRODUCTION

Nest monitoring is nearly ubiquitous in studies of avian reproductive ecology (Martin and Geupel 1993, Martin et al. 1996, Jehle et al. 2004). Two common goals of nest monitoring studies are to describe nest site habitat characteristics and to estimate daily survival of nests (Martin and Geupel 1993). Vegetation characteristics measured at multiple spatial scales around monitored nests are often used to identify important habitat features for a species of interest (e.g., Martin 1993, Klaus and Buehler 2001, Bulluck and Buehler 2008, Etterson et al. 2014, Peak and Thompson 2014). Daily survival estimates from monitored nests are commonly used to estimate nest success and productivity for a study population (e.g., Mayfield 1961, 1975, Johnson 1979, Shaffer 2004). In nearly all nest monitoring studies, it is not possible to monitor every nest in the population or area of interest. Therefore, an explicit or, more commonly, implicit assumption in studies of songbird reproductive ecology is that the monitored nests are a representative (i.e. unbiased) sample of nests in the population of interest. However, few studies of breeding birds have assessed whether this assumption is valid, primarily due to the difficulty of obtaining a known unbiased sample for comparison (but see Daw et al. 1998, Powell et al. 2005).

Studies of songbird reproductive ecology are often designed to maximize sample size, a goal that is constrained by available resources (i.e. time and manpower). To maximize the likelihood of finding nests, observers often target specific vegetation types or locations within cover-type patches based on published information or prior experience (e.g., Martin and Guepel 1993, Powell et al. 2005). As a result, observers may search only areas where nests are relatively easily found, resulting in biased samples of nest locations and nesting habitat characteristics, perpetuating incomplete knowledge of a species' nesting ecology. In addition, nests that are unintentionally but systematically excluded from a sample may experience different survival rates, biasing estimates of daily nest survival. Radio-tagging and following female Wood Thrushes (*Hylocichla mustelina*) to nests using ground-based radio-tracking was shown in one study to reduce nest location bias, with nests found at higher elevations, farther from streams, and in different vegetation types than nests found using standard nest-searching methods (Powell et al. 2005). However, radio-telemetry has not been widely adopted for finding songbird nests, despite potential biases in standard searching methods (Powell et al. 2005).

To determine whether the sample of nests found using radio-telemetry (hereafter, 'telemetry') was different from nests found using standard nest-searching techniques, we compared Golden-winged Warbler (*Vermivora chrysoptera*) nests found using both methods in 3 populations in the western Great Lakes region in central North America. We used nests found via each method to assess nest location, nest-site vegetation composition and structure, and nest success. We also assessed how the cost to find a nest differed between nest-searching techniques.

METHODS

Study Species

Golden-winged Warblers are small (~9 g) Neotropical migrants that nest in northeastern to north-central North America (Confer et al. 2011). Golden-winged Warblers are currently listed as Endangered, Threatened, or of High Management Concern in 10 states and in Canada (Buehler et al. 2007), and as Threatened by the International Union for the Conservation of Nature (IUCN 2013). The U.S. Fish and Wildlife Service lists the Golden-winged Warbler as a Species of Concern and is currently considering a 2010 petition to list the species as Federally Endangered. Significant population declines over the last 50 years have been linked to habitat loss (Confer et al. 2011). Golden-winged Warbler nest success is strongly influenced by nest location, with nest success increasing with distance into shrubland and away from edges (Streby et al. 2014). Unbiased information about nesting habitat use and nest productivity is necessary to inform and improve management across the species' breeding range.

As with most songbirds, standard methods for finding Golden-winged Warbler nests include observing adult behavior and targeted searching in known territories and areas structurally similar to known nesting sites (Martin and Guepel 1993, Bullock and Buehler 2008). Golden-winged Warblers are known to nest on the edges of mature forest and young secondary growth or shrubby wetlands, especially in areas of high herbaceous cover, low basal area, and low canopy cover (Ficken and Ficken 1968, Klaus and Buehler 2001, Martin et al. 2007, Bullock and Buehler 2008, Confer et al. 2011). Other than an occasional nest observed <10 m from an edge into mature forest, Golden-winged Warblers are not thought to nest in mature forest, and have, perhaps erroneously, been described as early-successional specialists (Confer and Knapp 1981). Therefore, current management plans designed to benefit Golden-winged Warblers center on increasing the quantity of early-successional forest to compensate for aging secondary growth forest across the species' breeding range (Martin et al. 2007, Kubel and Yahner 2008).

Study Area and Methods

We searched for nests during May and June of 2011 and 2012 at Tamarac National Wildlife Refuge (NWR) in northwestern Minnesota, USA, in 2012 at Rice Lake NWR in northeastern Minnesota, and in 2012 in Sandilands Provincial Forest (PF) in southeastern Manitoba, Canada. Each site comprised a complex landscape consisting of mature forest (primarily deciduous forest >50 yr old), upland early-successional stands in various stages of regeneration, shrubby wetlands, forested wetlands, mature coniferous forest, a few open grasslands, and lakes and rivers. We searched for nests in 12 upland early-successional stands of 0.6–26.0 ha and 8 shrubby wetlands of 3.3–17.0 ha, most of which were entirely surrounded by mature forest. Following nesting habitat descriptions from previous studies (e.g., Confer et al. 2011), the upland areas that we searched were primarily young, shrubby, early-successional stands dominated by sedges, forbs, and hazel (*Corylus* spp.) interspersed with quaking aspen (*Populus tremuloides*), bigtooth aspen (*P. grandidentata*), and oaks (*Quercus* spp.); the shrubby wetlands that we searched were of similar vegetation structure dominated by alder (*Alnus* spp.) and willow (*Salix* spp.).

From mid- to late-May, after female Golden-winged Warblers arrived from migration but before most nesting began, we used mist nets (20–45 nets each day) to capture females in early-successional forest stands and shrubby wetlands. We placed nets primarily in areas with low, dense vegetation or in areas where female Golden-winged Warblers were consistently observed foraging. Netting was principally passive (i.e. no call broadcast), but we regularly moved nets from locations where we did not capture females, and moved all nets daily or every 2 days to maximize coverage of our study area. We banded all Golden-winged Warblers (male and female) that we captured with standard aluminum U.S. Geological Survey leg bands and plastic color bands. We attached a 0.39-g (3.9–4.3% of body mass) radio-transmitter (Blackburn Transmitters, Nacogdoches, Texas, USA) to each female Golden-winged Warbler using the figure-eight harness design of Rappole and Tipton (1991) as modified by Streby et al. (2015). We used hand-held antennas and radio receivers to track females with ground-based telemetry in the weeks after capture. We tracked each female daily until we located her nest. We did not track her again until that nesting attempt failed or succeeded. For each nest, we recorded the number of days since initiation of nesting at that site in that year. Following nest detection by either nest-searching method, we monitored nests every 4 days until the estimated fledging date. When possible, we monitored nests from a distance using binoculars and approached nests from multiple directions so as not to produce trails. We recorded the capture location of each female and the location of each nest using hand-held Global Positioning System (GPS) units (100 points averaged for an accuracy of <3 m). We assumed that nests found using telemetry tracking of females captured soon after arrival from spring migration were a representative (i.e. unbiased) sample of nests in the population. Previous work in this system (Streby et al. 2013) demonstrated that radio-telemetry had no measurable impact on clutch size, brood size, fledgling survival, and several other productivity parameters for radio-tagged female Golden-winged Warblers when compared with unmarked females.

From mid-May to early July we searched for nests using standard nest-searching methods, including walking transects and using behavioral cues of adult birds (e.g., Martin and Geupel 1993). We concentrated our searching effort in areas with habitat characteristics similar to those described in prior studies and in areas where researchers familiar with the study area indicated high densities of singing males (J. Loegering personal communication). We included nests that were independently found using both standard nest searching and telemetry in both categories for statistical analyses.

To compare lateral vegetation characteristics at nests located using both nest-searching methods, we estimated lateral vegetation density using a 2.00×0.25 m profile board modified from MacArthur and MacArthur (1961) with 8 equal sections of alternating orange and white squares. We placed the board vertically 2.5 m from the nest in each cardinal direction and recorded the percentage (rounded to 10%) of each square obscured by vegetation at a distance of 5.0 m, placing the nest between the observer and the board for each observation. We used the mean of these observations to produce one estimate of lateral vegetation cover at each nest. We compared vertical vegetation cover at nests found using each nest-searching method by taking a photograph of the canopy from 2 m above each nest using a digital camera and deriving percent canopy cover using ImageJ (National Institutes of Health, Bethesda, Maryland, USA). Within ImageJ, we analyzed each canopy photograph by splitting the color channels to isolate vegetation from sky, then making the image binary by turning pixels of vegetation black and those of sky white, and finally measuring the percentage of pixels that were black.

We used a Kolmogorov-Smirnov test to compare the distribution of nest locations in relation to forest edge for nests found using each nest-searching method in program R (R Development Core Team 2012). We defined the forest edge as the border between an early-successional stand or shrubby wetland and a stand of trees >0.25 ha in size with a canopy >5 m tall (most forest stands were >20 m tall; Peterson et al. in press). We measured distances between nests and mature-forest edge for nests <25 m from forest edge. For nests >25 m from an edge we calculated distance to edge using Geographic Information System (GIS) software (ArcMap 9.3; ESRI, Redlands, California, USA) and a cover-type layer that we derived using aerial photographs. We used 1-m resolution digital orthophoto quadrangles (2009; Minnesota Department of Natural Resources, St. Paul, Minnesota, USA) for Tamarac and Rice Lake NWRs, and georeferenced 1-m resolution satellite images obtained from Google Earth 6.2 (2010; Google, Mountain View, California, USA) for Sandilands PF. We ground-truthed aerial photographs and satellite images using >2,500 locations visited in our study sites during the course of research activities.

We used Student's *t*-tests to compare the mean number of days after the nesting season began that nests were located, lateral vegetation cover, and canopy cover for nests found during searching and using telemetry. Additionally, we used Student's *t*-tests to compare lateral vegetation cover and canopy cover between nests that were undersampled using standard nest-searching methods (i.e. nests found using telemetry that were >25 m into mature forest) and those that were adequately sampled using standard nest-searching methods (i.e. nests found in early-successional stands or <25 m into mature forest).

We used the logistic exposure method (Shaffer 2004) to fit models of nest success using 5 explanatory variables (linear nest age, quadratic nest age, nest-searching method, distance to forest edge, and nest attempt) with proc GENMOD (SAS Institute 2008). We did not include lateral vegetation cover or canopy cover in candidate models because neither of these variables was found to be significant in a previous analysis (Streby et al. 2014). We produced 24 candidate models using all relevant combinations of variables and ranked models using Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002). Using the model estimates for each variable derived from the logistic exposure method (Shaffer 2004), we calculated daily nest survival rate (S_d) as:

$$S_d = \exp(\alpha + \beta_1 x_1 + \beta_2 x_2 \ldots) / (1 + \exp(\alpha + \beta_1 x_1 + \beta_2 x_2 \ldots)),$$

where α is the estimated intercept and β_1 is the estimated coefficient for variable x_1. We calculated nest success rate (i.e. the likelihood of survival to the mean nest age at time of fledging) as:

$$S_d \wedge 24.$$

We calculated mean nest success and associated 95% confidence intervals (CI) based on 2,000 simulated seasons of nest searching in which we found 50 nests using each method. For each nest in our simulations, we stochastically calculated S_d using a normal distribution derived from the mean and variance of the β coefficients estimated in the logistic exposure model. We then used the mean nest success and associated 95% CI from the resulting distribution of estimated nest success across our 2,000 simulated seasons to compare nest success between methods. To assess whether differences in nest survival between nests located via nest searching and using telemetry occurred because of nest-searching activities, we compared the likelihood of failure within the first 4-day monitoring period after discovery between nests found using each method using a chi-square (χ^2) test of independence.

To compare the cost effectiveness of radio-telemetry vs. standard nest searching, we calculated the cost per nest found using each method by including the costs of equipment and effort. We included the cost of effort for both methods as US$11.50 per person-hour, the amount that we paid field technicians. We did not include the cost of common field equipment (e.g., binoculars and backpacks). Therefore, for standard nest searching we included only the cost of effort. We categorized mist nets (US$90 per net), mist-net poles (US$5 per net), and radio receivers and antennas (US$1,000 per radio and antenna) as reusable equipment when calculating equipment costs. We calculated total costs for telemetry using effort, radio-transmitters (US$150 per transmitter), and 3 potential scenarios regarding ownership (no reusable equipment owned, half of the required reusable equipment owned, and all of the reusable equipment in ownership). We calculated nest-searching efficiency as the number of hours required to find a nest, and defined high crew experience as >1 season of Golden-winged Warbler nest-searching experience per person, medium crew experience as 0.25–1.00 season of experience per person, and low crew experience as <0.25 season of experience per person. According to Breeding Bird Survey data, the breeding density of Golden-winged Warblers was highest at Tamarac NWR (14.1 individuals per route), followed by Rice Lake NWR (10.6 individuals per route), and lowest in Sandilands PF (not detected on route; Sauer et al. 2014).

RESULTS

Using telemetry, we found 51 nests at Tamarac NWR, 21 nests at Rice Lake NWR, and 11 nests at Sandilands PF. Nests found using telemetry for which we recorded a capture location of the female ($n = 60$) were a median of 103 m from the capture point (minimum = 3 m, maximum = 3,013 m; IQR = 202). Thirteen nests (16%) found using telemetry were known renesting attempts. Using standard

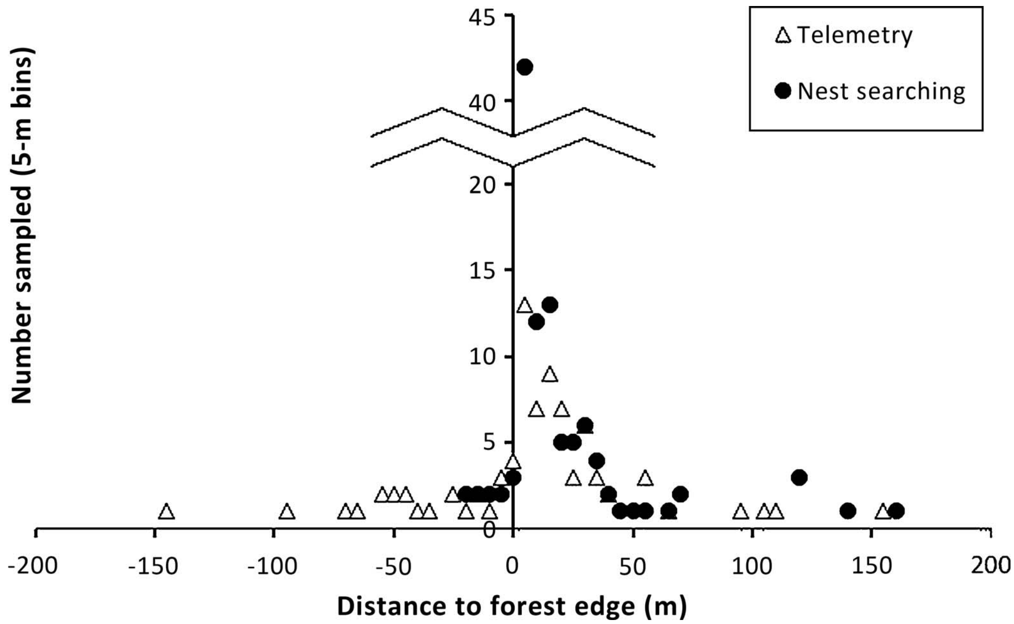

FIGURE 1. Distance from mature forest edge to Golden-winged Warbler nests found using standard nest-searching methods (black circles) and radio-telemetry (white triangles) in 2011 and 2012 at 3 sites in the western Great Lakes region, USA. Negative distances are to nests found inside mature forest stands.

nest-searching methods, we found 82 nests at Tamarac NWR, 22 nests at Rice Lake NWR, and 7 nests at Sandilands PF. One nest (1%) found using standard nest-searching techniques was a known renesting attempt. Eleven nests found using telemetry (13%) were also found using standard nest searching.

Nests that were not known renesting attempts were found at similar times after the nesting season began using both radio-telemetry ($\bar{x} = 15$ days, $n = 70$) and standard nest searching ($\bar{x} = 14$ days, $n = 110$; $t = 0.96$, $P = 0.33$). Age at time of discovery was similar for nests found using telemetry ($n = 83$, $\bar{x} = 6.06$ days) and nest searching ($n = 111$, $\bar{x} = 6.10$ days; $t = 1.77$, $P = 0.96$). Nests found using telemetry ($n = 83$) and nests found using standard nest-searching methods ($n = 111$) were distributed differently in relation to distance to the forest edge ($D = 0.202$, $P = 0.04$). Specifically, standard nest-searching methods under-sampled nests >25 m into mature forest and oversampled nests 0–5 m from the forest edge (Figure 1).

Lateral vegetation density was similar between nests detected using standard nest-searching methods ($\bar{x} = 46.3$, $n = 106$) and those found using telemetry ($\bar{x} = 45.9$, $n = 83$; $t = 0.14$, $P = 0.89$). Lateral vegetation density was also similar between nests found >25 m into mature forest ($\bar{x} = 47.0$, $n = 14$) and nests found using both methods <25 m into mature forest or in shrubland ($\bar{x} = 45.9$, $n = 164$; $t = 0.22$, $P = 0.83$). Percent canopy cover was similar between nests located using standard nest searching ($\bar{x} = 24.6$, $n = 110$) and telemetry ($\bar{x} = 29.8$, $n = 83$; $t = 1.31$, $P = 0.19$). However, percent canopy cover was significantly different between nests found >25 m into mature forest ($\bar{x} = 59.8$, $n = 14$) and those found <25 m into mature forest or in shrubland ($\bar{x} = 24.5$, $n = 169$; $t = 4.95$, $P < 0.001$).

Nest success was best explained by the model with a linear age variable and a nest-searching method variable (Table 1). Linear age was the most important variable for explaining nest success among all candidate models (cumulative Akaike weight [w] = 0.678), followed by nest-searching method (cumulative w = 0.515), nest attempt (cumulative w = 0.442), nest distance from edge (cumulative w = 0.367), quadratic age (cumulative w = 0.264), and constant survival over time (cumulative w =

TABLE 1. Akaike's Information Criterion corrected for small sample size (AIC_c) model selection results for models predicting nest survival of Golden-winged Warblers in the western Great Lakes region, USA, 2011–2012. Models with $\Delta AIC_c > 2$ are omitted. K is the number of model parameters, and w is the Akaike model weight.

Model	Log-likelihood	K	ΔAIC_c	w
Age + Method	−353.51	4	0.00 [a]	0.14
Age	−354.73	3	0.44	0.11
Age + Attempt	−353.79	5	0.56	0.10
Age + Method + Attempt	−352.91	4	0.80	0.09
Age + Method + DTE [b]	−353.00	3	0.98	0.08
Age + DTE	−354.44	2	1.85	0.06
Age + Method + DTE + Attempt	−352.46	4	1.90	0.06

[a] The lowest AIC_c = 713.02.
[b] Distance to forest edge.

0.024). For the top-ranked model, nest success decreased over time (regression coefficient = –0.0627 ± 0.0165) and nests found using telemetry were more likely to succeed than nests found using standard nest searching (regression coefficient = 0.3072 ± 0.1977). Mean nest success for simulated nest-searching seasons estimated from the best-fit model was 0.43 for nests found using radio-telemetry (95% CI: 0.39–0.47), 10% higher than the estimate of mean nest survival for nests found using standard nest searching (0.33; 95% CI: 0.29–0.36). Nests were equally likely to fail in the first monitoring period for those found using both radio-telemetry (8/83) and nest searching (12/111; $\chi^2 = 1.21$, df = 1, $P = 0.73$).

The cost-effectiveness and efficiency (i.e. nests found per hour) of telemetry compared with standard nest searching was dependent on the amount of preowned equipment and the level of experience of the nest-searching crew (Figures 2A and 2B). The cost of finding nests in Manitoba, where breeding densities were low, was higher than the cost of finding nests at the 2 Minnesota sites using both nest-searching methods. Whereas the cost of wages was sometimes reduced by using transmitters, telemetry was more expensive than standard nest searching at each of our study sites. On average, the total cost of telemetry could be reduced by up to 29% depending on how much reusable equipment was already owned (Figure 2A). With the exception of 2012 at Tamarac NWR, where we employed a highly experienced nest-searching crew, nest searching and telemetry yielded similar numbers of nests (Figure 2C).

DISCUSSION

There have been substantial advancements in the analysis of nest data in recent years (Johnson 2007), yet nest-searching techniques have remained the same for decades, despite demonstrated biases in nest searching and nest monitoring (e.g., Powell et al. 2005, Pietz et al. 2012, Streby and Andersen 2013) that could be rectified by using radio-telemetry. Our results demonstrate that radio-telemetry is an effective method to reduce the bias caused by the exclusion of nest-searching areas due to a priori assumptions of nest-site choice. Golden-winged Warblers are commonly described as habitat specialists that preferentially nest on the edges of shrubby secondary growth or shrubby wetlands and mature forest (Ficken and Ficken 1968, Klaus and Buehler 2001, Martin et al. 2007, Bullock and Buehler 2008, Confer et al. 2011). Using that knowledge to inform standard nest-searching protocols biased the sample of nests that we found toward forest edges and away from mature forest far from edge and early successional stands. Of radio-tagged females, 30% nested in mature forest, a cover type that we initially excluded from our nest-searching effort based on published descriptions of nesting-habitat associations. Excluding areas with presumed low or no nesting activity is a common tactic to increase sample size and cost-effectiveness in studies of forest-nesting songbirds. However, 18% of radio-tagged female Golden-winged Warblers in our study nested >25 m into mature forest, suggesting that simply expanding our search area a few meters into mature forest still would have excluded the area hosting almost 1 in 5 nests in our study population.

We did not find a difference in canopy cover between nests that we found using each method, likely because 82% of nests found using telemetry were in stands where we searched for nests or stands of similar vegetation structure. However, the 18% of nests that we found >25 m into mature forest outside our targeted nest-searching stands and wetlands were in areas of much greater canopy cover. As low-to-moderate canopy cover is traditionally a key descriptor of Golden-winged Warbler nesting habitat (e.g., Confer et al. 2011), this difference is important in that standard nest-searching methods perpetuate an incomplete description of habitat characteristics important to this species. Furthermore, locating nests in areas with moderate-to-high canopy cover may change some of the ecological considerations for conserving Golden-winged Warblers. For example, the nest predator community in forests is likely different than the predator community in shrublands, the cover-type description on which most conservation plans for this species are based. We suspect that some of the perceived nesting habitat specialization of Golden-winged Warblers stems from continued searching in locations identified in previous studies that considered an incomplete range of habitats used for nesting. Only recently have observations of radio-tagged male Golden-winged Warblers using more mature forest than expected in Minnesota (Streby et al. 2012) and Pennsylvania (Frantz 2013) suggested a range-wide underestimation of mature forest use by breeding Golden-winged Warblers.

We found nests at similar times in relation to the start of the season and nest initiation using both methods; neither method provided more exposure days for calculating nest success. However, the difference in estimated nest success for our samples found using nest searching vs. telemetry was considerable. Despite finding more nests farther into mature forest, where Golden-winged Warbler nest success tends to be lowest (Streby et al. 2014), nests found via nest searching had 11% lower estimated nest success than nests found using telemetry. This suggests that the difference in nest success estimates that we observed is not due to differences in the areas sampled with respect to edge, but is instead reflective of some other difference in the nests found using each method. As we observed no relationship between nest-searching method and survival in the first 4-day monitoring period, there is no evidence that nest searching itself caused the difference in survival between these 2 samples. After discovery, each sample of nests was monitored using the same methods and had similar

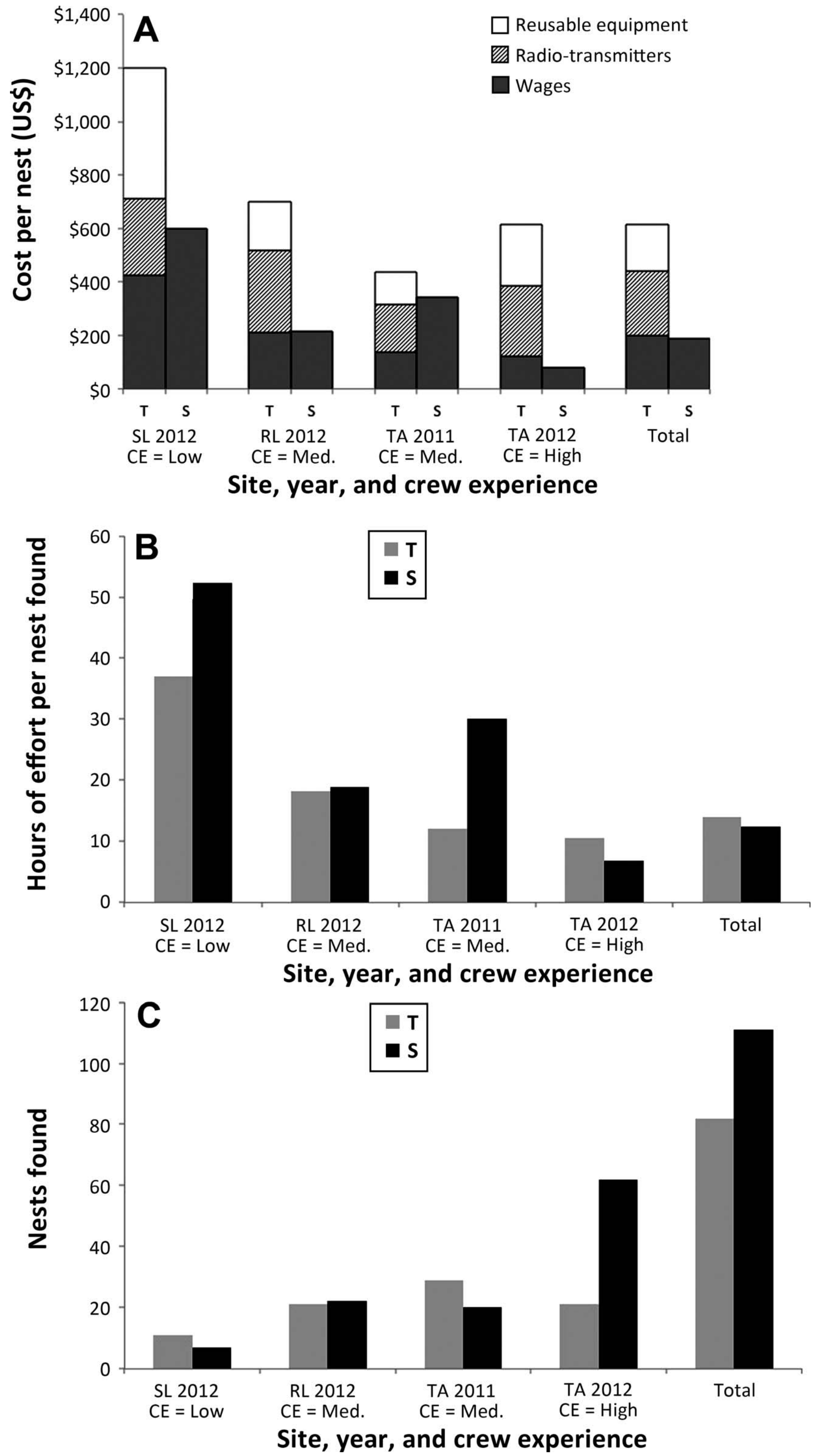

FIGURE 2. Cost effectiveness (**A**), efficiency (**B**), and total number of nests found (**C**) for 2 methods of locating Golden-winged Warbler nests (radio-telemetry [T] and standard nest searching [S]) in 2011 and 2012 at 3 sites with different crew nest searching experience (CE) in the western Great Lakes region, USA and Canada (Sandilands Provincial Forest [SL], Rice Lake National Wildlife Refuge [RL], and Tamarac National Wildlife Refuge [TA]). All costs are in US$. Costs of radio-telemetry include reusable equipment (mist nets, mist-net poles, radio receivers, and antennas), wages, and radio-transmitters. High crew experience = >1 season of Golden-winged Warbler nest-searching experience per person, medium (med.) crew experience = 0.25–1.00 season of Golden-winged Warbler nest-searching experience per person, low crew experience = <0.25 season of Golden-winged Warbler nest-searching experience per person.

vertical and lateral vegetative cover. We speculate that the most likely explanation for nest success being higher for radio-marked birds is that nests found during standard searching by humans were also more likely to be found by predators. It may be that there is some characteristic of nests found using nest searching that we were unable to quantify (e.g., more conspicuous adult behavior or less cover at scales that we did not measure) that made them easier to locate by us and by predators.

Obtaining a representative sample of nests is an important objective when studying nesting habitat associations and nest productivity in songbirds. Systematic nest searching can be impractical in sparse populations or for highly cryptic species. Increasing searching effort may increase sample size, but can result in biased samples because observers can only find nests where they look for them. Similarly to Powell et al. (2005), by finding nests a median of 103 m from a female's capture point, we likely reduced the influence of where observers searched on nest location, providing a more representative sample of nest locations and, by extension, a more accurate description of nesting habitat characteristics. However, although telemetry appears to reduce bias when searching for Golden-winged Warbler nests, it is doubtful that it eliminates all biases. Further study of nest-searching methods may improve understanding of the best method for obtaining a representative sample of nests.

In addition to reducing bias in nest locations, another advantage of telemetry was that it allowed us to find subsequent nesting attempts after initial nest failure. In studies that monitor postfledging survival, nest-searching effort reduces dramatically after young begin to fledge from first nests. Without targeted effort to observe females whose first nesting attempt failed, standard nest-searching methods may be inadequate for locating renesting attempts. Telemetry, in comparison, requires a negligible amount of effort to locate renesting attempts and is more easily performed concurrently with other research activities. Documenting consecutive nesting attempts by individual females is important because nest-site selection can differ later in the nesting season (Powell et al. 2005, Streby et al. 2014), and accurate estimates of renesting rates are important for estimating population productivity (Thompson et al. 2001, Peak and Thompson 2014).

Telemetry would also likely be useful for locating nests in areas of difficult terrain or in wetlands and areas with dense vegetation that limit access, researcher mobility, or detectability of birds and nests. Even when implementing methods that encourage systematic nest searching (e.g., transects), it is difficult to guarantee that observers will not subconsciously focus effort away from areas that are relatively difficult to search. Furthermore, observers often restrict their nest-searching effort to known territories of singing males. Size, shape, and location of song territories can be affected by differences in detectability in a heterogeneous landscape. Kubel and Yahner (2007) found that Golden-winged Warbler males were detectable at a maximum distance of 100–150 m in secondary-growth forest. However, avian detectability can be affected significantly by vegetation structure (e.g., Diehl 1981, Oelke 1981, Schieck 1997) and other factors. As a result, observers may bias their nest-searching efforts toward areas of high singing-male detectability, such as open secondary growth, while ignoring male territories in areas with low detectability such as mature forest with a dense and heterogeneous understory. Streby et al. (2012) found such a bias while mapping Golden-winged Warbler territories in Minnesota; song territories were larger and included more mature forest when they were delineated using radio-telemetry than when they were delineated with spot mapping (i.e. observations of color-banded males).

Initiation and subsequent success or failure of a study requiring observation of nests is often dependent on adequate funding and access to necessary resources. Although standard nest searching was more cost effective at locating nests in our study, our estimates of cost did not include the cost of locating a biased sample of nests using standard nest searching. Our telemetry data indicated that we oversampled nests in the locations where they were concentrated and relatively easy to find (i.e. the forest–shrubland edge) and undersampled nests where they occurred at lower density, artificially increasing the number of nests found per dollar spent with standard nest searching. Obtaining a representative sample of nests via standard nest searching would likely require additional expenditure of resources directed at searching for nests where they were at a lower density and more difficult to detect. There were also scenarios in our assessment in which telemetry equaled or surpassed nest searching in cost effectiveness while simultaneously obtaining a less biased sample. For example, telemetry was at least as cost effective as standard searching when searchers were inexperienced, when Golden-winged Warbler population density was low, and when netting and telemetry equipment were already owned, the latter of which would be the case in any study after the first season. Of course, the cost of standard nest searching can be very inexpensive if crews are composed of volunteers or unpaid interns, although in such situations the number of nests located can be quite small. For example, we had inexperienced technicians who found no nests in hundreds of hours of searching, suggesting that financially investing in experienced nest searchers is likely necessary to accomplish primary project objectives. In the future we expect that radio-telemetry will become even more cost effective, as radio-transmitter prices will likely continue to decrease and hourly wages will likely increase. We also note that when we used both methods to search for nests, we found some nests twice, effectively doubling the cost of finding those nests.

Using the mean costs of finding a nest via telemetry (assuming all preowned equipment) and nest searching, the 11 nests that we found using both methods accounted for ~8% of the total nest-searching budget.

Our results add to a growing literature of telemetry-based studies that demonstrate important biases in data collected using standard observational methods to find nests (Powell et al. 2005) and to determine the fates of nests (Streby and Andersen 2013) and fledglings (Streby et al. 2009, Peterson et al. 2012). Herein, we have demonstrated that the reduced biases and other benefits of locating nests via telemetry do not necessarily come with a prohibitive increase in financial cost, which suggests that, in many instances, locating nests of forest-nesting songbirds via telemetry is a viable alternative to standard nest-searching methods. Furthermore, the reduced bias of finding nests via telemetry compared with standard nest searching resulted in a more accurate understanding of Golden-winged Warbler nesting habitat associations with which to inform management.

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LITERATURE CITED

Buehler, D. A., A. M. Roth, R. Vallender, T. C. Will, J. L. Confer, R. A. Canterbury, S. B. Swarthout, K. V. Rosenberg, and L. P. Bulluck (2007). Status and conservation priorities of Golden-winged Warbler (*Vermivora chrysoptera*) in North America. The Auk 124:1439–1445.

Bulluck, L. P., and D. A. Buehler (2008). Factors influencing Golden-winged Warbler (*Vermivora chrysoptera*) nest-site selection and nest survival in the Cumberland Mountains of Tennessee. The Auk 125:551–559.

Burnham, K. P., and D. R. Anderson (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second edition. Springer, New York, NY, USA.

Confer, J. L., and K. Knapp (1981). Golden-winged Warblers and Blue-winged Warblers: The relative success of a habitat specialist and a generalist. The Auk 98:108–114.

Confer, J. L., P. Hartman, and A. Roth (2011). Golden-winged Warbler (*Vermivora chrysoptera*). In The Birds of North America Online (A. Poole, Editor), Cornell Lab of Ornithology, Ithaca, NY, USA. http://bna.birds.cornell.edu/bna/species/020 doi:10.2173/bna.20

Daw, S. K., S. DeStefano, and R. J. Steidl (1998). Does survey method bias the description of Northern Goshawk nest-site structure? Journal of Wildlife Management 62:1379–1384.

Diehl, B. (1981). Bird populations consist of individuals differing in many respects. In Estimating Numbers of Terrestrial Birds (C. J. Ralph and J. M. Scott, Editors). Studies in Avian Biology 6:225–229.

Etterson, M. A., R. Greenberg, and T. Hollenhorst (2014). Landscape and regional context differentially affect nest parasitism and nest predation for Wood Thrush in central Virginia, USA. The Condor: Ornithological Applications 116:205–214.

Ficken, M. S., and R. W. Ficken (1968). Territorial relationships of Blue-winged Warblers, Golden-winged Warblers, and their hybrids. Wilson Bulletin 80:442–451.

Frantz, M. W. (2013). Is spot mapping missing important aspects of Golden-winged Warbler (*Vermivora chrysoptera*) breeding habitat? M.S. thesis, Indiana University of Pennsylvania, Indiana, PA, USA.

IUCN (2013). The IUCN Red List of Threatened Species, version 2013.1. www.iucnredlist.org

Jehle, G., A. Yackel Adams, J. A. Savidge, and S. K. Skagen (2004). Nest survival estimation: A review of alternatives to the Mayfield estimator. The Condor 106:472–484.

Johnson, D. H. (1979). Estimating nest success: The Mayfield method and an alternative. The Auk 96:651–661.

Johnson, D. H. (2007). Estimating nest success: A guide to the methods. In Monitoring Bird Populations Using Mist Nets (C. J. Ralph and E. H. Dunn, Editors). Studies in Avian Biology 29:65–72.

Klaus, N. A., and D. A. Buehler (2001). Golden-winged Warbler breeding habitat characteristics and nest success in clearcuts in the southern Appalachian Mountains. Wilson Bulletin 113:297–301.

Kubel, J. E., and R. H. Yahner (2007). Detection probability of Golden-winged Warblers during point counts with and without playback recordings. Journal of Field Ornithology 78:195–205.

Kubel, J. E., and R. H. Yahner (2008). Quality of anthropogenic habitats for Golden-winged Warblers in central Pennsylvania. Wilson Journal of Ornithology 120:801–812.

MacArthur, R. H., and J. W. MacArthur (1961). On bird species diversity. Ecology 42:594–598.

Martin, K. J., R. S. Lutz, and M. Worland (2007). Golden-winged Warbler habitat use and abundance in northern Wisconsin. Wilson Journal of Ornithology 119:523–532.
Martin, T. E. (1993). Nest predation and nest sites: New perspectives on old patterns. BioScience 43:523–532.
Martin, T. E., and G. R. Geupel (1993). Nest-monitoring plots: Methods for locating nests and monitoring success. Journal of Field Ornithology 64:507–519.
Martin, T. E., C. R. Paine, C. J. Conway, and W. M. Hochachka (1996). BBIRD Field Protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT, USA.
Mayfield, H. (1961). Nesting success calculated from exposure. Wilson Bulletin 73:255–261.
Mayfield, H. F. (1975). Suggestions for calculating nest success. Wilson Bulletin 87:456–466.
Oelke, H. (1981). Limitations of estimating bird populations because of vegetation structure and composition. In Estimating Numbers of Terrestrial Birds (C. J. Ralph and J. M. Scott, Editors). Studies in Avian Biology 6:316–321.
Peak, R. G., and F. R. Thompson III (2014). Seasonal productivity and nest survival of Golden-cheeked Warblers vary with forest type and edge density. The Condor: Ornithological Applications 116:546–559.
Peterson, S. M., H. M. Streby, and D. E. Andersen (2012). Effects of brood parasitism by Brown-headed Cowbirds may persist in the post-fledging period. Wilson Journal of Ornithology 124: 179–183.
Peterson, S. M., H. M. Streby, and D. E. Andersen (In press). Spatially explicit models of full-season productivity and implications for landscape management of Golden-winged Warblers in the western Great Lakes region. In Golden-winged Warbler Ecology, Conservation, and Management (H. M. Streby, D. E. Andersen, and D. A. Buehler, Editors). Studies in Avian Biology.
Pietz, P. J., D. A. Granfors, C. A. Ribic, and F. R. Thompson III (2012). Knowledge gained from video-monitoring grassland passerine nests. In Video Surveillance of Nesting Birds (C. A. Ribic, F. R. Thompson III, and P. J. Pietz, Editors). Studies in Avian Biology 43:3–22.
Powell, L. A., J. D. Lang, D. G. Krementz, and M. J. Conroy (2005). Use of radio-telemetry to reduce bias in nest searching. Journal of Field Ornithology 76:274–278.
Rappole, J. H., and A. R. Tipton (1991). New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62:335–337.
R Development Core Team (2012). R: A Language and Environment for Statistical Computing. The R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org
SAS Institute (2008). SAS/STAT 9.2 User's Guide. SAS Institute, Cary, NC, USA.
Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link (2014). The North American Breeding Bird Survey, Results and Analysis 1966–2013, version 01.30.2015. USGS Patuxent Wildlife Research Center, Laurel, MD, USA. http://www.mbr-pwrc.usgs.gov/bbs/
Schieck, J. (1997). Biased detection of bird vocalizations affects comparisons of bird abundance among forested habitats. The Condor 99:179–190.
Shaffer, T. L. (2004). A unified approach to analyzing nest success. The Auk 121:526–540.
Streby, H. M., and D. E. Andersen (2013). Testing common assumptions in studies of songbird nest success. Ibis 155: 327–337.
Streby, H. M., J. P. Loegering, and D. E. Andersen (2012). Spot mapping underestimates territory size and use of mature forest by breeding male Golden-winged Warblers. Wildlife Society Bulletin 36:40–46.
Streby, H. M., T. A. McAllister, S. M. Peterson, G. R. Kramer, J. A. Lehman, and D. E. Andersen (2015). Minimizing marker mass and handling time when attaching radio-transmitters and geolocators to small songbirds. The Condor: Ornithological Applications 117:249–255.
Streby, H. M., S. M. Peterson, C. F. Gesmundo, M. K. Johnson, A. C. Fish, J. A. Lehman, and D. E. Andersen (2013). Radio-transmitters do not affect seasonal productivity of female Golden-winged Warblers. Journal of Field Ornithology 84: 316–321.
Streby, H. M., S. M. Peterson, and P. M. Kapfer (2009). Fledging success is a poor indicator of the effects of bird blow flies on Ovenbird survival. The Condor 111:193–197.
Streby, H. M., J. M. Refsnider, S. M. Peterson, and D. E. Andersen (2014). Retirement investment theory explains patterns in songbird nest-site choice. Proceedings of the Royal Society of London, Series B 281:20131834. http://dx.doi.org/10.1098/rspb.2013.1834
Thompson, B. C., G. E. Knadle, D. L. Brubaker, and K. S. Brubaker (2001). Nest success is not an adequate comparative estimate of avian reproduction. Journal of Field Ornithology 27:527–536.