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IS SPOT MAPPING MISSING IMPORTANT ASPECTS OF GOLDEN-WINGED
WARBLER (*Vermivora chrysoptera*) BREEDING HABITAT?

A Thesis

Submitted to the School of Graduate Studies and Research

in Partial Fulfillment of the

Requirements for the Degree

Master of Biology

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Indiana University of Pennsylvania

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The Golden-winged Warbler (*Vermivora chrysoptera*) is an imperiled migratory songbird that nests in young forest habitats of eastern North America. As such, this species has recently been the focus of an intensive multi-year, range-wide, breeding ecology study. A major focus of this research involved spot-mapping color banded males to examine relationships between nesting success and territory-scale habitat variables. I compared differences in space and habitat use of individual male Golden-winged Warblers that were monitored using both spot mapping and radio telemetry. An individual's telemetry delineated use area was on average 3.6 times larger than its spot-mapped territory. Almost half (46%) of all telemetry locations were located outside their respective male's spot-mapped territory. Number of saplings was higher in telemetry use areas (22.49 ± 2.14) than spot-mapped territories (11.80 ± 1.86). Although the exact motive for extra-territorial movements is unknown, foraging and/or suggestive observations of extra-pair copulation are likely motivating factors. The results of my study suggest Golden-winged Warblers are seeking resources outside their spot-mapped delineated territories. Furthermore, Golden-winged Warblers were found to have more telemetry locations in mature forest than found through spot-mapping. Ultimately, spot mapping alone does not accurately reflect Golden-winged Warbler space use and habitat needs.

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CHAPTER 1

INTRODUCTION

Understanding habitat and space use requirements is an essential component for developing effective habitat management guidelines for imperiled songbirds (Garshelis 2000). Breeding habitat requirements of songbirds are most often studied at the breeding territory scale (eg. Roth and Lutz 2004; Kubel 2005; Bulluck and Buehler 2008). A breeding territory is defined as a fixed area that is defended continuously during the breeding season (Noble 1939; Brown and Orians 1970), and to which access is limited to the defending individual, its mate, and offspring (Brown and Orians 1970). While much can be learned about a species' breeding habitat requirements by quantifying resource use within breeding territories, recent studies suggest that individuals may access important habitat components outside their defended territories (Anich et al. 2009a; Streby et al. 2012).

New arrivals to a breeding habitat must quickly seek out available sites to establish a territory, map resources for foraging bouts, find a mate, and identify conspecifics in the area for possible extra-pair copulation mating opportunities (Hahn and Silverman 2006; Betts et al. 2008). Once a breeding territory is established, movements outside of the breeding territory are normally seen as irregular or occasional "forays" not considered part of its home range (Stuchbury et al. 2005). Birds are usually inconspicuous when leaving their breeding territory (Williams 1990; Neudorf et al. 1997; Mays and Ritchinson 2004), which means they can go easily undetected using monitoring methods that require prominent visuals of displaying males. Nonetheless, most passerines are affected by factors outside of their breeding territory (Hinsley et al. 1995;

Betts et al. 2006, 2007). As such, studies that fail to consider extra-territorial movements may not accurately define an animal's ecology, behavior, and space use, all important aspects for the development of effective species-specific conservation plans.

Spot-mapping, or territory mapping by visual observation of displaying males (Bibby et al. 2000), has been the choice method to study avian habitat and space use. The dependency on visual confirmation of an individual limits the inferences researchers can make using spot mapping data. Spot-mapping does not account for all areas used by a bird (Anich et al 2009a; Streby et al. 2012), which was not fully appreciated until recent advances in radio telemetry technologies that made transmitters small enough to be used on passerines (Anich et al. 2009a, 2009b). Since then, radio telemetry has demonstrated that some species regularly make extra-territorial movements (Hanski and Haila 1988; Williams 1990; Smiseth and Amundsen 1995). These technological advances are enabling avian researchers to shift focus to broader spatial scales (i.e., home range) that allow for the characterization of habitats used outside breeding territories, and ultimately a more complete understanding of a species breeding ecology (Whitaker and Warkentin 2010).

Another central challenge to avian ecology and habitat management is relating ecological phenomena across scales when observing habitat use and selection (Levin 1992). Habitat use is how an individual uses habitat to meet its life history needs (Jones 2001). Habitat selection refers to a hierarchical process of behavioral responses that may result in the disproportionate use of habitats to influence survival and fitness of individuals (Hutto 1985; Block and Brennan 1993). As such, habitat-use patterns are the end result of habitat-selection processes (Jones 2001). Essentially, habitat selection

studies attempt to understand how animals “scale” their environments, which all animals display selection at some minimum spatial scale (Otis 1998). A species’ habitat requirements may vary depending on the scale (Johnson 1980; Wiens 1981), and assessing habitat selection at a single habitat scale may lead to false conclusions (Kotliar and Wiens 1990; Zimmerman and Glanz 2000). Studies investigating habitat selection at multiple scales have elucidated habitat selection as a complex decision-making process(see Limpert et al. 2007; Kesler and Haig 2007; Steen et al. 2010; Michel et al. 2008; Altmooos and Henle 2010; Hoss et al. 2010). Therefore, conducting habitat use studies at multiple spatial scales appears to be necessary for a complete understanding of a species’ breeding ecology.

Population declines of the Golden-winged Warbler (*Vermivora chrysoptera*) are believed to be correlated to loss of breeding habitat, competition and hybridization with the Blue-winged Warbler (*V. cyanoptera*), and Brown-headed Cowbird (*Molothrus ater*) parasitism(Confer et al. 2003, Buehler et al. 2007). Of these threats, loss of breeding habitat is believed to play the largest role in Golden-winged Warbler declines (Smith et al. 1993; Buehler et al. 2007). As such, management of early successional habitat that supports breeding Golden-winged Warblers is a critical conservation priority (Roth et al. 2012). In 2008, the Golden-winged Warbler Working Group initiated a 3-year, range-wide study to identify habitat features of breeding territories that most influence Golden-winged Warbler reproductive success (Roth et al. 2012).

As with other passerine breeding ecology studies, spot-mapping has been the most commonly used method to delineate breeding territories of Golden-winged Warblers (Confer et al 2003, Patton et al. 2010). Although spot-mapping is an effective method for

delineating core breeding territories, recent evidence from a radio telemetry study in Minnesota suggests that male Golden-winged Warblers may leave their core territories throughout the day to use resources elsewhere (Streby et al. 2012). A similar radio telemetry study found space use of the Swainson's Warbler (*Limnothlypis swainsonii*) was much larger than what was observed through spot-mapping (Anich et al. 2009a). Therefore, it is possible that current methods used to examine Golden-winged Warbler habitat use across its range are missing important aspects of Golden-winged Warbler breeding ecology.

A study in Minnesota found Golden-winged Warblers territories delineated by spot-mapping to be considerably smaller than telemetry-based home ranges (Streby et al. 2012). This study was conducted in a study area with one of the highest known densities of Golden-winged Warblers (~1 territory/ha) (Streby et al. 2012). Streby et al. (2012) also found that breeding Golden-winged Warblers used mature forest habitats more than previously reported. Golden-winged Warbler territory size may be related to the amount of optimal habitat available (MacDonald and Carr 1989; Smith and Shugart 1987; DeLotelle et al. 1987; Canterbury 1990; Brooker and Rowley 1995) or density of male Golden-winged Warblers in an area (Confer 1992). Given that territory size and population density are often inversely related (Maher and Lott 2000), it is reasonable to predict that Golden-winged Warblers in habitats with high nesting densities may need to travel outside their defended territories to access resources compared to individuals in areas with low nesting densities. Given the potential for conservation plans to be misinformed if based solely on data generated using visual observation methods (i.e. spot-mapping) (Streby et al. 2012), it is important that potential differences between spot-

mapping and radio telemetry based techniques be examined in other regions of Golden-winged Warbler breeding range.

I used radio-telemetry and spot-mapping methods to examine habitat and space use of territorial male Golden-winged Warblers in north-central Pennsylvania. Unlike the recent study in Minnesota, my study occurred in an area with a low Golden-winged Warbler nesting density (0.14 pair/1 ha) (J. Larkin, unpublished data). My objectives were to (1) compare Golden-winged Warbler space use between radio telemetry and spot-mapping techniques and (2) to quantify differences in habitat characteristics between telemetry- and spot-mapped delineated areas at two spatial scales: microhabitat and macrohabitat. Results from my study will help elucidate whether the different extra-territorial space use patterns observed in the high density Golden-winged Warbler population in Minnesota are consistent in the low-density breeding population of north-central Pennsylvania. Ultimately, determining the propensity to which Golden-winged Warblers use areas outside their spot-mapped breeding territories will be important for informing regional habitat management guidelines.

Chapter 2

LITERATURE REVIEW

Population Decline in the Golden-winged Warbler

The Golden-winged Warbler is an early successional, disturbance-dependent species that breeds in a shrub-scrub habitat of sparse trees with an herbaceous understory of forbs and grasses (Confer 1992). This species has experienced population declines for the past 40 years with an average annual decline of -2.9% per year in the United States (Sauer et al. 2011). In the Appalachian region such as Pennsylvania, the Golden-winged Warbler has declined 72% within the last 20 years with an average annual decline of -6.8% from 1966-2009 (Pennsylvania Breeding Bird Atlas 2009; Sauer et al. 2011). This may be in part due to decline of early successional habitats in Pennsylvania since the 1970s (Yahner 2003). The U.S. Fish and Wildlife Service recognize the Golden-winged Warbler as a “species of management concern” and it is on the Partners-in-Flight Continental Watch List (Rich et al. 2004). As such, the species has recently been petitioned for protection under the U.S. Endangered Species Act (Sewell 2010; Parham 2011).

Loss of breeding habitat in areas devoid of the Blue-winged Warbler is thought to be a primary cause of Golden-winged Warbler population declines. Natural fire suppression, advanced succession on abandoned farmland and timber harvests, and decline of natural habitat conditions has led to significant reductions in Golden-winged Warbler breeding habitat throughout most of its historic breeding range (Delcourt and Delcourt 1997, Buehler et al 2007; Hunter et al. 2001). Golden-winged Warbler breeding habitat was historically associated with abandoned meadows created by beaver (*Castor*

canadensis), regenerating burned areas, and other natural disturbance-generated habitat (Brewster 1886; Short 1963). Today, Golden-winged Warblers are most often associated with anthropogenic disturbances (timber harvests, utility rights-of way, and abandoned farmland) that emulate natural disturbances (Hunter et al. 2001).

Competition and hybridization with the Blue-winged Warbler is thought to be an overriding factor driving Golden-winged Warbler decline (Confer and Larkin 1998; Confer et al. 2003). Throughout much of the Golden-winged Warbler breeding range, expanding Blue-winged Warbler populations tend to replace Golden-winged Warbler populations within 50 years of initial contact (Gill 1980, 1997). However, there are areas in the heavily forested, higher elevations of the central and southern Appalachian Mountains that support breeding populations of Golden-winged Warblers in the absence of Blue-winged Warblers (Roth et al 2012). There exists one well documented case in southern New York, where Golden-winged and Blue-winged Warblers have coexisted stably for over a century (Eaton 1914; Confer et al. 1998). Koonce (2005) suggested that unspecified habitat factors may play a role in the replacement of Golden-winged Warblers by Blue-winged Warblers but is unlikely the sole factor.

In addition to the loss of breeding habitat and hybridization with Blue-winged Warblers, the Golden-winged Warbler faces lower nesting success in some regions due to nest parasitism by the Brown-headed Cowbird (*Molothrus ater*). In New York, Brown-headed Cowbird parasitism lowered Golden-winged Warbler fledgling rate by 17%, whereby Golden-winged Warbler fledgling rates in nonparasitized, nondepredated nests were higher (3.3 as opposed to 1.3 fledglings per nest) (Confer et al. 2003). Golden-winged Warblers nesting in post-agricultural shrub-scrublands may be the most

vulnerable to parasitism as cowbirds normally are more abundant in agricultural settings (Thompson et al. 2000).

Habitat Selection of Golden-winged Warblers

The Golden-winged Warbler breeds in ephemeral young forest and shrubland habitats with some scattered trees or mature forest edge (Confer 1992, Roth et al. 2012). Recently, it has become evident that long-term sustainability of breeding populations in the Appalachian Mountains are linked to expansive forested landscapes (Roth et al. 2012). In Pennsylvania, forest area has remained constant since the 1970s, but the early successional habitat Golden-winged Warblers rely on has been declining (Yahner 2003). In these young forest habitats, Golden-winged Warblers will also use residual overstory trees in interior portions of timber harvests as song perches (Kubel 2005). Golden-winged Warblers currently breed in many young forest and shrubland habitats such as abandoned farmlands, timber harvests, reclaimed minelands, alder bogs, tamarack swamps, and open woodlands with dense understory (Hunter et al. 2001). The creation of young aspen forests and maintaining shrub-scrub habitat are thought to be the best way to manage Golden-winged Warbler populations in the north-central portion of its range (Martin et al. 2007). Golden-winged Warbler abundance was highest in young aspen stands (1-10 years of age) and lowest in mature edge cover and swamp habitats (Martin et al. 2007).

Much research has focused on Golden-winged Warbler hybridization with Blue-winged Warblers (Gill 1997; Shapiro et al. 2004). A study at Sterling Forest State Park in New York compared phenotypic distribution, nesting, success, and genetic purity of Golden-winged Warblers and Blue-winged Warblers between uplands and swamp forests

(Confer et al. 2010). Golden-winged Warblers and Blue-winged Warblers have co-existed in southern New York and Sterling Forest State Park for over 100 years (Eaton 1914; Confer et al. 1998). Both wetland and upland Golden-winged Warbler territories consisted of patchy herb-shrub habitat and usually had a forested edge (Confer et al. 2010). Preliminary results suggested swamp forests supported a higher proportion of pure Golden-winged Warbler phenotype-haplotype matches than upland habitat (Confer et al. 2010). Management of swamp forests may be critical source habitats that help sustain the declining Golden-winged Warbler population in this region (Confer et al. 2010).

A recent study in West Virginia identified micro and macro scale habitat characteristics for Golden-winged Warblers breeding on actively grazed shrublands (Aldinger 2010). Vegetation density ($\geq 38.1\%$ at territories and $\geq 51.9\%$ at nests), microscale woody vegetation cover ($\geq 4.5\%$ at nests), and macrohabitat grass cover (37.5-87.5% at nests) were found to be important components of Golden-winged Warbler territories and nest sites (Aldinger 2010). Proximity to a shrub may be important to Golden-winged Warbler nest site selection, and the average height of the shrub layer at nest sites was $1.5 \pm 0.1\text{m}$ (Aldinger 2010; Aldinger, unpub. data).

To reverse the population decline of the Golden-winged Warbler and increase population viability, research is now focused on determining habitat features that will specifically attract breeding Golden-winged Warblers (Buehler et al. 2007). Current research supports past findings that Golden-winged Warblers establish territories at higher elevations with greater percentages of grass and canopy cover than Blue-winged Warblers (Patton et al. 2010). In New York, herb and shrub cover were found to be

positively correlated with Golden-winged Warbler clutch size while Blue-winged Warbler proximity was found to have a negative effect (Confer et al. 2003). Dominant plant species within breeding Golden-winged Warbler territories were identified so researchers can better understand how to create habitat that attract Golden-winged Warblers (Patton et al. 2010). Plant species indicative of sites with Golden-winged Warblers included orchardgrass (*Dactylis glomerata*), green ash (*Fraxinus pennsylvanica*) seedlings and saplings, and black locust (*Robinia pseudoacacia*) saplings (Patton et al. 2010).

The results of these studies and those of others have focused on habitat features within core breeding territories (e.g. Klaus and Buehler 2001; Kubel and Yahner 2008). Territory boundaries likely extend beyond song perches, with peripheral areas likely providing important edge attributes for nesting (Rossell et al. 2003). Golden-winged Warbler nesting sites in Michigan were usually located in peripheral areas near their territorial boundaries (Will 1986). Golden-winged Warbler territories have been known to extend 5-30 m into adjacent older forests (Rossell et al. 2003), and the species' association with forested edges may be indicative of the disturbance-based habitat within which it evolved (Patton et al. 2010). Because Golden-winged Warblers most often are monitored in early successional habitat due to observational bias (Streby et al. 2012), radio telemetry may help identify habitat features outside core breeding territories that can be incorporated into habitat management prescriptions.

Territory and Territoriality in The Golden-winged Warbler and Other Species

Even when not defending a territory or resources, most songbirds like to maintain a space between themselves and conspecifics (Pearson 1991; Ostreiher 1999). Howard

(1920) introduced scientific inquiry into territorial behavior, which is a primary form of aggressive spacing behavior. Avian territory is normally defined as any defended area during the breeding season (Hinde 1956). A territory is defended continuously for some duration of time where an individual exhibits acts of display or aggressive behavior to prevent rival individuals from entering or using the space (Brown and Orians 1970). Therefore, primary use of a territory is limited to the defending individual bird, its mate, and progeny (Brown and Orians 1970). Golden-winged Warblers can nest in clusters of individual territories (Confer and Knapp 1981; King et al. 2009). Nest clustering is common in songbirds and may result from evolutionary benefits of multiple mate opportunities (Melles et al. 2009).

Wood Warbler territories generally include a breeding area where the nesting, courtship, mating, and food-seeking occur, which are known as all-purpose territories (Hinde 1956). A typical all-purpose Golden-winged Warbler territory is between 0.6-2.7 hectares (ha) although they have been recorded as large as 5 ha (Confer 1992; Patton et al. 2010). Territory size in mountain wetlands of North Carolina was 0.4-1.6 ha which is consistent with other ranges reported (Rossell et al. 2003). The lower size limit of a Golden-winged Warbler territory in any habitat may represent the minimum area required to provide sufficient breeding resources (Verner 1977). Size of Golden-winged Warbler territories may be related to the amount of optimal habitat (Canterbury 1990), density of males in an area (Confer 1992), or may serve as a function of the distribution of attractive features (like water and prominent trees) (Rossell et al. 2003).

Although Golden-winged Warbler densities are rarely reported, a study in northern Wisconsin observed high Golden-winged Warbler nesting densities (0.55 males

per ha) in habitats with only tree seedlings (<2.5 cm mean diameter) (Roth and Lutz 2004). In contrast, a study in eastern Ontario reported much lower nesting densities (0.04 males per ha) in habitats comprised of saplings and medium-sized aspen (King et al. 2009). A similar study calculated densities as males per point count station with the highest at 0.79 (0.20 males per ha) in a young (1-10 years old) aspen stand (Martin et al. 2007; King et al. 2009).

An important aspect of Golden-winged Warbler ecology is territorial relationships between Blue-winged Warblers and their hybrids (Confer et al. 2010; Patton et al. 2010). Blue-winged Warblers and Golden-winged Warblers are usually found in small, isolated “colonies” which may be dependent on the availability of breeding habitat and other factors (Short 1963). Golden-winged and Blue-winged Warblers differ phenotypically by size, color, and facial pattern (Ficken and Ficken 1968). Facial pattern seems to be important for species recognition in territorial behavior and visual face recognition was important in evoking aggression (Ficken and Ficken 1968). However, hybrids are just as likely to form pairs relative to their abundance in the population as phenotypic Golden-winged Warblers, regardless of whether they express a Golden-winged or Blue-winged facial pattern (Vallender et al. 2007, 2009). Golden-winged and Blue-winged Warbler hybrid phenotypes exhibit degrees of intermediacy between the two pure phenotypes such as the Brewster’s Warbler (*V. leucobronchialis*) or the rarer variation, Lawrence’s Warbler (*V. lawrencei*). Even when the Golden-winged and Blue-winged Warblers look phenotypically pure, they may express introgression (Shapiro et al. 2004; Dabrowski et al. 2005; Vallender et al. 2007).

Golden-winged Warblers broadcast their presence and control of a territory through vocalizations or song (Ficken and Ficken 1973). Golden-winged Warblers and Blue-winged Warblers each have unique Type 1 and similar Type 2 songs. Later in the season and particularly following territorial encounters, the Type 2 song is sung (Ficken and Ficken, 1967). Territorial encounters are most intense and frequent before nest building (Ficken and Ficken 1968). As such, song playback for Golden-winged Warbler detection is more effective earlier in the nesting season and predator mobbing more effective later (King et al. 2009). This may be due to males aggressively defending territories in the beginning of the nesting season, then defending the mate and offspring from a predator during nesting (King et al. 2009).

Territorial defense of food resources is adaptive and subject to change, corresponding to maintaining a balance of costs and benefits where benefits must exceed costs (Carpenter and MacMillen 1976). Brown (1964) introduced a cost-benefit approach to territoriality. The type of territoriality evolved in a species depends on the resources for which competition exists, and upon the degree to which they are “economically defendable” (Brown 1964). As such, the problem for a species like the Golden-winged Warbler then becomes that of demonstrating which particular resources are in short supply, which are not, and how it is beneficial for certain ones to be defended but not others (Brown 1964).

There is variation of territoriality across species. For example, a study showed that Pomarine Skuas (*Stercorarius pomarinus*) defended small areas when their food source [lemmings (*Lemmus trimucronatus*)] were abundant, and defended larger territories when lemmings were scarce (Wiley and Lee 2000). A study of Ovenbirds

(*Seiurus aurocapillus*) revealed that their territories were the same as their feeding area (Stenger 1958). The study validated the food value theory, where the function of territorial behavior is to space out birds enough to ensure adequate food supply for successful rearing of young (Stenger 1958). However, food resources don't explain all territorial aggression. A study of breeding nectar-eating Honeyeaters (*Phylidonyrus novaehollandiae* and *P. nigra*) in Australia found that they aggressively defended their territories even when their main food source was experimentally made scarce (Armstrong 1992). An alternative explanation is that the honeyeaters were responding to changes in likelihood of losing their territories if not defended since territories normally are not re-acquired easily (Armstrong 1992; Krebs 1982; Beletsky and Orians 1989).

Since territory owners have an investment to protect such as food resources and a chance to mate, they usually do not succumb easily to a newcomer (Beletsky and Orians 1987). The extent of knowledge of an area or investment in an area contributes then to territorial dominance (Beletsky and Orians 1989). Territorial males also assert themselves more effectively in their territories than when they are in a new place by using familiar details to aid during aggressive encounters. For example, Stellar's Jays (*Cyanocitta stelleri*) won more confrontations closer to their nesting territories, and the ability to win decreased with distance from the nesting site (Brown 1975).

In an extensive literature review of territoriality in birds, population density as a determinant of territoriality was reported in only 7% of papers (Maher and Lott 2000). Density independent factors can influence territoriality, and birds may choose other options when habitat is crowded such as not breed or disperse (Brown 1987). However, many strong examples exist of the impact of population density. Nesting American Tree

Sparrows (*Spizella arborea*) used only 15% to 18% of their territories when population density was low. The American Tree Sparrow's activities concentrated in the core area but they also defended a less frequently used buffer zone (Weeden 1965). When American Tree Sparrow density was high, competition for breeding space increased and caused denser packing of smaller territories, which eliminated buffer zones (Weeden 1965).

Two other vertebrate studies concluded that increased population density can stop territoriality due to increased rates of intruder pressure (Cole and Noakes 1980; Magurran and Seghers 1991). High population costs (combined with low fighting costs) can also promote large, overlapping home ranges (Morrell and Kokko 2005). When fighting costs are high and population density is low, the most adaptive behavior may be to avoid fight locations which can generate exclusive territories in a population able to resist invasion by more aggressive (fighting) strategies (Morrell and Kokko 2005). In most cases, territoriality is found to increase population stability but it may come at the cost of reduced equilibrium densities (López-Sepulcre and Kokko 2005).

The last component to territoriality is determining what influences territory size. Most studies indicate a negative relationship between food availability and territory size (Adams 2001). Territory residents may decide what size an area to defend based on food availability, and increased food density may attract more competitors, causing the resident to make its territory smaller (Myers et al. 1979). However, it was also common to find no correlation between food abundance and territory size (Adams 2001). One study, in contrast, found that male rock pipits (*Anthus petrosus*) given supplemental food

within their territories at hidden sites established larger territories (into less-preferred habitat) than males that received none (Arvidsson et al. 1997).

The lack of consistency between food availability and territory size may result from non-food related variables influencing territory size (Adams 2001). For example, the availability of perch sites (Yosef and Grubb 1994) and the dispersion of potential mates are plausible influences (Butchart et al. 1999). Removal of competitors in one study caused increases in pomacentrid reef fish (*Parma victoriae*) territory size at all algal food abundances since manipulation of food supply had no effect (Norman and Jones 1984).

There are several possible reasons as to why only some species adjust territory size relative to food abundance. If the species obtained food away from the territory, it may reduce their reliance on food resources within the territory (Myers et al. 1979). Two non-avian studies suggest territories can serve functions other than protection of the food supply (Waldschmidt 1983; Wolff 1985). A study of spiders indicated animals may have to rely on predictors of expected food supply since they cannot accurately assess the food supply directly (Riechert 1981). Species may adjust territory by having to respond to characteristics of vegetation to indicate expected food supply (Seastedt and MacLean 1979; Franzblau and Collins 1980; Stamps 1994). Since most studies indicate that responses to changes in food abundance are less likely for contiguous absolute territories (like Golden-winged Warblers have) than noncontiguous territories, multiple factors must contribute to the wide-range of variation seen in these foraging studies (Adams 2001).

Radio Telemetry and Golden-winged Warbler Habitat Selection

Radio transmitters have relatively recently become small enough to allow new research on passerine ecology (Streby and Anderson 2010). Researchers are learning more about post-fledgling ecology through the use of radio telemetry, which helps improve our understanding of less studied aspects of the avian life cycle (Suedkamp et al. 2008; Vitz and Rodewald 2010; Vitz and Rodewald 2011). The central challenge in ecology is relating ecological phenomena across scales (Levin 1992). Habitat selection studies are about how animals “scale” their environment: at some minimum observation scale, all animals will exhibit habitat selection (Otis 1998). This is why habitat requirements may vary depending on spatial scale (Johnson 1980; Wiens 1981), and assessing habitat selection at a single spatial scale may lead to false conclusions (Kotliar and Wiens 1990; Zimmerman and Glanz 2000). Studies investigating habitat selection at multiple spatial scales has helped to elucidate habitat selection as a complex process occurring at various scales (for examples from other species, see Limpert et al. 2007; Steen et al. 2010; Michel et al. 2008; Altmöös and Henle 2010; Kesler and Haig 2007; Hoss et al. 2010).

The first radio-telemetry based study that examine Golden-winged Warbler breeding ecology only quantified habitat selection at the landscape scale (Streby et al. 2012). Additionally, spot mapping and radio telemetry locations were used to compare Golden-winged Warbler space use, territory size, and land cover composition. Four of eighteen transmittered adult males were intensively monitored. There was no evidence of male mortality, giving a nesting-season survival of 1.0 for 2010 (Streby and Anderson 2010). Nineteen females were also monitored and had a daily survival of 0.987 ± 0.008

during the 2010 nesting season, with one predated by a hawk and two believed predated by nest predators (Streby and Anderson 2010). Territories were 2.8 times larger and included more mature forest using telemetry than spot-mapping estimates (Streby et al. 2012). Additionally, home ranges included more mature forest using telemetry suggesting mature forest may be a bigger component to Golden-winged Warbler breeding habitat than indicated by spot-mapping techniques (Streby et al. 2012).

A study in Costa Rica quantified Golden-winged Warbler habitat selection during the non-breeding season using radio telemetry (Chandler and King 2011). Information on habitat selection at the home range level (2nd order) was provided by point count surveys while habitat selection within the home ranges (3rd order) was provided by radio telemetry. The following variables were measured to quantify habitat characteristics: elevation, canopy height, percentage canopy cover, slope, aspect and diameter at diameter breast height (dbh) of trees. Microscale variables measured were: hanging dead leaf index, vine tangle index, and epiphyte index. At each telemetry location, habitat type was recorded as primary forest, secondary forest, naturally disturbed forest, or agroforestry system. Golden-winged Warblers selected microhabitat features associated with intermediate disturbance within their home ranges suggesting their foraging preference for hanging dead leaves (Chandler and King 2011).

Golden-winged Warblers on their wintering grounds preferred areas of high basal area (0.055 in 2m plot) and where vine tangles were present within their home ranges, features commonly found in large canopy gaps and advanced secondary forest (Chandler and King 2011). Golden-winged Warbler abundance was highest in naturally disturbed forest and advanced secondary forest with abundance positively associated with number

of dead hanging leaves (Chandler and King 2011). Within the same study, Golden-winged Warbler non-breeding territory size averaged 8.8ha with little overlap between neighboring home ranges (Chandler 2011). Their data suggested that Golden-winged Warblers are territorial during the non-breeding season. Golden-winged Warblers as dead leaf foragers and their reliance on this patchily-distributed, high quality food resource may explain their large non-breeding season home range sizes and territoriality (Chandler 2011).

CHAPTER III

METHODS

Study Area

Core breeding territories and habitat use areas of Golden-winged Warblers were delineated and sampled at Bald Eagle State Park and Sproul State Forest in north-central Pennsylvania. Bald Eagle State Park consists of 2387 hectares in Bald Eagle Valley of northern Centre County (PA DCNR 2011). A 700 ha lake encompassed 29% of the park (PA DCNR 2011). The remaining 71% consisted of forests, wetlands, fields, powerline right-of-ways, and recreational areas (PA DCNR 2011). Bald Eagle State Park is nested between two physiographic provinces: Mountainous High Allegheny Plateau and the Ridge and Valley province to the south and east (Briggs 1999). My study sites (n=6) were located on a 219 ha portion of the park that was within the Ridge and Valley Province. This province is characterized by long, narrow, mountainous ridges separated by valleys that vary in width and elevation (Way 2009; Pennsylvania Bureau of Topographic and Geologic Survey 2011) with shallow, stony soil (Braun 1950). Ridges and side slopes were dominated by tree species associated with northern hardwoods or oak-hickory forests (Braun 1950; Abrams and Ruffner 1995). Mixed red oak-hickory forests occurred on lower slopes where common species included red oak (*Quercus rubra*), white oak (*Quercus alba*), black gum (*Nyssa sylvatica*), hickory (*Carya* spp.) and red maple (*Acer rubrum*) (Fike 1999; Rhoads and Block 2005). Northern hardwoods were dominated by American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), black and yellow birch (*Betula lenta* and *B. alleghaniensis*), and eastern hemlock (*Tsuga canadensis*) (Fike 1999; Stoleson and Larkin 2010). My study sites were located at an

elevation of approximately 200 meters, and were comprised of a young forest, managed and natural shrublands, and remnant forest patches. Invasive shrubs such as bush honeysuckle (*Lonicera* spp.), autumn-olive (*Elaeagnus umbellata*), and multiflora rose (*Rosa multiflora*) dominated all 6 study sites. Common native woody species included red osier dogwood (*Cornus sericea*), silky dogwood (*C. amomum*), gray dogwood (*C. racemosa*), arrowwood viburnum (*Viburnum dentatum*), blackberry (*Rubus* spp.), elm (*Ulmus* spp.), black walnut (*Juglans nigra*), hawthorn (*Crataegus* spp.), and ash (*Fraxinus* spp.).

The second study area was located in Sproul State Forest, primarily located in western Clinton and northern Centre counties (PA DCNR 2011). Sproul S.F. consists of 123,611 hectares and features steep, rugged hillsides cut by the Susquehanna River and its tributaries (Briggs 1999; PA DCNR 2011). The entire study area was located in the Appalachian Mountainous High Plateau province (Briggs 1999). Provincial elevations range from 174-732 m (Briggs 1999). Sproul is predominately northern hardwood or dry oak forest that contain some scattered white pine (*Pinus strobus*) and/or hemlock (*Tsuga canadensis*) (PA DCNR 1999). On drier upper slopes and ridgetops, these oak forests commonly have white oak (*Quercus alba*), black oak (*Quercus velutina*), and chestnut oak (*Quercus montana*) and often have a dense shrub layer comprised of mountain laurel (*Kalmia latifolia*), blueberry (*Vaccinium* spp.), sweet fern (*Comptonia peregrina*), and blackberry (*Rubus* spp.) (Rhoades and Block 2005). Sweet birch (*Betula lenta*) is dominant on rocky upper slopes and was present on my study sites (Braun 1950). Golden-winged Warblers at Sproul State Forest were restricted to regenerating timber harvests and portions of a 4000 ha area that burned due to an arson fire in 1990 (Larkin, per. comm.). My study sites (n=3) in Sproul S.F. were located at a 610m elevation and consisted of approximately 270 ha of the

regenerating burned area located along Jews Run Road. Regenerating forests were dominated by a young forest mosaic of blackberry (*Rubus* spp.), blueberry (*Vaccinium* spp.), mountain laurel (*Kalmia latifolia*), sweet fern (*Comptonia peregrina*), hay-scented fern (*Dennstaedtia punctilobula*), teaberry (*Gaultheria procumbens*), sassafras (*Sassafras albidum*), birch (*Betula* spp.), black locust (*Robinia pseudoacacia*), and red maple (*Acer rubrum*) saplings (Fike 1999; PA DCNR 1999; Rhoades and Block 2005). There was very little development in this region except for a few hunting cabins, a major gas pipeline, several gated and ungated gravel roads, and numerous gas wells.

Definitions

Ornithologists tend to be inconsistent with what constitutes habitat use and habitat selection in published literature, so it is important to identify how my radio telemetry study addressed these two concepts (Jones 2001). *Habitat* refers to a distinctive set of physical environmental factors that a species uses for its survival and reproduction (Block and Brennan 1993). *Habitat use* refers to how an individual uses habitat to meet its life history needs. *Habitat selection* refers to a hierarchical process of behavioral responses that may result in the disproportionate use of available habitats to influence survival and fitness of individuals (Hutto 1985; Block and Brennan 1993). As such, habitat-use patterns are the end result of habitat-selection processes (Jones 2001).

A *territory* is a fixed area that is defended continuously for some period of time in the Golden-winged Warbler's breeding season (Noble 1939; Brown and Orians 1970). Based on this criteria, a territory is normally limited exclusively to the defending Golden-winged Warbler, its mate, and progeny (Brown and Orians 1970). I refer to areas that were delineated via spot-mapping as spot-mapped territories. A home range is usually defined as an area traversed by an individual in its "normal" activities of foraging,

mating, and caring of young (Burt 1943). Excursions outside of an individual's normal use area are usually excluded from home range calculations (Burt 1943). Usually outlying locations are removed from consideration by using a smaller set of all the recorded locations (i.e., 95%), but this criterion is arbitrary and often lacks biological basis (Anderson 1982; White and Garrott 1990). For the purposes of my study, *home range* (telemetry use area) was defined as areas repeatedly traversed by an individual and all extra-territorial movements (Kenward 2001).

Capture and Handling

Between 1 May and 1 July 2011, male Golden-winged Warblers were captured using targeted mist-netting with song playback and a warbler decoy (Anich et al. 2009a). Captured individuals were fitted with a metal U.S. Geological Survey band, as well as 1-3 unique color bands for identification purposes. Additionally, males that weighed >10 g were fitted with a radio transmitter (Holohill models BD-2N (0.43 g), LB-2X (0.31 g)). Radio transmitters were attached with a glue-on method that required minimal handling (~5 min), and was approved by the Institutional Animal Care and Use Committee (IACUC #03-0708-R, Indiana University of Pennsylvania). The process involved clipping a small patch of feathers from the interscapular region, cleaning the area with acetone, placing a small piece of cotton mesh to the underside of the transmitter, and attaching the transmitter to the feather stubble using cyanoacrylate glue (Scotch[®] Maximum Strength Adhesive) (Sykes et al. 1990, Johnson et al. 1991; Anich et al. 2009b). To ensure the glue had dried, the transmitter was held gently in place for 5 minutes before releasing the individual at the point of capture. This method has been successfully used elsewhere on warbler-sized birds (Anich et al. 2009a, 2009b).

According to the Guidelines for Use of Wild Birds in Research, transmitters for small birds should be less than 5% the bird's body mass (Fair et al 2010). Adult, male Golden-winged Warblers weigh between 8-11 g. The transmitter units (Holohill models BD-2N (0.43 g), LB-2X (0.31 g)) was less than 5% of the Golden-winged Warbler's weight with the additional piece of cotton. To be conservative regarding the application of radio-transmitters, transmitters were only placed on males that weighed ≥ 10 g.

Territory and Telemetry Use Area Delineation

Golden-winged Warblers territories were spot-mapped every other day through visual observation of feeding, perching, and singing. Each banded male was spot mapped for a 30 to 60 minute sampling period (Barg et al. 2005), between 0500-1900 hours eastern standard time (EST). We tried to record at least 5 different spot-mapping locations per visit.

Radio telemetry data were collected on alternate days for the life of each transmitter using the homing method (Mech 1983; White and Garrott 1990). The homing method involves approaching the Golden-winged Warbler on foot based on radio signal strength until a visual observation is documented but not approaching close enough to introduce bias in behavior (White and Garrot 1990; Vitz and Rodewald 2010). Golden-winged Warblers were approached close enough for a visual or to estimate the bird's location. If a visual observation was not possible, I approached the perceived location from several directions to confirm the individual's actual location (Anich et al. 2009a). Telemetry equipment consisted of a 3 element yagi antenna and radio receivers (Lotek Suretrack STR_1000 and Communication Specialist). Telemetry monitoring was conducted between 0500 and 1900 EST. The order and time of territories monitored

were alternated to prevent any time of day effects on activity (Shields 1977). We attempted to record a minimum of 30 telemetry locations for each Golden-winged Warbler (Seaman et al. 1999; Garton et al. 2001).

Because it is important to sample locations at an interval long enough to allow an individual to move from any point in its territory or home range to any other point, I allowed at least 1-minute to elapse between locations (Lair 1987; Holzenbein and Marchinton 1992; McNay et al. 1994; Silva-Opps and Opps 2011). All observations (spot map and telemetry) were flagged and Universal Transverse Mercator (UTM) coordinates recorded using a Garmin eTrex version 3.30 global positioning system (GPS). Other data recorded included bird identification number, radio frequency, time of day, behavior of bird (if seen), and habitat type.

I used all spot map locations for each male to delineated territories and telemetry use areas were delineated by created using 100% and 50% Minimum Convex Polygons (Mohr 1947). Area is positively correlated with sample size using the MCP method and can be highly influenced by an outlying point (Worton 1987; Barg et al. 2005; Börger et al. 2006). While MCPs are known to overestimate home range size (White and Garrot 1990), I used this method to ensure the liberal quantification of area needed to support male Golden-winged Warblers. I argue such information is very important for better informing management decisions for this species, as most existing estimates of breeding habitat space use for Golden-winged Warblers are the result of spot-mapped data.

Calculating Sample Size Estimates

I determined if an appropriate sample size was met for each individual telemetry use area by plotting home range size vs. number of locations. I defined appropriate

sample size as the point after which additional locations resulted in a minimal increase (<1%) in telemetry use area size (Harris et al 1990; Seaman et al 1999; Laver 2005; Schrecengost et al 2009). To produce home range asymptotes for continuous radio tracking data, radio locations were added sequentially in the computer program Ranges 7 (Anatrack, Dorset, United Kingdom) using incremental area analysis (South et al 2008).

Habitat Sampling

Habitat sampling was completed in Golden-winged Warbler spot-mapped territories and in telemetry use areas at the end of the breeding season (late-June into July). Habitat structure and composition of Golden-winged Warbler habitat use areas found through spot-mapping and radio telemetry were sampled in the same manner using a standardized protocol developed by the Golden-winged Warbler Working Group. Using a systematic random sampling design, we ran transects through spot-mapped delineated territories and sampled vegetation at 30 or more points per territory (Figure 1). Appropriate spacing between points and transects were determined in ArcMapGIS (ESRI 2011, Redlands, CA) using aerial photographs with overlaying minimum convex polygons (MCPs) before going in the field. A random compass bearing and starting point was also determined prior to entering the field. A 50 m marked rope at meter increments along with a handheld GPS were used to maintain accurate spacing between sampling points and transects. In order to ensure statistical independence between spot-mapped territories and telemetry use areas, any habitat sampling points that were less than 12 m outside spot-mapped breeding territory were excluded from sampling. Habitat sampling was conducted at each telemetry location (Figure 2). Additionally, telemetry locations

outside of spot-mapped territories were characterized as typical or non-typical Golden-winged Warbler breeding habitat.

At each habitat sampling point, percent cover of vegetation (grass, forbs, ferns, goldenrod), shrubs <2 m tall, shrubs >2 m tall, saplings (<10 cm dbh), and canopy cover was visually estimated within a 1 m radius circle along with distance to a microedge (any change in vegetation strata). Canopy cover was the percentage of the plot shaded by overhead tree foliage. Percent cover of blueberry (*Vaccinium* spp.), mountain laurel (*Kalmia latifolia*), and sweet fern (*Comptonia peregrina*) was estimated at Sproul and percent cover of honeysuckle/autumn olive (*Lonicera tatarica*/*Elaeagnus umbellata* collectively), multiflora rose (*Rosa multiflora*), and vine were recorded at Bald Eagle. At every 5th sampling point, we recorded the number of shrubs 1–2 m tall, shrubs >2 m tall, and number of saplings within a 5 m radius. Shrubs were counted based on individual stumps in which the shrub originated. In the case of shrubs that grow in large masses, the number of shrub “equivalents” was estimated based on its typical growth form. Also at every 5th sampling point in spot-mapped territories and at all telemetry locations that occurred outside spot-mapped territories, the number of snags and number of “in” trees (basal area) were recorded within 11.3 m using a 2.5 m²/ha prism .

Figure 1. Diagram of a hypothetical Golden-winged Warbler territory with random transects (lines) and 1m radius vegetation sampling plots (black dots), and 5 m radius sampling plots (large circles). A systematic random sampling design used at Bald Eagle State Park and Sproul State Forest during the 2011 Golden-winged Warbler breeding season.

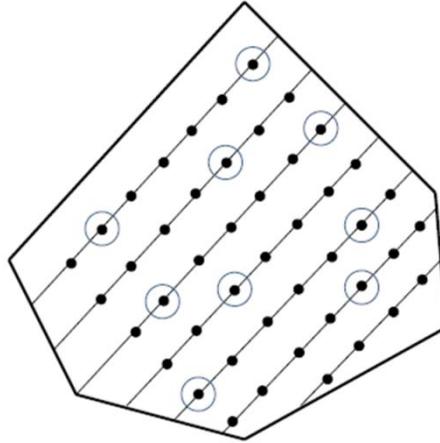
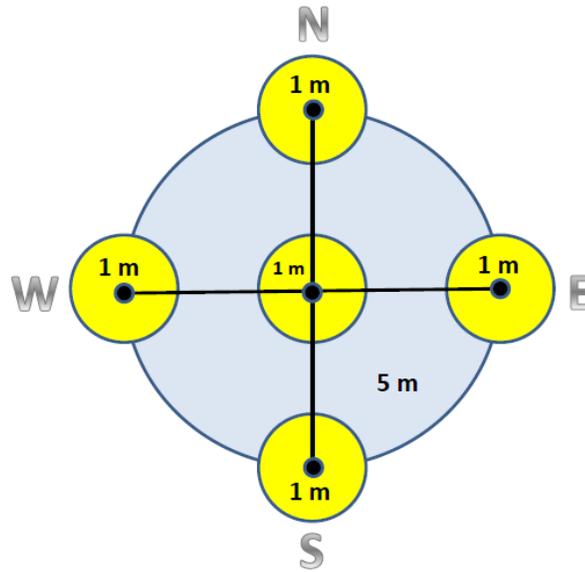


Figure 2. Habitat sampling protocol used at Bald Eagle State Park and Sproul State Forest during the 2011 Golden-winged Warbler breeding season. The diagram illustrates a habitat sampling plot at a telemetry location outside a spot-mapped territory. There was a 1 m radius center point and four additional 1 m radius sampling points 5 m away from point center. The larger circle represents the 5 m radius sampling plot.



Data Analysis

Golden-winged Warbler telemetry use areas were generated using 100% and 50% Minimum Convex Polygons (MCPs) in ArcMapGIS version 10 (ESRI 2011, Redlands, CA). I used Selected Cores Analysis in Ranges 7 with the re-calculated Ac (RAc) peel centre method to determine what points to remove for 50% MCPS (South et al. 2008). The re-calculated Ac method focused on the area of densest locations by recalculating the arithmetic mean position after excluding each furthest radio location (South et al. 2008). I required a minimum of three days overlap between spot-mapping and telemetry monitoring of an individual for inclusion in any analyses. I used a paired-t test to determine if there were size differences between telemetry use areas and spot-mapped territories. All data were log transformed prior to analysis if they could achieve normality (Shapiro-Wilk $p > 0.05$) (Tabachnick and Fidell 1996; Zar 2010).

I used the intersect tool in ArcMap GIS to measure area overlap among spot mapped territories and among telemetry use areas. I used a non-parametric Wilcoxin Signed Rank test to compare amount and number of overlap for an individual's spot-mapped territory and telemetry use area among all *Vermivora* spp. spot-mapped territories (excluding an individual's respective spot-mapped territory or telemetry use area).

Habitat variables from each telemetry location were averaged for each individual male Golden-winged Warbler. Habitat data collected was compared between spot-mapped territories and telemetry use areas that fell outside of spot-mapped territories. Number of shrubs 1-2 m and number of shrubs >2 m were combined into one variable called total number of shrubs. Habitat variables were tested for normality prior to

running paired samples t-tests. Raw data for fern, *Rubus* spp., tree cover, microedge, sapling cover, number of saplings, and number of trees was normal ($p > .05$) and did not require transformation. The rest of the percentage-based habitat variables (grass, forb, goldenrod, bareground, shrub cover >1 m, shrub cover <1 m) received an arcsine transformation (Zar 2010). All count-based habitat variables (number of trees, number of saplings, number of shrubs, and snags) received a log transformation. Only goldenrod, bareground and shrub cover <1 m achieved normality ($p > .05$). Therefore, I used a non-parametric Wilcoxin Signed Rank test for grass, forb, *Rubus* spp., shrub cover >1 m, number of shrubs, and number of snags. Holm's correction method (1979) was used to correct the error rate to account for multiple comparisons ($\alpha / (n - 1)$) since sequential Bonferroni corrections do not lose as much power (Walsh 2004).

I used Indicator Species Analysis in PC-ORD (McCune and Mefford 2011) to categorize sapling and tree species at Sproul State Forest as indicative of spot-mapped territories or portions of telemetry use areas outside spot mapped territories. I also ran the Indicator Species Analysis on shrub species in a separate analysis. I used Monte Carlo randomization test to determine the statistical significance of indicator values (Dufrêne and Legendre 1997; McCune and Mefford 2011). Indicators were considered significant at $p < 0.05$. I used 1000 randomizations in the Monte Carlo test. Even if genera was significant at $p < 0.05$, I did not consider them to be meaningful indicators unless they had indicator values of at least 25, meaning that a genus was present in at least 50% of the samples in the spot-mapped territories or telemetry use areas (Dufrêne and Legendre 1997; similar to Patton et al. 2010).

To examine the macro-habitat characteristics of areas used by intensively monitored Golden-winged Warblers (n = 12), I compared proportion of cover types (early-successional and mature forest) contained within territories estimated using spot-mapping and telemetry with a χ^2 -test of independence as done in Streby et al. (2012). The same comparison was made for all radio-tracked Golden-winged Warblers (n=22). I compared only use of each cover type between the two monitoring methods and not use relative to availability (Streby et al. 2012). Contiguous areas of ≥ 0.25 ha of mature trees were classified as mature forest in my study. In addition, I compared the amount and percent of forested cover between spot-mapped territories and telemetry use areas at Sproul State Forest using a non-parametric Wilcoxin Signed Rank test (n = 9) where mature forest surrounds the study area and is easy to classify at a large spatial scale. I used National Land Cover Dataset 2001 Percent Tree Canopy Version 1.0 (Homer et al 2004), ground truthing, and review of aerial (year 2011) photographs in ArcMap GIS to classify all locations.

CHAPTER IV

RESULTS

During the 2011 field season, over 639 telemetry and 1575 spot mapping observations were recorded among 22 and 53 male Golden-winged Warblers, respectively. Nearly half (46%) of all telemetry locations were located outside their respective male's spot-mapped territory ($n = 21$). Thirteen of the 22 radio-tagged individuals had a minimum of 3 days overlap between spot-mapping and telemetry observations. One of these 13 individual was strictly extra-territorial movement after his nest had fledged, and was excluded from analyses. Thus, 12 of the 22 males monitored via radio telemetry and spot mapping were included in my analyses. Average of all asymptote values from observation-area curves suggested a minimum of 40 radio locations (mean = 39.92 locations \pm 4.8) were needed to determine maximum size of Golden-winged Warbler telemetry use areas. Seven of the 12 individuals included in my analyses had >40 radio locations. However, only two of the twelve individuals may not have had a sufficient number of radio locations to determine maximum telemetry use areas, both needing at least 1 additional radio location (see DESL and JBZ in Table 2).

Spot-mapped Territory vs. Telemetry Use Area Size

Telemetry use areas (100% MCPs) were larger than spot mapped territories ($t_{11} = 4.156, p = 0.002$; Table 1). Spot-mapped territories at Sproul ($n=9$) ranged from 0.65-3.69 ha (mean = 1.92 ha \pm 0.29 SE) whereas telemetry use areas ranged from 1.40-19.76 ha (mean = 7.28 ha \pm 2.24). Spot mapped territories at Bald Eagle ($n=3$) were between 0.83-1.48 ha (mean = 1.18 ha \pm 0.19), whereas telemetry use areas ranged from 2.25-5.41 ha (mean = 3.38 ha \pm 1.02). Average 100% MCP spot mapped territory and telemetry

use areas for both study sites combined were $1.74 \text{ ha} \pm 0.24$ and $6.30 \text{ ha} \pm 1.74$ respectively. Core telemetry use areas (50% MCP) ($0.50 \text{ ha} \pm 0.08$) were also larger than core spot-mapped territories ($0.26 \text{ ha} \pm 0.05$) ($t_{11} = 2.341$, $p = 0.039$) (Table 1).

Spot-mapped Territory vs. Telemetry Use Area Overlap

Most ($n=11$) spot-mapped territories overlapped or fell within the boundaries of their respective telemetry use area regardless of the 100% or 50% MCP spatial scale (Figures 3 and 4). The one exception was an individual from Sproul that had a core spot-mapped territory that was larger than its telemetry use area. While spot-mapped territories exhibited minimal overlap among individual males, telemetry use areas revealed extensive space use overlap among several males (Figure 5). Individual telemetry use areas overlapped with more than double ($2.0 \text{ territories} \pm 0.58$) the number of *Vermivora* spp. territories than spot-mapped territories did alone ($0.67 \text{ territories} \pm 0.26$) ($Z = -2.226$, $p = 0.026$) (Table 3, Figure 5). Individual telemetry use areas also had a greater amount of overlap (in ha) over *Vermivora* territories than spot-mapped territories did alone ($Z = -2.497$, $p = 0.013$) (Table 3).

Figure 3. A 100% MCP spot-mapped territory (smaller polygon; 1.88 ha) a 100% MCP telemetry use area (larger polygon; 19.76 ha) for a male Golden-winged Warbler in Sproul State Forest, spring 2011. This individual had a nesting female within his spot-mapped territory, but was observed via telemetry >700 m and 340 m from its spot-mapped territory.



Figure 4. A 100% MCP spot-mapped territory (smaller polygon; 1.48 ha) and a 100% MCP telemetry use area (larger polygon; 5.41 ha) for a Golden-winged Warbler at Bald Eagle State Park, spring 2011.

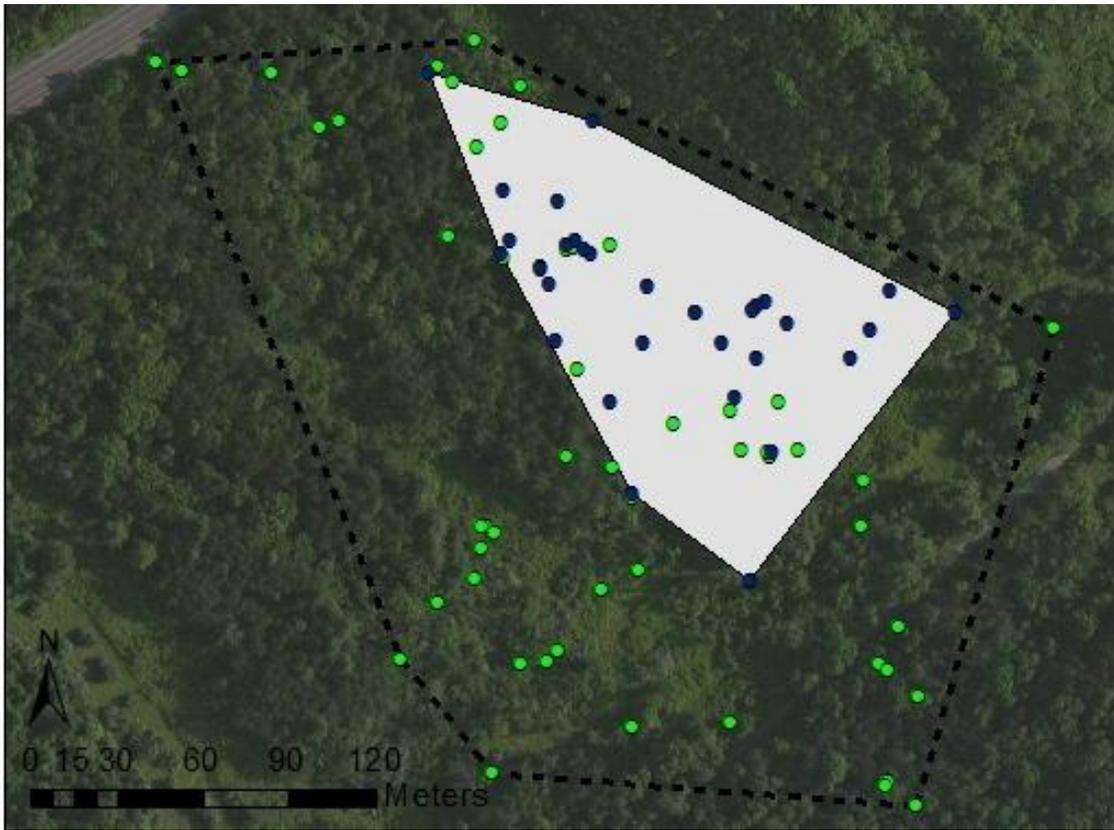


Table 1. Size comparisons between Golden-winged Warbler spot-mapped territories and telemetry use areas using 50% and 100% minimum convex polygons. Locational data were collected at Bald Eagle State Park and Sproul State Forest during spring 2011.

Individual ID	100% MCPs		50% MCPs	
	Spot-mapped territory (ha)	Telemetry use area (ha)	Spot-mapped territory (ha)	Telemetry use area (ha)
AP1	1.24	2.47	0.19	0.25
CO1	1.97	5.89	0.20	0.67
DESL	1.88	19.76	0.12	0.85
EXUN	3.69	2.42	0.69	0.63
GREB	1.50	3.39	0.28	0.37
GWB1	0.83	2.25	0.20	0.25
JBH	0.65	1.40	0.12	0.13
JBZ	2.37	3.04	0.49	0.40
LPK	0.98	11.53	0.24	0.40
MOV1	1.48	5.41	0.26	1.03
ORD	1.93	2.45	0.15	0.46
SM15	2.33	15.63	0.21	0.52
Mean (SE)	1.74 ± 0.24	6.30 ± 1.74	0.26 ± 0.05	0.50 ± 0.08

Table 2. Results* for incremental sample analysis to determine how many telemetry locations were needed to reach an asymptote in Golden-winged Warbler telemetry use areas. Analysis was computed using Ranges 7 demo (South et al. 1998). Locational data were collected at Bald Eagle State Park and Sproul State Forest during spring 2011.

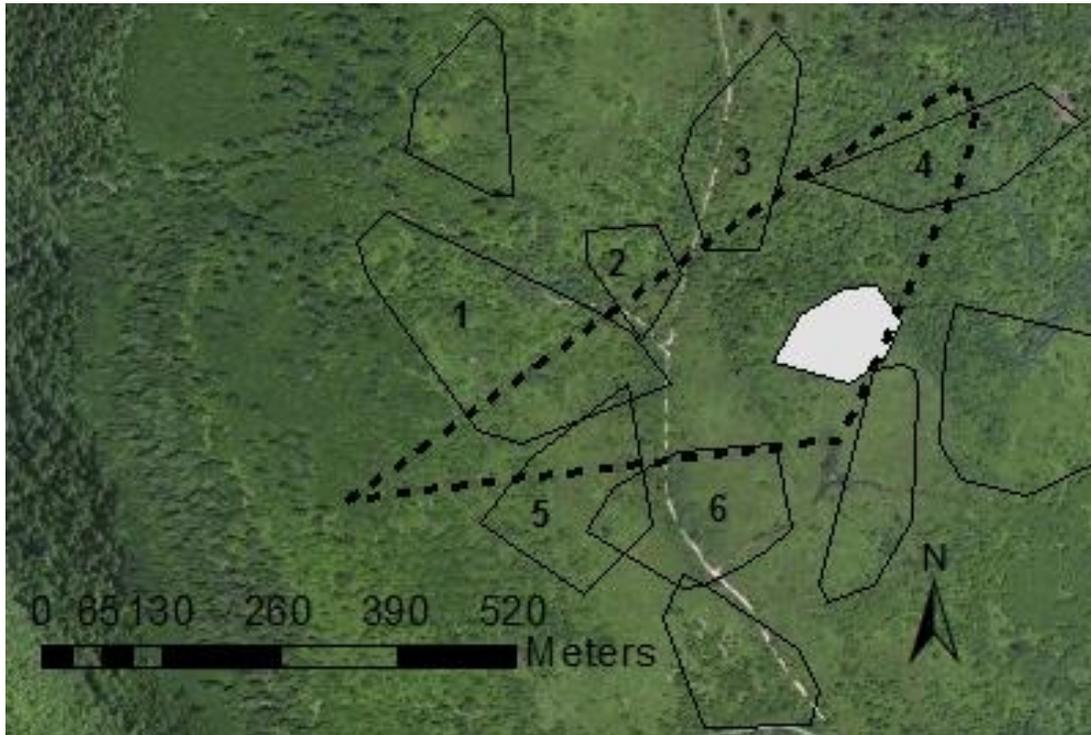
Individual ID	Study Area	Area (ha)	Radio Locations	Asymptote
AP1	Bald Eagle	2.47	37	37
C01	Sproul	5.89	35	32
DESL	Sproul	19.76	63	64
EXUN	Sproul	2.42	20	20
GREB	Sproul	3.39	43	32
GWB1	Bald Eagle	2.25	47	37
JBH	Sproul	1.40	57	55
JBZ	Sproul	3.04	57	58
LPK	Sproul	11.53	37	22
MOV1	Bald Eagle	5.41	53	51
ORD	Sproul	2.45	40	40
SM15	Sproul	15.63	31	35

*Because Ranges 7 produced marginally larger area estimates than ArcMap GIS calculations, the areas produced by Ranges 7 were used only for sample size estimates in my study.

Table 3. Number of *Vermivora* spp. spot-mapped territories (n=63) that overlapped with the 100% MCP spot-mapped and 100% telemetry use areas of 12 intensively monitored Golden-winged Warblers in north-central Pennsylvania during spring 2011. An * indicates marginal overlap for one individual (ORD).

Individual ID	No. Overlapping spot-mapped territories		Mean Overlap with spot-mapped territories	
	Spot-mapped territory	Telemetry use area	Spot-mapped territory (ha)	Telemetry use area (ha)
API	1	1	0.02	1.44
CO1	0	3	0.00	1.58
DESL	1	6	0.54	4.53
EXUN	1	1	0.54	0.16
GREB	0	1	0.00	0.49
GWB1	1	1	0.02	0.04
JBH	0	0	0.00	0.00
JBZ	0	0	0.00	0.00
LPK	0	6	0.00	3.71
MOV1	1	1	0.45	1.38
ORD	0	1*	0.00	<0.001*
SM15	3	4	0.43	2.07
Mean (SE)	0.67 ± 0.26	2.08 ± 0.62	0.17 ± 0.07	1.28 ± 0.44

Figure 5. A spot mapped territory (light grey) and telemetry use area (dashed polygon) for an individual male Golden-winged Warbler (Individual ID: LPK) at Sproul State Forest. Note the individual's spot mapped territory did not overlap with other *Vermivora* spp. territories (hollow polygons), but his telemetry use area overlapped with portions of six spot-mapped territories. Data were collected during spring 2011.



Comparison of Habitat Use between Spot-mapped Territories and Telemetry Use Areas

Vegetation was sampled at 107 and 56 telemetry locations that that occurred in areas outside spot-mapped territories at Sproul and Bald Eagle, respectively (Table 4, Table 5). Distance from telemetry-associated vegetation plots to respective spot-mapped territories at Sproul ranged from 12 m - 724 m (mean = 122 m \pm 17). Distance from telemetry-associated vegetation plots to respective spot-mapped territories at Bald Eagle ranged from 13 m - 97 m (mean = 48 m \pm 3.7). Distance from telemetry-associated vegetation plots to respective spot-mapped territories regardless of study area ranged from 12m – 724 m (mean = 100 m \pm 12). The number of saplings was lower in spot-mapped territories (mean 11.80 \pm 1.86) and higher in telemetry use areas (mean 22.49 \pm 2.14), $t(11) = -3.808$, $p = 0.003$, after a Bonferroni correction for multiple comparisons ($\alpha .05/16 = p < .003125$) (Table 5).

Table 4. Vegetation sampled within Golden-winged Warbler spot-mapped territories and at telemetry use areas outside spot-mapped territories to distinguish between habitat features used at Bald Eagle State Park and Sproul State Forest during spring 2011.

Individual ID	No. Spot-mapped territory veg plots (points along transects)	No. Telemetry use area veg plots (locations)
AP1	30	1
CO1	30	11
DESL	30	26
EXUN	46	1
GREB	30	15
GWB1	30	19
JBH	30	9
JBZ	45	7
LPK	30	17
MOV1	30	27
ORD	33	10
SM15	44	11
Mean (SE)	34.0 ± 1.93	12.83 ± 2.43

Table 5. Vegetation sampled within spot-mapped territories and outside them in telemetry use areas at Bald Eagle State Park and Sproul State Forest during spring 2011. After comparing habitat variables, only number of saplings (bolded) proved to be different between spot mapped territories and telemetry use areas after a Bonferroni correction for multiple comparisons.

Habitat Variable	BESP								Sproul S.F.			
	Spot-mapped Territory (n=12)		Telemetry Use Area (n=12)		Spot-mapped Territory (n=3)		Telemetry Use Area (n=3)		Spot-mapped Territory (n=9)		Telemetry Use Area (n=9)	
	Mean	(±S.E.)	Mean	(±S.E.)	Mean	(±S.E.)	Mean	(±S.E.)	Mean	(±S.E.)	Mean	(±S.E.)
Grass (%)	4.46	1.06	4.38	0.84	8.41	2.86	7.65	2.09	3.34	1.07	2.95	0.76
Forbs (%)	6.90	1.60	2.20	0.44	26.18	5.28	5.20	1.25	1.44	0.64	0.88	0.24
Ferns (%)	17.85	2.29	19.03	1.80	0.23	0.23	1.38	0.67	22.84	2.69	26.78	2.28
<i>Rubus</i> spp. (%)	39.30	3.50	29.53	2.38	0.58	0.71	2.36	0.89	50.25	3.68	41.46	2.86
Goldenrod (<i>Solidago</i> spp.) (%)	5.55	1.20	3.87	0.73	9.46	3.47	4.96	1.30	4.45	1.17	3.40	0.88
Bush Honeysuckle/Autumn Olive (<i>Lonicera tatarica/Elaeagnus umbellata</i>) (%)	--	--	--	--	10.98	4.23	29.57	3.61	--	--	--	--
Multifloral Rose (<i>Rosa multiflora</i>) (%)	--	--	--	--	3.46	2.23	5.55	1.74	--	--	--	--
Vine (n=2 for spot-mapped territory) (%)	--	--	--	--	16.73	4.80	9.71	1.55	--	--	--	--
Sweet Fern (<i>Comptonia peregrina</i>) (%)	--	--	--	--	--	--	--	--	2.63	0.86	1.52	0.36
Blueberry (<i>Vaccinium</i> spp.) (%)	--	--	--	--	--	--	--	--	4.19	1.27	10.34	1.72
Mountain Laurel (<i>Kalmia latifolia</i>) (%)	--	--	--	--	--	--	--	--	0.81	0.73	2.58	0.89
Bare Ground (%)	12.31	2.27	17.23	1.88	20.32	5.53	33.62	3.86	10.04	2.42	10.02	1.80
Shrub <1 m (%)	10.58	1.82	11.74	1.36	24.37	5.26	12.15	1.52	6.67	1.58	11.56	1.85
Shrub >1 m (%)	4.03	1.25	10.97	1.55	15.96	4.41	30.37	3.69	0.66	0.67	2.45	0.82
Sapling (%)	8.78	1.60	13.71	1.48	10.12	3.48	20.43	3.35	8.40	1.81	10.76	1.48
Tree (%)	14.82	2.84	23.83	2.58	10.79	4.67	37.72	5.24	15.96	3.40	17.73	2.78
Distance to microedge (m)	1.30	0.13	1.07	0.09	1.02	0.17	0.92	0.15	1.38	0.16	1.13	0.11
No. "in" trees	1.83	0.58	3.12	0.46	1.29	1.07	4.98	0.90	1.98	0.70	2.30	0.45
No. Snags within 11m	0.15	0.10	0.41	0.14	0.06	0.12	0.64	0.33	0.18	0.13	0.31	0.13
No. of shrubs 1-2 m	6.50	2.60	11.33	2.83	22.88	7.08	27.06	6.50	1.75	1.25	4.62	1.76
No. of shrubs >2 m	1.09	0.56	0.72	0.29	4.41	1.43	2.34	0.79	0.00	0.00	0.01	0.02
Total No. of shrubs	8.24	3.55	9.17	2.46	27.78	3.48	29.77	0.88	1.73	0.92	3.53	1.16
No. of saplings	11.93	2.55	20.72	2.95	6.76	3.88	23.70	4.76	13.38	3.11	19.66	3.72

Indicator Species Analysis

I only ran the indicator species analysis for males at Sproul (n=9) because there were too few males monitored at Bald Eagle (n=3). Additionally, plant species composition differed greatly between the two study sites, and thus, data from both sites could not be combined for analysis. Among 20 sapling species included in the indicator species analysis, three were indicators of telemetry use areas outside of spot-mapped territories (Table 6); red maple (*Acer rubrum*) (IV = 77.4, p = 0.009), sweet birch (*Betula lenta*) (IV = 77.1, p = 0.004), and sassafras (*Sassafras albidum*) (IV = 61.1, p = 0.0280). No sapling species were indicators of spot mapped territories. No tree species (n = 14) were indicators of spot-mapped territories or telemetry use areas (Table 7). No shrub species were indicators of spot-mapped territories or telemetry use areas outside of spot-mapped territories (Table 8).

Table 6. Indicator species analysis for sapling species (<10 cm dbh) in Golden-winged Warbler spot-mapped territories (Maxgroup 0) and in portions of telemetry use areas outside of spot-mapped territories (Maxgroup 1). Data collected at Sproul State Forest during spring 2011. Sapling species with a * p value were significant (p < 0.05).

Sapling Species ID	Maxgroup	Indicator Value (IV)	p * value
Red Maple (<i>Acer rubrum</i>)	1	77.4	0.009*
Sweet Birch(<i>Betula lenta</i>)	1	77.1	0.004*
Red Oak (<i>Quercus rubra</i>)	1	61.7	0.055
Sassafras (<i>Sassafras albidum</i>)	1	61.1	0.028*
Chokecherry (<i>Prunus virginiana</i>)	1	61.1	0.073
Black Cherry (<i>Prunus serotina</i>)	1	50.8	0.413
White Pine (<i>Pinus strobus</i>)	1	49.8	0.313
Black Locust (<i>Robinia pseudoacacia</i>)	1	46.9	0.526
White Oak (<i>Quercus alba</i>)	1	46.3	0.086
Pin Cherry (<i>Prunus pensylvanica</i>)	1	42.7	0.456
Black Gum (<i>Nyssa sylvatica</i>)	1	33.3	0.204
Hawthorne (<i>Crataegus</i> spp.)	0	14.8	1.000
Chestnut Oak (<i>Quercus prinus</i>)	1	11.1	1.000
Larch (<i>Larix laricina</i>)	1	11.1	1.000
Yellow Birch (<i>Betula alleghaniensis</i>)	1	11.1	1.000
Apple (<i>Malus</i> spp.)	1	11.1	1.000
Quaken Aspen (<i>Populus tremuloides</i>)	1	11.1	1.000
Witch Hazel (<i>Hamamelis virginiana</i>)	1	8.7	1.000
Red Pine (<i>Pinus resinosa</i>)	0	7.0	1.000
Spruce (<i>Picea</i> spp.)	0	5.6	1.000

Table 7. Indicator species analysis for tree (>10 cm dbh) species in Golden-winged Warbler spot-mapped territories (Maxgroup 0) and in portions of telemetry use areas outside of spot-mapped territories (Maxgroup 1). Data collected at Sproul State Forest during spring 2011.

Tree Species ID	Maxgroup	Indicator Value (IV)	p * value
Sweet Birch (<i>Betula lenta</i>)	1	67.11	0.156
Red Maple (<i>Acer rubrum</i>)	1	61.1	0.114
White Oak (<i>Quercus alba</i>)	1	39.5	0.211
Pin Cherry (<i>Prunus pensylvanica</i>)	1	34.6	0.437
Red Oak (<i>Quercus rubra</i>)	1	33.3	0.220
Black Locust (<i>Robinia pseudoacacia</i>)	1	29.2	0.650
Black Cherry (<i>Prunus serotina</i>)	1	26.5	0.717
White Pine (<i>Pinus strobus</i>)	1	23.6	0.771
Chestnut Oak (<i>Quercus prinus</i>)	1	22.2	0.475
Larch (<i>Larix laricina</i>)	1	11.1	1.000
Hickory (<i>Carya</i> spp.)	1	11.1	1.000
Paper Birch (<i>Betula papyrifera</i>)	0	11.1	1.000
Spruce (<i>Picea</i> spp.)	1	11.1	1.000
Red Pine (<i>Pinus resinosa</i>)	0	9.0	1.000

Table 8. Indicator species analysis for shrub species in Golden-winged Warbler spot-mapped territories (Maxgroup 0) and in portions of telemetry use areas outside of spot-mapped territories (Maxgroup 1). Data collected at Sproul State Forest during spring 2011.

Shrub Species ID	Maxgroup	Indicator Value (IV)	p * value
Blueberry (<i>Vaccinium</i> spp.)	1	60.4	0.122
Sweet Fern (<i>Comptonia peregrina</i>)	1	57.4	0.250
Mountain Laurel (<i>Kalmia latifolia</i>)	1	35.3	0.306

Percent Forest Cover in Spot-mapped Territories and Telemetry Use Areas

The chi-square test for independence indicated more locations were observed in mature forest when using telemetry than when using spot-mapping among intensively monitored Golden-winged Warblers ($\chi^2 = 5.97$, $df = 1$, $p = 0.015$ when $n = 12$). One spot-mapping location was located in mature forest for one individual (Alpha ID: MOV1). Ten telemetry locations were located in mature forest among 4 of the 12 individuals (Alpha ID: GREB; $n = 1$, LPK; $n = 1$, MOV1; $n = 6$, SM15; $n = 2$). More locations were observed in mature forest when using telemetry than when using spot-mapping among all radio-tracked Golden-winged Warblers ($\chi^2 = 9.359$, $df = 1$, $p = 0.002$ when $n = 22$). Two spot-mapping locations were located in mature forest (Alpha ID: APP1; $n=1$, MOV1; $n=1$). Twelve telemetry locations representing 6 of 22 individuals (Alpha IDs: APP1; $n= 1$, GFSL; $n = 1$, GREB; $n = 1$, LPK; $n = 1$, MOV1; $n = 6$, SM15; $n = 2$) were located in mature forest.

A non-parametric Wilcoxin Signed Rank test indicated that the percentage and amount of forested cover did not differ between spot-mapped territories and telemetry use areas ($Z(8) = -1.753$, $p = 0.08$; $Z(8) = -1.753$, $p = 0.08$). Spot-mapped territories averaged 0.19% (± 0.17) forest cover while telemetry use areas had 5.82% (± 3.6) forest cover. Spot-mapped territories had 0.004 ha \pm 0.003 forest cover while telemetry use areas had 0.67 ha \pm 0.58 forest cover.

Table 9. Amount and percent forested cover in spot-mapped territories and telemetry use areas (n = 9). Data collected at Sproul State Forest during spring 2011.

Individual ID	Spot-mapped territory (ha)	Telemetry use area (ha)	Spot-mapped territory (%)	Telemetry use area (%)
CO1	0.00	0.00	0.00	0.00
DESL	0.00	0.00	0.00	0.00
EXUN	0.00	0.00	0.00	0.00
GREB	0.00	0.26	0.00	7.67
JBH	0.00	0.00	0.00	0.00
JBZ	0.003	0.304	0.13	10.00
LPK	0.00	0.12	0.00	1.04
ORD	0.03	0.02	1.55	0.82
SM15	0.00	5.13	0.00	32.82
Mean (SE)	0.004 ± 0.003	0.67 ± 0.58	0.19 ± 0.17	5.82 ± 3.6

CHAPTER V

DISCUSSION

Spot-mapped Territory and Telemetry Use Area Comparison and Overlaps

My study revealed that Golden-winged Warblers regularly used areas outside their spot-mapped territories with nearly half (46%) of all telemetry locations occurring outside their respective spot-mapped territories. These findings are similar to those reported for a high density population in Minnesota (Streby et al. 2012), and demonstrate that extra-territorial movements by Golden-winged Warblers are not influenced by nesting densities. Since spot-mapping cannot easily detect these furtive movements, this method alone did not accurately represent all Golden-winged Warbler space use and movement within our study sites.

Telemetry use areas (mean = 6.3 ha \pm 1.74) in my study were more than 3 times higher than their respective spot-mapped territories (1.74 ha \pm 0.24), and higher than other reported Golden-winged Warbler territory sizes (Confer 1992; Rossell et al. 2003; Patton et al. 2010). Home ranges (e.g., telemetry use areas) are typically larger in passerines, and have been reported as 1.4-8 times the size of their breeding territories (Hanski and Haila 1988; Leonard et al. 2008; Anich et al. 2009a). Previous research on black bear space use found a strong correlation between home range size and the size of their peripheral areas (Powell et al. 1997). The peripheries would expand or contract as home range 'cores' contained or lacked important resources (Powell 2000). Cerulean Warblers (*Setophaga cerulea*) in one study were found to forage more often than expected in non-core areas of their territories (Perkins 2006), and sometimes non-core areas served as foraging "hotspots" (Barg 2002). These

studies suggest peripheral areas, like the telemetry use areas in my study, may have more importance than previously realized.

Core use areas (i.e. 50% MCPs) are generally considered the most important part of an animal's home range (Burt 1943; Samuel et al. 1985; Samuel and Green 1988) because food and other critical resources often are patchily distributed throughout the landscape (Mitchell 1997; Powell et al. 1997). Avian breeding territories vary in size, but usually denote areas of high use within a larger home range (Harris et al. 1990). Core areas (50% MCPs) for the Golden-winged Warblers I studied were larger when delineated by telemetry than spot-mapping in almost all cases (10 out of 12 individuals). Telemetry and spot-mapped delineated core areas almost always overlapped (11 out of 12 cases), suggesting that both methods can reliably delineate Golden-winged core breeding territories. However, spot-mapping was clearly ineffective at completely characterizing the spatial ecology of breeding Golden-winged Warblers compared to telemetry. Such disparity in space use sizes resulting from spot mapped and telemetry based methods should be considered in range-wide efforts currently underway to create and maintain Golden-winged Warbler breeding habitat.

There is usually an inverse relationship between territory size and population density (Maher and Lott 2000). Golden-winged Warblers in my low density study sites should not have been facing the same level of inter-specific competition as areas of high nesting densities in Minnesota, allowing them to establish territories large enough to provide high quality habitat. As such, Golden-winged Warblers in areas with low nesting densities should find more 'empty' habitats to establish a territory

and would have more freedom in movement to use areas of optimal habitat. Therefore, placement of breeding territories is likely due to finding optimal nesting habitat (Hildén 1965; Klopfer and Ganzhorn 1985) that does not necessarily have optimal conditions with respect to other important resources (e.g., foraging substrates). In low-nesting densities, this may allow flexibility to the individual to seek these additional resources outside a spot-mapped territory, with more benefits than costs associated to the movement. The large movements outside spot-mapped territories may reflect an ideal free distribution with little to no immediate influence from conspecific males (Fretwell and Lucas 1970). Territoriality would allow Golden-winged Warbler males to assess local density, but not prevent them from settling in the most ideal breeding habitat (Adams 2001).

My data also revealed disparities between telemetry use areas and spot-mapped territories regarding the amount of spatial overlap among individual males. Although Golden-winged Warbler breeding spot-mapped territories are often described as being separated by unoccupied habitat due to territoriality, telemetry revealed that these undefended areas actually are not empty- rather they appear to be shared space for Golden-winged Warblers with much overlap among individuals. In a telemetry study on Bulluck's Orioles (*Icterus bullockii*), individuals from different nests showed significant overlap among foraging sites, would travel as far as 1 km from their nests to forage, and did not appear to be territorial in these areas (Williams 1990). During my study I observed three males (Alpha IDs: AP1, APP1, GWB1) foraging in the same area (within a 10m radius circle) with no apparent aggressive

behavior. This would support the idea of some areas of a telemetry use area potentially being neutral foraging grounds (Williams 1990).

Golden-winged Warblers at our study sites exhibited greater telemetry use area overlap with *Vermivora* spp. territories than would have been noticed through spot-mapped territories. If one would consider these movements into other nesting territories as potential extra-pair copulation (EPC) mating opportunities, this may be a strong motivating factor for leaving the spot-mapped territory. For example, an individual in Sproul (Alpha ID: DESL) with the largest telemetry use area (19.76 ha) was found in close proximity to females belonging to two other males in spot-mapped territories on two separate occasions, despite having his own nesting female. In one instance, this individual was found 700 m from his nesting territory pursuing a female only to be chased away by a different defending male with his own nesting female. However, because females were unmarked, I cannot determine whether the female was his own or that of the defending male. Golden-winged Warbler females will attend males on foraging bouts (Streby et al. 2012), so this possibility cannot be ruled out. The same individual was found 338.9 m away from his territory in close proximity (25m) of a different male and female pair, but no aggressive interactions occurred.

Siring of extra-pair young often occur in neighboring territories (Birkhead and Møller 1992; Westneat and Sherman 1997; Whitaker and Warkentin 2010), but can also occur from several territories away (Currie et al. 1998; Pedersen et al. 2006; Dolan et al. 2007). The benefits of searching widely to increase the number of potential extra-pair mates can outweigh the risks associated with making such

movements if males have few adjacent females (Woolfenden et al. 2005). Furthermore, the spatial overlapping of telemetry use areas with spot-mapped territories of other males may allow for social interaction and aid gathering of social information important to the species, but would also compel individuals to be discrete in their movements (Whitaker and Warkentin 2010).

The “hidden lek” hypothesis explains why some species are known to aggregate their territories (Wagner 1998; Tarof et al. 2004). Golden-winged Warblers are known to nest in clusters of individual territories (Confer and Knapp 1981; King et al. 2009) which also may be connected with the idea of EPC being a common but not always observed ecological behavior. One study in Ontario indicated more than 30% Golden-winged Warbler nestlings were the result of EPCs, occurring in more than half (55%) of all nests (Vallender et al. 2007). Nest clustering is common in other songbirds and it has been hypothesized that this behavior has evolved so females can be closer to other potential mates (Melles et al. 2009). Although birds may cluster to monopolize the same resources (Keister and Slatkin 1974) or to avoid nest predation (Turner and Pitcher 1986), the idea of nest clustering in Golden-winged Warblers due to a “hidden lek” cannot be discredited, as there is no single explanation for the common occurrence of EPC in avian species (Griffith et al. 2002).

Not surprisingly, several factors thought to influence territory size may also influence opportunities for EPC such as density (Birkhead 1978), degree of breeding synchrony (Birkhead and Biggins 1987; Westneat et al. 1990), and features of the habitat (Sherman and Morton 1988; Ritchinson et al. 1994). Females of males that

face conflicting demands between mate guarding and foraging (Westneat 1994), or taking care of fledglings may experience more EPC attempts (Westneat et al. 1990; Ritchinson et al. 1994). Populations that experience high predation may find EPC valuable because it reduces the chance that an individual's reproductive effort will be completely unsuccessful (Seger and Brockman 1987; Ritchinson et al. 1994). Mayfield nesting success for Golden-winged Warblers in my study area from 2008-2011 was $35.6\% \pm 4.84$ (Larkin, unpublished data), which is relatively low compared to other studies.

Although females will accompany males on foraging bouts outside the territory (Streby et al. 2012), evidence from my study and previous observations suggest EPC mating opportunities may, in part, be a factor for the disparity between the size and degree of overlap of spot-mapped territories and telemetry use areas. Several observations were made in my study areas between 2008-2011 that suggested Golden-winged Warbler nests were sired by two males. All of these observations were made at Golden-winged warbler nest and involved the resident males and female actively feeding nestlings, while a second male was observed next to the nest and sometime also feed the nestlings. The following is an account of one such observation. In 2011, a territorial male Golden-winged Warbler (#704) had been exhibiting behavior typical of a paired male with a nest. On 15 June, a male and female Golden-winged Warbler with Lepidoptera were observed in #704's territory, and followed to the nest site. However, the male was identified as #662, a male never previously observed in this portion of the study area. Rather, #662 had been spot mapped multiple times on his territory 534 m away from the nest site. The #704 male

was also present around the nest site, but kept his distance from the #662 male. The #704 male tried to feed the nestlings, but #662 chased him away. Such observations along with those associated with my telemetry data provide strong evidence of EPC opportunities as an explanation, at least in part, for long-distance extra-territorial movements by male Golden-winged Warblers.

Micro- and Macrohabitat Variables Outside Spot-mapped Territories

Telemetry use areas outside spot-mapped territories contained nearly twice the average number of saplings (mean = 20.72 ± 2.95 to 11.93 ± 2.55 , respectively).

Although the exact motivating factor for a Golden-winged Warbler to leave its territory is not known, individuals may be seeking or opportunistically using saplings as a resource when traveling outside their spot-mapped breeding territories. Golden-winged Warblers are impacted by limited nesting habitat (Confer et al. 2003), and habitat characteristics associated with nest sites may reflect resource partitioning (Bulluck and Buehler 2008). Food resources are considered a limiting factor to many species (Wiens 1989; Rodenhouse and Holmes 1992; Newton 1998). There is generally an inverse relationship between territory size and food availability (Saitoh 1991; Powers and McKee 1994; Arvidsson et al. 1997), but this is not always the case (Adams 2001).

Most movements outside a breeding territory are typically for foraging purposes in passerines (Zach and Falls 1979; Westneat 1993, 1994). Males can lose weight as the nesting season progresses (Searcy 1979), so continual foraging bouts may maintain body condition and lead to better survival (Westneat 1994). Foraging was observed at 22% of our radio locations when a visual was made outside spot-

mapped territories. Plant species' physical and chemical characteristics affect the kinds of and distributions of forage substrates, which then affects how birds search and find food, and the abundances of these sought resources (Holmes et al. 1979). Therefore, it is important to identify these sapling species that Golden-winged Warblers may have been seeking within telemetry use areas.

A Golden-winged Warbler foraging ecology study that ran in conjunction with this study found that Golden-winged Warblers will forage on specific plant species within their territories (Bellush 2012). Although the reason(s) for the Golden-winged Warbler to leave their spot-mapped territory is unknown, there appears to be the potential for their extra-territorial movement to be characterized by specific plant species occurring outside their core breeding territories. Songbirds are known to seek out specific plant species (Holmes and Robinson 1981) from foliage density cues which are positively correlated to prey density (Marshall and Cooper 2004). Arthropod biomass is also strongly correlated to warbler abundance in time and space (Johnson and Sherry 2001). Insect prey availability determines foraging activity in insectivorous birds (Hutto 1981), and the Golden-winged Warbler is probably no different.

Golden-winged Warblers in my study were found to use more mature forest than realized through spot-mapping which is in agreement with results from a study in Minnesota (Streby et al. 2012). Ten telemetry locations met my criteria of being considered within mature forest among four of the twelve sampled individuals as opposed to one spot-mapping location for one individual. Although percent and amount forested cover did not differ between spot-mapped territories and telemetry

use areas in Sproul State Forest (n = 9), movements into mature forest were seen at both study sites despite low sample size. Mature forest likely provides an important role in Golden-winged Warbler's breeding ecology with such movements also observed in the less intensively monitored individuals (n = 22). For example, one radio-tagged Golden-winged Warbler at Bald Eagle (Alpha ID: APP1) traveled 1.6 km outside his territory to a forested area only to be observed in his spot-mapped territory the following morning.

Golden-winged Warblers in West Virginia that were monitored via telemetry visited mature forest stands surrounding managed grazing lands during extra-territorial movements (Aldinger, unpub. data). Additionally, a radio-tagged Golden-winged Warbler male and some its fledglings in West Virginia abandoned his spot-mapped nesting territory, and progressively ventured further into surrounding mature forest (Aldinger, per. comm.). Interestingly, mature forest breeding birds are known to move from their territories into patches of regenerating forests during the post-breeding period (Vitz 2003). Perhaps the movements into mature forests that I observed served as reconnaissance to identify areas to which adults would bring fledglings. Regardless of their motivation for using mature forest, my findings and those elsewhere warrant land managers to consider the importance of mature forests in range-wide efforts to create and maintain Golden-winged Warbler breeding habitat.

Management Implications

Habitat management presupposes at least some understanding of a species' needs (Garshelis 2000). My radio telemetry study of Golden-winged Warblers indicated that spot-mapping underestimated space use and movement of the Golden-

winged Warbler. These results along with Streby et al. (2012) suggest that Golden-winged Warblers will make large movements outside their spot-mapped territories regardless of nesting density. These findings warrant researchers of Golden-winged Warblers to incorporate monitoring methods that allow for a more complete characterization of Golden-winged Warbler breeding ecology and resource needs. This is particularly important if the research is intended to inform management.

Current conservation plans for Golden-winged Warblers that are based on habitat measured solely within spot-mapped territories are missing recommendations for an intermediate spatial scale. For example, Bakermans et al. (2011) provide detailed recommendations for managing Golden-winged Warbler habitat that were based on territory and landscape level data. However, no intermediate scale recommendations are provided (Bakermans et al. 2011). While insight for both territory and landscape scale needs of Golden-winged Warblers are clearly important for developing effective conservation plans, my results stress the likely importance of habitat cues at intermediate (clusters of territories) scales. An intermediate scale of habitat selection may be where individuals make important behavioral decisions related to breeding ecology (Rettie 1998).

Future radio telemetry studies should monitor both male and female Golden-winged Warblers via telemetry to better elucidate their motivations for leaving spot mapped breeding territories and to assess if their patterns of space use coincide. Some banded individuals (n=12) could not be radio tracked in my study since they weighed less than the 10 g body weight required for radio transmitter placement. Male Golden-winged Warblers that weighed under 10 g were radio-tracked recently

in West Virginia and exhibited space use patterns similar to mine (Aldinger, unpub. data). Future radio telemetry studies that examine the effects of sex and body condition on Golden-winged Warbler space use and movement patterns.

The number of saplings and plant species composition differentiated my telemetry use area from spot-mapped territories. Other habitat variables suggestive of representing a telemetry use area from a spot-mapped territory may not have been determined due to my small sample size. As such, future radio telemetry studies would benefit from larger sample sizes to better characterize Golden-winged Warbler habitat requirements at multiple spatial scales.

My results also merit caution when surveying Golden-winged Warblers during point counts. Initial Partners in Flight (PIF) detection distance for a singing Golden-winged Warbler was 200 m (Rosenberg and Blancher 2005) which was found to be more conservatively 100-150 m in non-open habitats (Kubel and Yahner 2007). Given that many of the telemetry locations recorded during this study were greater than 200 m away from territories, one may inaccurately presume no breeding individual present that is instead making routine extra-territorial movements outside of detection distance. These results emphasize the importance of conducting multiple visits to a location when using points counts to survey for Golden-winged Warblers, even when song playback is part of the survey protocol.

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