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Spot-mapping Golden-winged Warbler Territories

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Original Article

Spot-Mapping Underestimates Song-Territory Size and Use of Mature Forest by Breeding Golden-Winged Warblers in Minnesota, USA

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ABSTRACT Studies of songbird breeding habitat often compare habitat characteristics of used and unused areas. Although there is usually meticulous effort to precisely and consistently measure habitat characteristics, accuracy of methods for estimating which areas are used versus which are unused by birds remains generally untested. To examine accuracy of spot-mapping to identify singing territories of golden-winged warblers (*Vermivora chrysoptera*), which are considered an early successional forest specialists, we used spot-mapping and radiotelemetry to record song perches and delineate song territories for breeding male golden-winged warblers in northwestern Minnesota, USA. We also used radiotelemetry to record locations (song and nonsong perches) of a subsample ($n = 12$) of males throughout the day to delineate home ranges. We found that telemetry-based estimates of song territories were 3 times larger and included more mature forest than those estimated from spot-mapping. In addition, home ranges estimated using radiotelemetry included more mature forest than spot-mapping- and telemetry-based song territories, with 75% of afternoon perches located in mature forest. Our results suggest that mature forest comprises a larger component of golden-winged warbler song territories and home ranges than is indicated based on spot-mapping in Minnesota. Because it appears that standard observational methods can underestimate territory size and misidentify cover-type associations for golden-winged warblers, we caution that management and conservation plans may be misinformed, and that similar studies are needed for golden-winged warblers across their range and for other songbird species. © 2012 The Wildlife Society.

KEY WORDS golden-winged warbler, home range, Minnesota, radiotelemetry, song territory, spot-mapping, territory size, *Vermivora chrysoptera*.

Understanding species–habitat relationships is required for habitat management and conservation planning. For songbirds, species–habitat relationships are usually determined from either point counts, commonly used to determine presence and absence of birds at multiple spatial scales and as an index to monitor trends in abundance (e.g., Sauer et al. 2008) or spot-mapping (mapping of perches used for singing by territorial M; hereafter, song perches), which is more effort-intensive than point counts and is reputed to produce a census of birds in a surveyed area (Buckland 2006). Spot-mapping is often used as the benchmark by which other survey methods are tested (Franzreb 1976, Franzreb 1981, Howell et al. 2004, Buckland 2006). Spot-mapping has specifically been used to demonstrate bias in density estimates from other survey methods, including fixed-radius point counts (Howell et al. 2004). However, the assumption that spot-mapping is a reliable benchmark by which to test all other methods has itself not been tested.

Many studies report habitat characteristics most commonly associated with occupied locations identified using a variety of survey methods, and subsequently make management recommendations to maximize those habitat characteristics (e.g., Schlossberg et al. 2010). Habitat characteristics associated with used and unused areas are sometimes integrated in Geographical Information Systems (GIS) to model habitat quality and identify important areas for management consideration (Dettmers and Bart 1999). Although much attention is paid to consistency in methodology and terminology for describing habitat characteristics to be compared between used and unused areas, the assumption that spot-mapping and other survey methods effectively delineate used and unused areas or habitat characteristics again remains generally untested.

Recent radiotelemetry studies have demonstrated that songbirds use areas that differ in vegetation structure and food availability from those of song territories (Anders et al. 1998, Mazerolle and Hobson 2003, King et al. 2006, Streby

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and Andersen 2011). For example, although ovenbirds (*Seiurus aurocapilla*) are often considered edge-sensitive birds and males sing primarily in interior mature forest during morning hours (Van Horn and Donovan 1994), radiomonitored adult male ovenbirds frequently forage in forest edges later in the day (Mazerolle and Hobson 2003) and adult and fledgling ovenbirds use forest edges and young forest stands during the postfledging period, or the time between nesting and autumn migration (King et al. 2006, Vitz 2008, Streby and Andersen 2011). Radiotelemetry studies of wood thrush (*Hylocichla mustelina*; Anders et al. 1998, Lang et al. 2002) and scarlet tanager (*Piranga olivacea*; Vega Rivera et al. 2003) indicate that those species also use areas that differ in vegetation structure from those of adult male song territories during the nesting period, the postfledging period, or both.

In their recent review, Whitaker and Warkentin (2010) suggested that spot-mapping of song perches and other observational methods may lead to an incomplete understanding of songbird space use because they do not include extraterritorial movements. However, the assumption remains that observational methods, such as spot-mapping, at least adequately delineate space used within song territories. The potential underestimation of songbird space use by spot-mapping is not merely a case of confusion between song territories and breeding home ranges. To be clear, a song territory is defined as the area in which a socially monogamous male sings, and the territory is used for mating, nesting, and primary food acquisition (Nice 1941). In contrast, a breeding home range (hereafter; home range) includes the song territory and all extraterritorial areas used by a breeding pair during regular daily activities (Whitaker and Warkentin 2010). Although home ranges are generally larger than song territories (Ferry et al. 1981, Naguib et al. 2001), Anich et al. (2009) found that Swainson's warbler (*Limnothlypis swainsonii*) song territories were substantially larger when song perches were identified using radiotelemetry than when using spot-mapping. Whether this result can be extended to estimates of song territory size and habitat use generally in songbirds is not clear, but if spot-mapping does not accurately estimate territory size of songbirds, empirical comparisons of used and unused areas may be erroneous.

We studied a population of golden-winged warblers (*Vermivora chrysoptera*) in northwestern Minnesota, USA and used spot-mapping and radiotelemetry to monitor territorial males and estimate song-territory size and cover-type composition. In addition, we used radiotelemetry to estimate size and cover-type composition of home ranges of male golden-winged warblers. Golden-winged warblers are of high conservation concern and have experienced range-wide declines for >40 years (Buehler et al. 2007), prompting studies of the species' habitat requirements. Golden-winged warblers are described as early successional forest specialists and singing males generally occupy upland or wetland areas dominated by shrubs and early successional trees (Confer 1992). Spot-mapped territories across the species' range consistently include open shrubby areas, often with sparse mature trees and sometimes mature-forest edge. Therefore, current management plans for golden-winged warblers call for an increase in quantity and area of early successional forest stands.

Our goal was to determine whether spot-mapping accurately estimated area and cover-type composition of golden-winged warbler song territories, and whether cover-type composition differed between song territories and home ranges. Specifically, our objectives were to 1) compare area and cover-type composition between golden-winged warbler song territories estimated using spot-mapping and radiotelemetry, 2) compare distances between subsequent perching locations identified during spot-mapping and radiotelemetry during early morning hours to assess whether low detection after longer movements is a limitation of spot-mapping, and 3) compare area and cover-type composition between song territories and home ranges estimated using radiotelemetry. We expected telemetry-based estimates of song-territory size would be larger than spot-mapping-based estimates, but that estimates produced by each method would be comprised primarily of open shrubby areas and early successional forest. We expected that birds would sometimes fly too far between subsequent perching locations for spot-mapping crews to detect more distant song perches, leading to smaller song territory estimates during spot-mapping than during radiotelemetry. In addition, we expected telemetry-based home ranges to be larger than song territories, but also to include primarily early successional shrubby areas.

STUDY AREA

We studied golden-winged warblers at Tamarac National Wildlife Refuge (NWR), Becker County, Minnesota. Tamarac NWR encompassed >19,000 ha of mature forest interspersed with regenerating forest stands of various seral stages, lakes, rivers, and a variety of shrubby and forested wetlands. We labeled a forest stand as "mature" if the overstory was dominated by trees >35-cm diameter at breast height, a moderately closed canopy, and generally a lack of substantial disturbance for >40 years. Tree species in mature forests were typically aspen (*Populus* spp.) and oak (*Quercus* spp.). The refuge was located at the western margin of golden-winged warbler range, but hosted an estimated 2,000 nesting pairs (approx. 2% of the global population [Rich et al. 2004]). We monitored golden-winged warblers in and around 2 upland, early successional, regenerating forest stands, which were 21 ha and 26 ha and hosted 20–25 and 25–30 breeding pairs, respectively. The smaller study stand was partially disturbed >30 year ago for gravel removal and partially disturbed 11 years prior to our study by forest harvest followed 1 year later by a prescribed burn. The larger stand was disturbed by harvest of jack pine (*Pinus banksiana*) and red pine (*P. resinosa*) 8 years prior to our study and then by a prescribed burn 6 years before our study. Both stands were on sandy soils and vegetation regeneration was, therefore, much slower than other harvested stands on higher quality soils in this region. During our study, both stands were dominated by patches of low shrubs, grasses, sedges,

and forbs, interspersed with individual and small patches of remnant mature oak and aspen trees and snags.

METHODS

We monitored movements and space use by territorial male golden-winged warblers at our study sites in 2010. From 15 May to 31 May, we used mist nets and call playback to capture territorial males, as described for this species by Murray and Gill (1976). We marked each captured male with a standard aluminum U.S. Geological Survey leg band and a unique combination of 3 plastic, darvic color leg bands. We marked a subsample of those males with 0.40-g radiotransmitters (4.4% of mean M mass) using a figure-8 harness design modified from Rappole and Tipton (1991). We captured, handled, banded, and attached radiotransmitters to birds following Institutional Animal Care and Use Committee Protocol number 1004A80575 (DEA) and number 0710A19381 (JPL) approved by the University of Minnesota Institutional Animal Care and Use Committee. We observed behavior related to color bands and radiotransmitters for approximately 10–20 minutes after releasing birds. Those behaviors differed markedly among individuals and ranged from picking at bands or radiotransmitters with the bill to difficulty flying during the first several attempts. We observed birds closely throughout this acclimation period and we were prepared to remove markers if these behaviors continued. We observed none of these behaviors for any individuals after 20 minutes. We observed many of the radiomarked birds engaged in intricate "dogfight" territorial interactions with neighboring males within 30 minutes of release, and it was not possible to identify which male was radiomarked until the agonistic interaction ended and the birds slowed or perched. Based on these observations, we concluded that color bands and radiotransmitters had minimal effects on behavior and movements of male golden-winged winged warblers following a brief acclimation period.

Spot-Mapping

We conducted spot-mapping and radiotelemetry with 2 independent crews; spot-mapping and radiotelemetry crews did not discuss or observe each other's methods, although some members of each crew had prior experience with both methods. We conducted spot-mapping with pairs of researchers for 3–4 hours beginning between dawn and sunrise on each of 10 days between 15 May and 5 June. Pairs of spot-mapping researchers walked systematically through each study site, stopped when a singing male was identified, followed that male for a 30–60-minute sampling period (Barg et al. 2005), and ideally recorded locations of 10 different song perches per visit. Researchers moved on after collecting 10 locations or when the bird was lost and could not be located within 15 minutes. Our methods differed from Barg et al. (2005), in that our crew did not attempt to record locations every minute. Because our goal was to delineate territories and not to assess relative use within the territory, our crew recorded each song perch only once regardless of how long the bird sang from a perch (commonly for >2 min). When monitoring a bird, one researcher identified the bird and located song perches and the second researcher used a handheld Global Positioning System (GPS) unit to record song-perch locations after the bird moved on. We observed no evidence that researchers disturbed males or forced them to move to areas that may have been otherwise unused. We combined locations from multiple days for individually identifiable (i.e., color-banded) males. Although we identified many additional territorial males at our sites, we analyzed only those for which we recorded ≥7 song perches for the season ($n = 28$).

Radiotelemetry

Using ground-based radiotelemetry, we monitored a subsample ($n = 12$) of the same male golden-winged warblers and recorded one location each day (at random times between 0600 hr and 1500 hr) throughout the same sampling period. In addition, for 3 days during 3–5 June, we monitored 4 of those radiomarked birds more intensively. We monitored each bird for 1 hour each day during 1 of 3 periods: 1) 0600–0900 hours (coinciding with timing of territory mapping), 2) 0900–1200 hours, and 3) 1200–1500 hours. We monitored each bird during a different period on each day, such that each bird was tracked for 1 hour during each period. Pairs of researchers located and monitored movements of one bird at a time; one researcher continuously and cautiously located the bird using radiotelemetry, while the second researcher recorded perching locations with a handheld GPS unit and recorded bird activity. We obtained visual confirmation of exact perches for >95% of locations ($n = 153$) during telemetry and we narrowed the location down to a single tree at all other locations ($n = 7$). As with our spot-mapping methods, we recorded a single perching location once each time it was used, and did not continuously record a location when a bird perched for several minutes. Potential disturbance was no different than that of the spot-mapping crew and we observed no evidence that radiotelemetry crews disturbed the monitored birds or forced them to move to areas they would not have otherwise used. For each subsequent perching location, we recorded whether we were able to identify that location by watching the bird fly from perch to perch (as with spot-mapping), or if radiotelemetry was required to identify the subsequent perching location. In addition, we recorded whether the monitored bird sang at each perch during early morning hours to map song territories for comparison to spot-mapped territories. We did not radiomark or monitor more birds due to logistical constraints. The 4 birds we intensively monitored were selected because they were the first 4 males for which we confirmed pairing success by observing their interactions with females during nest construction (we did not want to include unpaired, potentially nonterritorial, floater M). Although we tracked all 12 radiomarked males once daily throughout the nesting period, our intensive radiotelemetry monitoring occurred within the 12-day (50% of nesting cycle) incubation stage of the nesting cycle for the mates of those 4 males.

Statistical Analysis

We measured distances between subsequent perching locations and estimated minimum convex polygon (MCP) song territory and breeding home-range sizes using GIS software with recorded locations overlaid on aerial photographs (Minnesota Department of Natural Resources Data Deli; http://deli.dnr.state.mn.us/) and a cover-type layer (developed by Tamarac National Wildlife Refuge from aerial photographs with a min. mapping unit of 0.25 ha) for which we updated and modified stand delineation based on aerial photographs and ground-truthing at our sites. For song territories delineated using spot-mapping ($n = 28$) and radiotelemetry ($n = 4$), we used 100% MCP because we assumed males did not sing at full volume (golden-winged warblers often sing quietly while foraging throughout their broader breeding home range [H. M. Streby, personal observation]) outside their song territories. For radiotelemetry-based home ranges, we calculated 95% MCP by removing the 5% of points farthest from the geographic center of each home range, and then creating the MCP to reduce probability of including perches not within the area of normal daily use. We estimated radiotelemetry-based home-range size using locations from 1, 2, and all 3 monitoring periods to assess importance of time of day for investigating space use.

We compared distances (m) between subsequent perching locations from spot-mapping and radiotelemetry methods, for each of the 4 intensively tracked males and all 4 males combined, with Student's *t*-tests. We compared MCP territory sizes estimated using spot-mapping and radiotelemetry methods with a 2-tailed *t*-test assuming unequal variance. We report territory sizes in hectares as mean ± standard error. We compared proportion of cover types (early successional and mature forest) contained within territories estimated using each method with a χ^2 test of independence. Because availability of cover types to wide-ranging adult songbirds would vary considerably depending on where study-area boundaries were arbitrarily placed (Jones 2001), we compared only use of each cover type between our 2 methods and not use relative to availability (i.e., selection). In addition, we compared numbers of perches used by golden-winged warblers located in different cover types between radiotelemetry-estimated territories and home ranges using a χ^2 test of independence. Importantly, we did not include individual or small patches of a few mature remnant trees within early successional stands as mature forest. Because official minimum-area requirements for defining a stand of forest are ambiguous (Sasaki and Putz 2009), but delineating cover-types was necessary for our analysis, we considered contiguous areas of $\geq$0.25 ha of mature trees to be mature forest in this study.

RESULTS

Using spot-mapping, we monitored 28 territorial male golden-winged warblers (those for which we recorded $\geq$7 song perches) and recorded 7–27 ($\bar{x} = 13$) song perches for each bird. For the 4 intensively radiomonitored birds, we recorded 35–45 ($\bar{x} = 40$) perching locations. Between 0600 hours and 0900 hours, we recorded 14–17 ($\bar{x} = 16$) perching locations including 7–10 ($\bar{x} = 8$) song perches for each bird. We also recorded 9–18 ($\bar{x} = 13$) perching locations for each bird between 0900 hours and 1200 hours, and 8–15 ($\bar{x} = 11$) perching locations between 1200 hours and 1500 hours.

During radiotelemetry monitoring between 0600 hours and 0900 hours, we required radiotelemetry (i.e., we were unable to maintain visual contact as is required for spot-mapping) to locate 68% ($n = 22$) of subsequent song perches, and 85% ($n = 30$) of subsequent perches from which birds did not sing. Distances between subsequent perching locations were greater ($t_{94} = 1.99$, $P < 0.01$) during radiotelemetry ($\bar{x} = 39.2$ m, $n = 59$) than during spot-mapping ($\bar{x} = 17.7$ m, $n = 38$) cumulatively for all 4 birds and individually for each bird (each $P < 0.05$; Fig. 1). This pattern was not driven by extraterritorial movements because 59% ($n = 20$) of movements >30 m were to perches from which birds subsequently sang. Although 57% ($n = 34$) of all movements recorded between 0600 hours and 0900 hours were >30 m during radiotelemetry, only 11% ($n = 4$) of recorded movements were >30 m during spot-mapping. Despite using fewer song perches ($t_3 = 2.16$, $P < 0.01$) to estimate song-territory sizes from radiotelemetry data, radiotelemetry-based song-territory estimates (0.45 ± 0.08 ha, $n = 4$) were 3 times larger ($t_3 = 3.18$, $P = 0.03$) than spot-mapping-based estimates (0.16 ± 0.02 ha, $n = 28$).

Golden-winged warbler song territories included more mature forest when movements were monitored with radiotelemetry than with spot-mapping (Fig. 2). We observed more song perches within mature forest when we located perches using radiotelemetry than when using spot-mapping ($\chi^2 = 5.76$, df = 1, $P = 0.016$). In addition, radiotelemetry-based home ranges included more mature forest (37%) than either radiotelemetry-based (22%) or spot-mapped (5%) song territories. More perches (song and nonsong) identified using radiotelemetry were located in mature forest during early morning ($\chi^2 = 5.23$, df = 1, $P = 0.022$), late morning ($\chi^2 = 12.11$, df = 1, $P = 0.001$), and afternoon ($\chi^2 = 49.68$, df = 1, $P < 0.001$) compared with perches identified during spot-mapping (Fig. 3). Importantly, 75% of afternoon perches were located in mature forest and birds

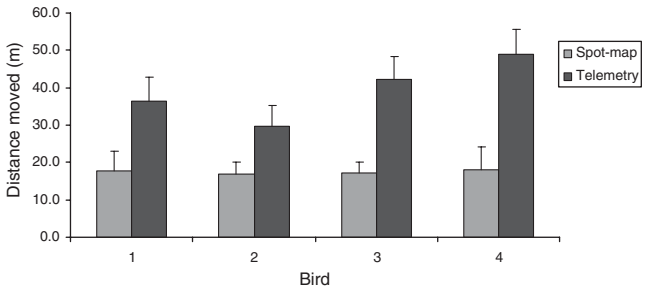

Figure 1. Movements (distance between subsequent perches recorded between 0600 hr and 0900 hr) by 4 territorial male golden-winged warblers that were monitored using spot-mapping and radiotelemetry during 2010 at Tamarac National Wildlife Refuge, Minnesota, USA. Movements were longer for each bird (all $P < 0.05$) and more variable among birds during radiotelemetry than during spot-mapping.

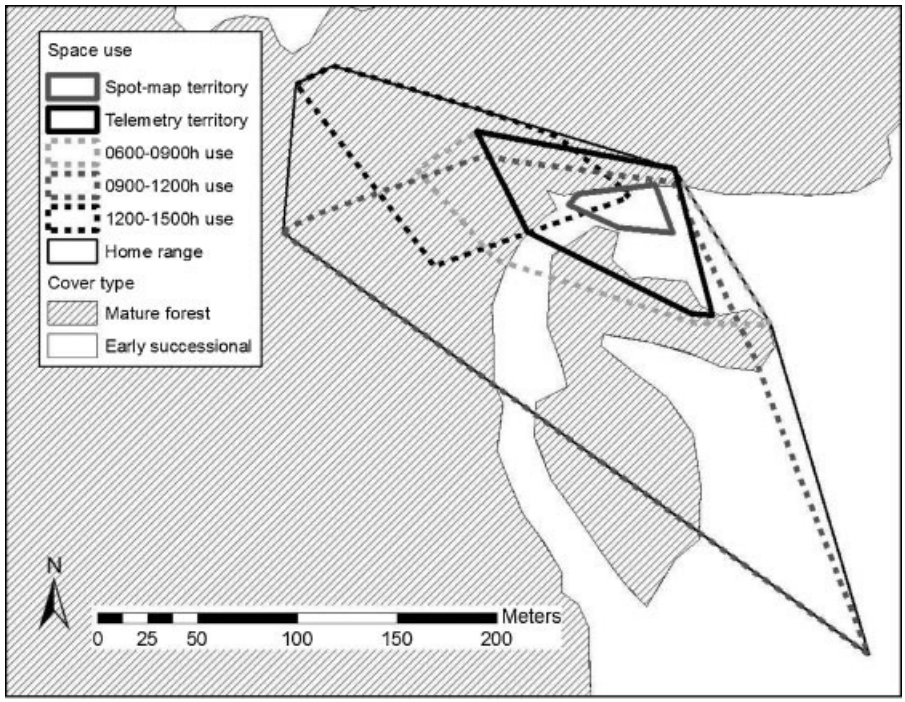

Figure 2. Space use by a territorial male golden-winged warbler estimated using spot-mapping (song territory) and radiotelemetry (song territory, home range, and areas used during different portions of the day) during the 2010 nesting season at Tamarac National Wildlife Refuge, Minnesota, USA.

rarely returned to song territories during that period. Therefore, use of mature forest later in the day appeared to be not for brief extraterritorial forays, but for extended periods of foraging, primarily in mature-forest canopy.

None of the 28 territories we spot-mapped overlapped with each other. Only 2 of the birds we monitored intensively using radiotelemetry were neighbors, and their song territories overlapped slightly (<5%) with each other. The home ranges of each of the 4 intensively radiomonitored birds included the entirety of, or a portion of, 4–7 other territories we spot-mapped, including some beyond immediate neighbors. Although not included in territory and home-range analyses, the additional 8 birds we radiomonitored once daily all followed similar space-use patterns throughout the nesting period.

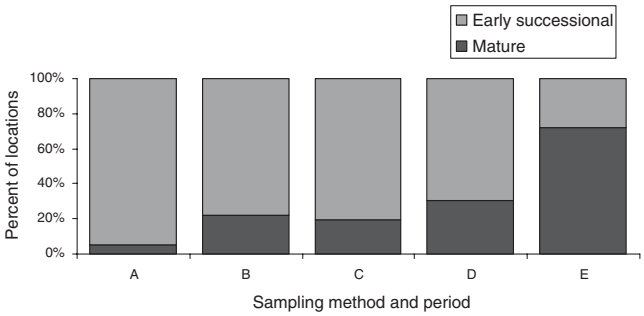

Figure 3. Percent of perches used by breeding male golden-winged warblers recorded in early successional stands and mature-forest stands during (A) spot-mapping of song territories, and radiotelemetry mapping of (B) song territories, and home ranges in the (C) early morning, (D) late morning, and (E) early afternoon in 2010 at Tamarac National Wildlife Refuge, Minnesota, USA.

DISCUSSION

Spot-mapping, the standard by which other songbird surveys are often tested, substantially underestimated territory size and use of mature forest by golden-winged warblers in our study. Our radiotelemetry-based estimates of song territories were 3 times larger than our spot-mapped song territories despite radiotelemetry estimates being based on fewer song-perch locations. Separate analysis suggested that our radiotelemetry-based territories would have continued to increase in area with additional song-perch locations (H. M. Streby, unpublished data), suggesting that even our radiotelemetry methods underestimated size of golden-winged warbler song territories in our study population. Therefore, we do not contend that our radiotelemetry-based estimates of space use are a perfect standard, merely that they demonstrate that the currently accepted standard can be insufficient. Our spot-mapped estimates of territory size were small relative to the range reported in previous studies of golden-winged warblers. However, our study area hosts one of the highest known densities of breeding golden-winged warblers (Rich et al. 2004), and spot-mapped territories are similarly small in other areas with high nesting densities (Roth and Lutz 2004). Considering the general inverse relationship between density and territory size in songbird populations, it is likely that radiotelemetry-based estimates of territory size could be considerably larger in less dense golden-winged warbler populations, but more research is needed.

To our knowledge, only one previous study compared songbird song-territory sizes estimated using spot-mapping to those estimated using radiotelemetry (Anich et al. 2009). Swainson's warbler song territories estimated using

radiotelemetry during that study were much larger than those estimated using spot-mapping in previous Swainson's warbler studies at different locations. Our direct comparison of concurrent spot-mapping and radiotelemetry-based estimates of territory size for golden-winged warblers produced similar results.

Our radiotelemetry-based song-territory estimates included more mature forest than did the same territories we estimated using spot-mapping. Our results and post hoc discussions between the spot-mapping and radiotelemetry crews suggest 2 likely explanations: 1) detectability of birds decreased with increased distance and vegetation density between subsequent perches; and 2) researchers can be biased by a priori presumptions of species–cover-type associations. Our results suggest that there is a significant decline in detectability during spot-mapping of golden-winged warblers when a bird moves >30 m between song perches, which is likely exacerbated when a bird moves into or through dense vegetation. Failure to include longer distance movements between song perches likely reduced estimates of song-territory size for obvious reasons. Our spot-mapping crews rarely ventured more than a few meters into mature forest when they lost sight of a bird because they knew golden-winged warblers to be "early-successional specialists." A bird singing from farther into mature forest was often assumed to be a different bird singing from a different nearby early successional stand. In addition, spot-mapping crews reported observations of a bird using a small area, flying out of sight, and then returning to the original area, at which time the crew commenced recording song perches. Those more distant perches were quickly and easily located by the radiotelemetry crew and birds commonly commenced singing after such large movements.

Using radiotelemetry, we observed males singing throughout the late morning and early afternoon even when far from their apparent song territory, albeit less often and more quietly. It is possible that this soft singing is related to seeking extra-pair copulations (Norris and Stutchbury 2001), but we observed only foraging during this period and no interactions with female conspecifics (except for two males that we observed with their color-banded mates >100 m from their territories). In addition, using radiotelemetry during early morning hours, we observed males singing in multiple concentrated areas within the larger than expected (based on spot-mapping) song territories. Our observations suggest that counts of birds resulting from spot-mapping and point counts of unmarked individuals may be biased upward by counting males singing outside their territories or singing in multiple concentrated areas within larger than expected song territories. Indeed, this probably would have affected our spot-mapping crew if the birds we monitored were not color-banded.

Kubel and Yahner (2007) reported that male golden-winged warblers in Pennsylvania, USA responded to song playback only 68% of the time during the first 5 hours after dawn and concluded that detectability of this species is low during point counts and when using song playback. Male golden-winged warblers in our study responded to song playback >95% of the time within the first 3 hours after dawn and rarely after 4 hours past dawn during >100 playback attempts (H. M. Streby, unpublished data). Our radiotelemetry results indicate that not only did golden-wing warblers not respond to song playback during late morning, but they were, in fact, usually not within their territories at that time, suggesting that point counts and song playback may be less effective for monitoring this species beyond 3 hours past dawn.

Comparisons of habitat characteristics between used and unused areas, or between areas used by different species, are common in songbird research (e.g., Dettmers and Bart 1999, Patten et al. 2010, Schlossberg et al. 2010). A recent review of 57 studies about habitat use by grassland birds pleaded for standardized techniques and terminology in measuring habitat variables (Fisher and Davis 2010). However, such studies also depend on the accuracy of techniques for estimating which areas are used and not used by birds. If common survey methods do not adequately define used and unused areas, even the most precise measurements of vegetation variables may not be useful. Furthermore, if different habitat characteristics are important later in the day or later in the season than when point counts and spot-mapping are conducted, those habitat characteristics would not be considered in habitat models and management planning. We conclude that expanding studies of songbird territory selection beyond observations of singing males will likely result in a broader understanding of species–habitat relationships, and provide more complete information for potentially more effective management planning, particularly for declining species or species of high conservation concern.

MANAGEMENT IMPLICATIONS

For management purposes, the difference in golden-winged warbler territory size estimated using spot-mapping and radiotelemetry may be less important than the difference in cover-type composition. Mature forest is sometimes described as the boundary or periphery of areas used by golden-winged warblers (Ficken and Ficken 1967, Confer 1992). Confer and Knapp (1981) reported that golden-winged warbler territories in New York, USA occasionally extended 5–30 m into mature forest. Although our spot-mapped song territory estimates are consistent with that observation, all of the song territories we estimated using radiotelemetry extended >10 m into mature forest, and half of them extended >100 m into mature forest, with home ranges extending even farther.

Currently, management strategies targeting recovery of golden-winged warblers primarily call for creating early successional forest through forest harvest or allowing grasslands and farm fields to regenerate. Our results suggest that mature forest may be a larger component of golden-winged warbler breeding habitat than previously thought. Further investigation is needed to assess whether this is the case in other regions within the species' breeding range. If so, habitat-management plans designed to benefit golden-winged warblers may require revision to include consideration for an

apparent importance of mature forest during the breeding season.

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LITERATURE CITED

Anders, A. D., J. Faaborg, and F. R. Thompson, III. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile wood thrushes. Auk 115:349–358.

Anich, N. M., T. J. Benson, and J. C. Bednarz. 2009. Estimating territory and home-range sizes: do singing locations alone provide an accurate estimate of space use? Auk 126:626–634.

Barg, J. J., J. Jones, and R. J. Robertson. 2005. Describing breeding territories of migratory passerines: suggestions for sampling, choice of estimator, and delineation of core areas. Journal of Animal Ecology 74:139–149.

Buckland, S. T. 2006. Point-transect surveys for songbirds: robust methodologies. Auk 123:345–357.

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. Bullock. 2007. Status and conservation priorities of golden-winged warbler (*Vermivora chrysoptera*) in North America. Auk 124:1439–1445.

Confer, J. L. 1992. Golden-winged warbler (*Vermivora chrysoptera*). Account 20 *in* A. Poole, editor. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA. <http://bna.birds.cornell.edu.floyd.lib.umn.edu/bna/species/020>. Accessed 5 Mar 2011.

Confer, J. L., and K. Knapp. 1981. Golden-winged warblers and blue-winged warblers: the relative success of a habitat specialist and a generalist. Auk 98:108–114.

Dettmers, R., and J. Bart. 1999. A GIS modeling method applied to predicting forest songbird habitat. Ecological Applications 9:152–163.

Ferry, C., B. Frochot, and Y. Leruth. 1981. Territory and home range of the blackcap (*Sylvia atricapilla*) and some other passerines, assessed and compared by mapping and capture–recapture. Studies in Avian Biology 6:119–120.

Ficken, M. S., and R. W. Ficken. 1967. Singing behaviour of blue-winged and golden-winged warblers and their hybrids. Behaviour 28:149–181.

Fisher, R. J., and S. K. Davis. 2010. From Wiens to Robel: a review of grassland-bird habitat selection. Journal of Wildlife Management 74:265–273.

Franzreb, K. E. 1976. Comparison of variable strip transect and spot-map methods for censusing avian populations in a mixed-coniferous forest. Condor 78:260–262.

Franzreb, K. E. 1981. A comparative analysis of territorial mapping and variable-strip transect censusing methods. Studies in Avian Biology 6:164–169.

Howell, C. A., P. A. Porneluzi, R. L. Clawson, and J. Faaborg. 2004. Breeding density affects point-count accuracy in Missouri forest birds. Journal of Field Ornithology 75:123–133.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. Auk 118:557–562.

King, D. I., R. M. Degraaf, M. L. Smith, and J. P. Buonaccorsi. 2006. Habitat selection and habitat-specific survival of fledgling ovenbirds (*Seiurus aurocapilla*). Journal of Zoology 269:414–421.

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.

Lang, J. D., L. A. Powell, D. G. Krementz, and M. J. Conroy. 2002. Wood thrush movements and habitat use: effects of forest management for red-cockaded woodpeckers. Auk 119:109–124.

Mazerolle, D. F., and K. A. Hobson. 2003. Do ovenbirds (*Seiurus aurocapillus*) avoid boreal forest edges? A spatiotemporal analysis in an agricultural landscape. Auk 120:152–162.

Murray, B. G., Jr., and F. B. Gill. 1976. Behavioral interactions of blue-winged and golden-winged warblers. Wilson Bulletin 88:231–254.

Naguib, M., R. Altenkamp, and B. Griessmann. 2001. Nightingales in space: song and extra-territorial forays of radio tagged song birds. Journal für Ornithologie 142:306–312.

Nice, M. M. 1941. The role of territory in bird life. American Midland Naturalist 26:441–487.

Norris, D. R., and B. J. M. Stutchbury. 2001. Extraterritorial movements of a forest songbird in a fragmented landscape. Conservation Biology 15:729–736.

Patten, L. L., D. S. Maehr, J. E. Duchamp, S. Fei, J. W. Gasset, and J. L. Larkin. 2010. Do the golden-winged and blue-winged warbler exhibit species-specific differences in their breeding habitat use? Avian Conservation and Ecology 5(2). <http://www.ace-eco.org/vol5/iss2/art2/>. Accessed 5 Mar 2011.

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.

Rich, T. D., C. J. Beardmore, H. Berlanga, P. J. Blancher, M. S. W. Bradstreet, G. S. Butcher, D. W. Demarest, E. H. Dunn, W. C. Hunter, E. E. Inigo-Elias, J. A. Kennedy, A. M. Martell, A. O. Panjabi, D. N. Pashley, K. V. Rosenberg, C. M. Rustay, J. S. Wendt, and T. C. Will. 2004. Partners in Flight North American landbird conservation plan. Cornell Lab of Ornithology, Ithaca, New York, USA.

Roth, A. M., and S. Lutz. 2004. Relationship between territorial male golden-winged warblers in managed aspen stands in northern Wisconsin, USA. Forest Science 50:153–161.

Sasaki, N., and F. E. Putz. 2009. Critical need for new definitions of "forest" and "forest degradation" in global climate change agreements. Conservation Letters 2:226–232.

Sauer, J. R., J. E. Hines, and J. Fallon. 2008. The North American Breeding Bird Survey, results and analysis 1966–2007. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Schlossberg, S., D. I. King, R. B. Chandler, and B. A. Mazzei. 2010. Regional synthesis of habitat relationships in shrubland birds. Journal of Wildlife Management 74:1513–1522.

Streby, H. M., and D. E. Andersen. 2011. Seasonal productivity in a population of migratory songbirds: why nest data are not enough. Ecosphere 78:1–15. <http://www.esajournals.org/toc/ecsp/2/7>. Accessed 19 Jul 2011.

Van Horn, M. A., and T. M. Donovan. 1994. Ovenbird (*Seiurus aurocapilla*). Account 88 *in* A. Poole, editor. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA. <http://bna.birds.cornell.edu.floyd.lib.umn.edu/bna/species/088doi: 10.2173/bna.88>. Accessed 5 Mar 2011.

Vega Rivera, J. H., W. J. McShea, and J. H. Rappole. 2003. Comparison of breeding and post-breeding movements and habitat requirements for the scarlet tanager (*Piranga olicacea*) in Virginia. Auk 120:632–644.

Vitz, A. C. 2008. Survivorship, habitat use, and movements for two species of mature forest birds. Dissertation, The Ohio State University, Columbus, USA.

Whitaker, D. M., and I. C. Warkentin. 2010. Spatial ecology of migratory passerines on temperate and boreal forest breeding grounds. Auk 127:471–484.

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