Management Implications of Brood Division in Golden-winged Warblers*

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Abstract. Brood division in the postfledging period is a common avian behavior that is not well understood. Brood division has been reported in Golden-winged Warblers (*Vermivora chrysoptera*), but it is not known how common this behavior is, whether males and females exhibit different strategies related to parental care and habitat use, or how brood division might influence management strategies. We radiomarked fledglings and monitored divided broods of Golden-winged Warblers from fledging until independence from parental care at three sites in the western Great Lakes region from 2010 to 2012 to assess differences in strategies between male and female parents and to consider possible management implications. Male- and female-reared sub-broods exhibited different space use during the dependent postfledging period despite similar fledgling survival, cover-type use, and microhabitat use. By independence, female-reared sub-broods traveled over twice as far from the nest (mean = 461 ± 81 SE m) as male-reared sub-broods (164 ± 41 m). Additionally, female-reared sub-broods traveled over three times as far from the natal patch edge (354 ± 72 m) as male-reared sub-broods (108 ± 36 m). Without accounting for differential space use by male- and female-reared sub-broods, we would have reported broods traveling 292 (± 46 m) from the nest and 214 (± 40 m) from the natal patch edge—distances that do not reflect how far females move sub-broods. Parental strategies differ between sexes with regard to movement patterns, and we recommend incorporating the differences in space use between sexes in future management plans for Golden-winged Warblers and other species that employ brood division. Specifically, management actions might be most effective when they are applied at spatial scales large enough to incorporate the habitat requirements of both sexes throughout the entire reproductive season.

Key Words: behavior, parental care, postfledging care, songbird, *Vermivora chrysoptera*.

Brood division is a widespread avian behavior that is characterized by adults provisioning and caring for a subset of their brood over all or a substantive portion of the postfledging period, after young leave the nest but before they reach independence from adult care, forming two stable "sub-broods" attended separately by male and female parents (Harper 1985, Leedman

* Peterson, S. M., H. M. Streby, and D. E. Andersen. 2016. Management implications of brood division in Golden-winged Warblers. Pp. 161–171 *in* H. M. Streby, D. E. Andersen, and D. A. Buehler (editors). Golden-winged Warbler ecology, conservation, and habitat management. Studies in Avian Biology (no. 49), CRC Press, Boca Raton, FL.

and Magrath 2003, Peterson 2014). Will (1986) reported that Golden-winged Warblers (*Vermivora chrysoptera*) exhibited brood division, but the extent to which this behavior occurs in Golden-winged Warblers and how it influences productivity and habitat use are unknown. Recently, Peterson (2014) observed division in 98.5% of broods in northern Minnesota and southern Manitoba, Canada, with equal parental effort where male and female parents cared for similar numbers of fledglings and provisioned fledglings at similar rates, suggesting that brood division is nearly obligate in Golden-winged Warblers.

Most studies of brood division in birds have focused on differences or similarities in adult care and the potential evolutionary benefits of employing this behavior (McLaughlin and Montgomerie 1985, Lessells 2002, Leedman and Magrath 2003, Draganoiu et al. 2005). In Golden-winged Warblers, parental care, such as provisioning of young and parental attendance, is similar between male and female parents (Peterson 2014), suggesting that both sexes are similarly capable of rearing young to independence. Furthermore, brood division in Golden-winged Warblers appears to most closely fit the evolutionary strategy proposed by Lessells (1998), in which brood division decreases the likelihood of survival for any individual parent when compared with brood abandonment, but increases survival of the other parent of a brood and for fledglings in both sub-broods (Peterson 2014).

An aspect of brood division that has potential conservation implications but has received little attention is how sub-broods partition space. Elsewhere, four studies of three species reported spatial patterns of division in broods (McLaughlin and Montgomerie 1985, Weatherhead and McRae 1990, Evans Ogden and Stutchbury 1997, Rush and Stutchbury 2008). Weatherhead and McRae (1990) observed that divided broods of American Robins (*Turdus migratorius*) traveled similar distances from the nest independent of parental sex. In contrast, female Hooded Warblers (*Setophaga citrina*; Evans Ogden and Stutchbury 1997, Rush and Stutchbury 2008) and female Lapland Longspurs (*Calcarius lapponicus*; McLaughlin and Montgomerie 1985) traveled farther from the nest with their sub-broods compared to males. How Golden-winged Warbler sub-broods partition space is unknown, but if female- and male-reared sub-broods exhibit different spatial use patterns, conservation strategies may need to account for these differences to maximize their impact. In extreme cases, failure to recognize brood division may lead to flawed conservation plans for a species and failure to achieve the desired management effect.

We studied brood division in three populations of Golden-winged Warblers in the western Great Lakes region of central North America. Golden-winged Warblers are Neotropical migratory songbirds that breed in northeastern and north-central North America and spend the nonbreeding season in southern Central America and northern South America (Confer et al. 2011). Golden-winged Warbler populations outside of the core population in the western Great Lakes region are declining rapidly, resulting in Golden-winged Warblers being listed as Endangered, Threatened, or of high management concern in 10 states and Canada (Buehler et al. 2007). Golden-winged Warblers are single-brooded, fledging young from no more than one clutch per year, and each parent cares for both nestlings and fledglings (Confer et al. 2011).

Primary nesting habitat of the species consists of shrubby, early successional uplands, shrubby wetlands, and adjacent forests with dense undergrowth (Streby et al. 2014). Golden-winged Warbler postfledging habitat differs from that used for nesting, with birds selecting mature forest and mid-successional forest over other cover types, but also using early successional forests and wetlands (Chapter 8, this volume). Current Best Management Practices in the western Great Lakes region are based on a positive association of nesting Golden-winged Warblers with forest, shrubland, shrub-forest wetlands, and pasture-hay fields within 244 m of a managed upland patch and ≥50% forest cover within 2.4 km of a habitat patch (A. M. Roth et al., unpubl. plan). To provide available postfledging habitat, A. M. Roth et al. (unpubl. plan) suggested creating a dynamic forest landscape comprising different aged stands, maintaining 15%–20% of the total managed area in early seral stage, forested cover types.

Brood division during the 25-day postfledging period of parental care in Golden-winged Warblers appears to be nearly obligate, with rare observations of both parents provisioning the same fledglings (Will 1986, Peterson 2014). Sub-broods often form crèches with ≥1 conspecific sub-brood and fledglings of other species (Will 1986, H. M. Streby, unpubl. data). Similar to other songbirds (Ricklefs 1968, Anders et al. 1998, King et al. 2006, Streby and Andersen 2013a), Golden-winged Warbler fledgling survival is lowest in the first few days after fledging, with 75% of fledgling mortality occurring in the first three days after fledging from the nest (Chapter 8, this volume).

We monitored fledgling movements via radiotelemetry throughout the dependent postfledging period before independence to assess differences between male- and female-reared sub-broods of Golden-winged Warblers. We specifically compared patterns in movements, space use of locations on the landscape and within vegetation strata, structure and composition of vegetation used by fledglings, and fledgling survival. Based on the patterns we observed in habitat and space use by Golden-winged Warbler sub-broods, we suggest breeding habitat management implications for the western Great Lakes region.

METHODS

Study Sites

From 2010 to 2012, we studied Golden-winged Warbler breeding-season ecology at Tamarac National Wildlife Refuge (NWR) in Becker County, Minnesota (47.049°N, 95.583°W). In 2011 and 2012, we expanded our study to include sites at Rice Lake NWR in Aitkin County, MN (46.529°N, 93.338°W) and Sandilands Provincial Forest (PF) in southeastern Manitoba, Canada (49.637°N, 96.247°W). At each study site, we focused our efforts in 8–16 plots of 2.5–25 ha shrubby uplands and wetlands and the surrounding forest in a predominantly forested landscape. For a more detailed description of the landscapes present at our study sites, see Chapter 8 (this volume).

Field Methods

We located Golden-winged Warbler nests (n = 50) using nest-searching methods described by Martin and Geupel (1993). We found additional nests (n = 28) by passively mist-netting adult female Golden-winged Warblers after their arrival from spring migration but before most started nesting, and attaching a VHF radio transmitter that was ~4.1% of mean adult mass with a figure-eight harness (Rappole and Tipton 1991, Streby et al. 2015) and by subsequently monitoring the radiomarked females (Streby et al. 2013). Radio transmitters used in this study had no measureable impact on female productivity (Streby et al. 2013). We recorded nest locations using handheld Global Positioning System (GPS) units (GPSMAP 76 or eTrex Venture HC, Garmin Ltd., Schaffhausen, Switzerland), and we averaged locations using 100 points to achieve <5 m accuracy. We delineated cover types in ArcGIS 10.0 Geographic Information System (GIS) software (Environmental Systems Research Institute, Redlands, CA). For Tamarac NWR and Rice Lake NWR, we used 1-m resolution digital orthophoto quadrangles (2009; Minnesota Department of Natural Resources, St. Paul, MN). For Sandilands PF, we used 1-m resolution georeferenced satellite images obtained from Google Earth™ 6.2 (2010; Google Inc., Mountain View, CA). For each nest, we defined the natal patch as the contiguous patch of shrubland cover in which the nest was situated. For five nests located <25 m into mature forest (7%), we defined the natal patch as the nearest contiguous patch of shrubland cover. We excluded two nests that were >25 m into mature forest from this analysis. Natal patches ranged from 0.25 to 30 ha in area.

We monitored nests on 4-day intervals until near the estimated fledge date, when we visited nests daily. When nestlings were 6–9 days old (counting hatch day as day 1), we banded all nestlings in the nest with standard U.S. Geological Survey leg bands, measured their mass to the nearest 0.01 g with a digital scale (AWS-100, American Weigh Scales Inc., Norcross, GA), and attached a radio transmitter to 1–5 randomly selected nestlings using the figure-eight harness design (~4.6% of mean nestling mass; Rappole and Tipton 1991, Streby et al. 2015). In addition, we used mist nets to capture, band, and attach radio transmitters to fledglings from unknown nest locations (n = 14) detected by fledgling vocalization or adult behavior. We used these individuals only in analyses that did not require knowledge of nest location such as vegetation characteristics and minimum daily distance moved. We estimated the age of captured fledglings based on observed development of fledglings banded in the nest and subsequently monitored throughout the postfledging period.

We recorded daily fledgling locations using ground-based radiotelemetry, as described in Streby and Andersen (2013b). We avoided locating fledglings in inclement weather to minimize the chance that our activities would cause fledglings to move to locations where their survival might be compromised by exposure to excessive cold or moisture. For each fledgling, we recorded locations using handheld GPS units as described above for nest locations. For each encounter of a fledgling, we recorded vegetation strata as ground, understory, midstory, or canopy, and whether the location was in nonshrubland forest such as mature forest, forested wetland, and sapling-dominated clear-cuts. We defined the understory strata as the vegetation layer from ground to 2 m, midstory as the vegetation layer from >2–15 m, and the canopy as the vegetation layer >15 m. At each fledgling location, we estimated lateral vegetation density by recording the amount of vegetation obscuring a 2-m profile board (MacArthur and Macarthur 1961, Streby and Andersen 2013a, for more detailed methods see Chapter 8, this volume). We used ImageJ (National Institutes of Health, http://imagej.nih.gov/ij/) to derive percent vertical cover as the percent of sky covered by vegetation >2 m above the ground from digital photographs taken vertically from 2 m above the ground at fledgling locations. For each photograph, we divided color channels to differentiate between sky and vegetation, converted vegetation and sky to binary pixels, and measured the percentage of pixels occupied by vegetation. We used ArcGIS to calculate daily distance from nest for all fledglings for which we knew the location of the nest from which they fledged. We used ArcGIS to measure the daily distance from the edge of the natal patch to daily locations, with locations inside the natal patch considered to be negative distances from the edge of the patch.

We identified sex of the parent attending individual fledglings by plumage while observing adult and fledgling interactions. We excluded 50 broods from our analyses for which fledglings were depredated before we observed parental care, and two broods without brood division where fledglings were provisioned by both parents during multiple observations. We recorded observations daily over the 25-day period that Golden-winged Warbler fledglings are dependent upon adults (Will 1986).

Postfledging Periods

Our initial observations indicated that space use was similar between male- and female-reared sub-broods shortly after fledging from the nest, but space use appeared to differ between male- and female-reared sub-broods by the time fledglings became independent of adults (Peterson 2014). Changes in space use suggested a shift in parental movement strategies during the postfledging period. Peterson (2014) analyzed these data and identified a period of greater-than-expected directionality of movements on days 9 and 10 that indicated a change in female space use in relation to the nest site (Figure 10.1a). Therefore, to ensure that we compared differences in male and female parental behavior both before and after the apparent change in parental strategies occurred, we divided the postfledging period into two periods—an early postfledging period from days 1 to 8, and a late postfledging period from days 9 to 25.

Statistical Analyses

We tested for differences between male- and female-reared sub-broods in distance from nest and vegetation characteristics at daily fledgling locations including percent vertical cover, lateral vegetation density, nonshrubland forest use, and strata occupied by fledglings in broods for which we tracked both sub-broods via radiotelemetry (hereafter, "paired sub-broods"). We used data from this sample of broods to avoid potential bias from nonindependence of locations for sub-broods that we tracked without knowing the location of the sub-brood under the care of the other parent. After testing for differences between paired sub-broods, we used our entire sample of sub-broods to describe patterns over time for each variable as a function of parental sex. For sub-broods in which we monitored >1 fledgling, we used the mean value for all fledglings (usually two) in that sub-brood for each variable in analyses. All results are presented as mean $\pm$ SE.

Daily distance from a nest and natal patch edge are likely to be temporally autocorrelated because the distance from the nest one day is likely to be more similar to the distance from the nest the subsequent day than the distance from any randomly selected day. Thus, we used a sign test to assess differences between paired sub-broods in daily distance from nest and natal patch (Dixon and Mood 1946). We calculated mean distance from nest and natal patch edge near the end of the postfledging period using the mean distance

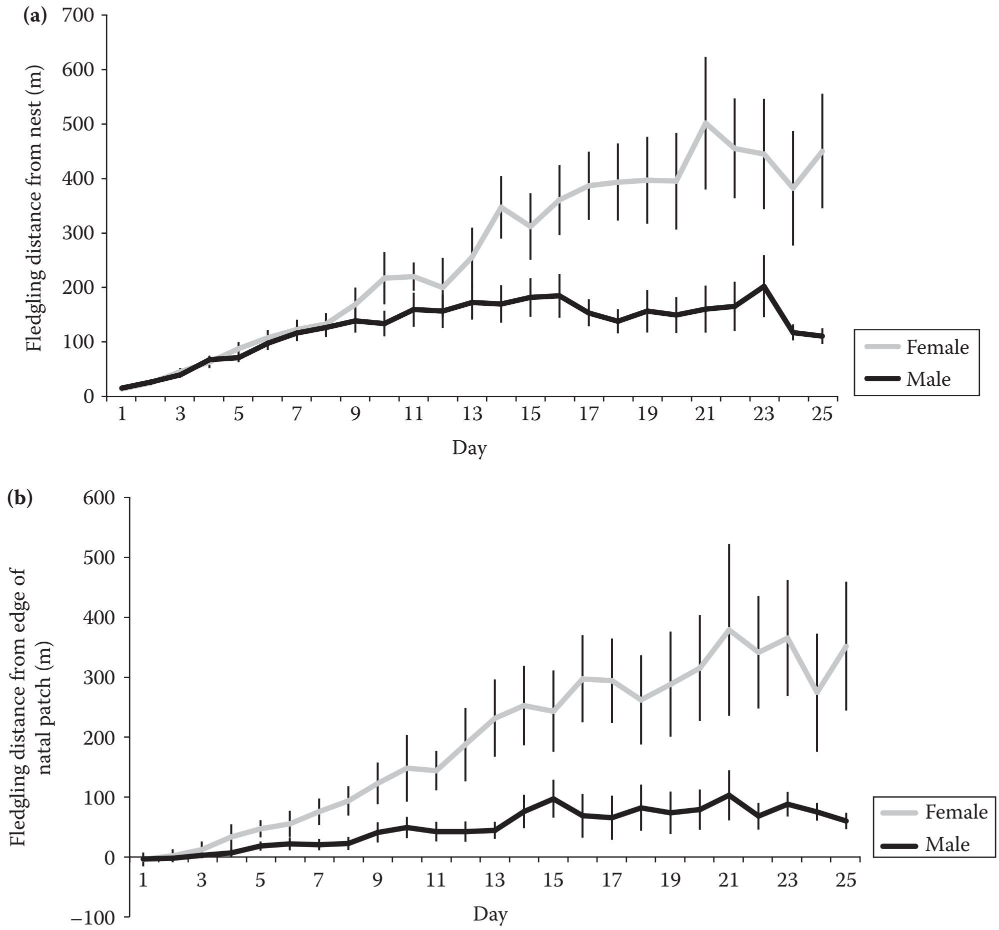

Figure 10.1. Trends in (a) daily distance from nest and (b) daily distance from the edge of the natal cover patch in male-reared sub-broods (Male) and female-reared sub-broods (Female) in three populations of Golden-winged Warblers in the western Great Lakes region 2010–2012 (data presented as mean ± SE).

of fledglings in each sub-brood over the last five days of the postfledging period prior to independence (i.e., days 21–25). We used a Pillai-M.S. Bartlett trace multivariate analysis of covariance (MANCOVA) to test for differences between male- and female-reared sub-broods in vegetation characteristics at fledgling locations using linear models in R (ver. 2.14.1, R Foundation for Statistical Computing, Vienna, Austria). Parental sex and fledgling age were explanatory variables and percent vertical cover, lateral vegetation density, nonshrubland forest use, and strata occupied by fledgling were response variables. For all MANCOVA tests that were statistically significant ($\alpha = 0.05$), we conducted an ANCOVA test on each dependent variable.

We could not compare survival between male- and female-reared sub-broods during the early postfledging period because in most cases, we were unable to identify the sex of the parental caregiver for fledglings that died during that period. In addition, our data indicated that space use was nearly identical for fledglings in male- and female-reared sub-broods in the early postfledging period, suggesting that predation pressure was likely similar between sub-broods. For the late postfledging period, we used the known fates module in program MARK (ver. 5.1, Colorado State University, Ft. Collins, CO) to estimate daily fledgling survival and 95% confidence intervals using the known fate module for a random fledgling per sub-brood (White and Burnham 1999).

In sub-broods with multiple marked fledglings that had different capture histories (2% of all sub-broods), we randomly selected a fledgling in that sub-brood to include in survival analyses. Fledgling survival during the late postfledging period was unrelated to fledgling age (Chapter 8, this volume); we therefore did not include fledgling age in our survival model. We compared 95% confidence intervals for male- and female-reared sub-broods to test for differences in fledgling survival. Previous models of fledgling survival in this study population determined that survival did not differ by site or year (Streby et al. 2014).

RESULTS

During the summers of 2010–2012, we monitored 66 Golden-winged Warbler fledglings from 60 sub-broods at Tamarac NWR, 30 fledglings from 28 sub-broods at Rice Lake NWR, and 27 fledglings from 24 sub-broods at Sandilands PF. In broods for which we monitored both sub-broods, both male- and female-reared sub-broods moved similar distances from the nest in the early postfledging period (sign test, $n = 18$, $P = 0.82$; Figure 10.1a). In contrast, female-reared sub-broods moved farther from the nest than male-reared sub-broods during the late postfledging period (sign test, $n = 15$, $P = 0.04$; Figure 10.1a). Female-reared sub-broods from broods in which we monitored both sub-broods were farther away from the natal patch edge than male-reared sub-broods throughout the entire postfledging period (sign test, $n = 19$, $P = 0.02$; Figure 10.1b). In the last five days of the postfledging period, female-reared sub-broods ($n = 22$) were 461 ± 81 m away from the nest and 354 ± 72 m from the natal patch edge, whereas male-reared sub-broods ($n = 29$) were 164 ± 41 m away from the nest and 108 ± 36 m away from the natal patch edge (Figure 10.1a,b). If we had not accounted for brood division and treated sub-broods as independent sample units ($n = 51$), we would have reported mean distance from the nest as 292 ± 46 m and mean distance from natal patch edge as 214 ± 40 m for the last five days of the postfledging period.

Male- and female-reared sub-broods used areas with similar vegetation characteristics (vertical cover, shrubland use, lateral vegetation density, and forest strata) in both the early postfledging period ($n = 18$ paired sub-broods, $F_{4, 221} = 0.95$, $P = 0.43$) and the late postfledging period ($n = 12$ paired sub-broods, $F_{4, 262} = 1.92$, $P = 0.11$). Vegetation characteristics at fledgling locations changed over time ($n = 19$ paired sub-broods, $F_{4, 488} = 50.02$, $P < 0.001$). Percentage of vertical cover at locations used by sub-broods increased from 40% at fledging to 60% at independence ($n = 19$ paired sub-broods, $F_{2, 499} = 12.23$, $P < 0.001$; Figure 10.2a). Lateral vegetation density at fledgling locations was ~65% and did not vary throughout the postfledging period ($n = 19$ paired sub-broods, $F_{2, 537} = 2.8$, $P = 0.06$; Figure 10.2b). Both male- and female-reared sub-broods used nonshrubland forest extensively, with use of this cover type increasing from 45% on day 1 to 85% by independence ($n = 19$ paired sub-broods, $F_{2, 541} = 25.47$, $P < 0.001$; Figure 10.2c). We observed fledglings occupying vegetation strata farther from the ground with increasing frequency throughout the postfledging period. The frequency of fledglings perched on the ground declined from 35% on day 1 to 0% by day 13 ($n = 19$ paired sub-broods, $F_{2, 539} = 37.15$, $P < 0.001$), frequency of use of midstory increased from 0% on day 1 to 15% by independence ($n = 19$ paired sub-broods, $F_{2, 539} = 18.25$, $P < 0.001$), and frequency of use of canopy increased from 0% on day 1 to 25% by independence ($n = 19$ paired sub-broods, $F_{2, 539} = 30.2$, $P < 0.001$) in the postfledging period (Figure 10.2d,e). Understory use did not change throughout the postfledging period, remaining at ~60% ($n = 19$ paired sub-broods, $F_{2, 539} = 1.305$, $P = 0.12$). Fledglings in both male- and female-reared sub-broods had similarly high daily survival for the period from nine days after fledging until independence (male $\bar{x} = 0.9887$, 95% CI = 0.9946–0.9766, $n = 54$; female $\bar{x} = 0.9873$, 95% CI = 0.9939–0.9736, $n = 46$).

DISCUSSION

We observed a significant difference in space use between male- and female-reared sub-broods of Golden-winged Warblers during the postfledging period in the western Great Lakes region, and the difference has implications for management. Spatial patterns are present not only in relation to a single point at the nest, but also at a scale relevant to management such as a clearcut or shrubby wetland patch, as we observed that female-reared sub-broods traveled farther from the natal patch edge than male-reared sub-broods. Current Best Management Practices in the western Great Lakes region suggest active management at a radius of 244 m around a patch

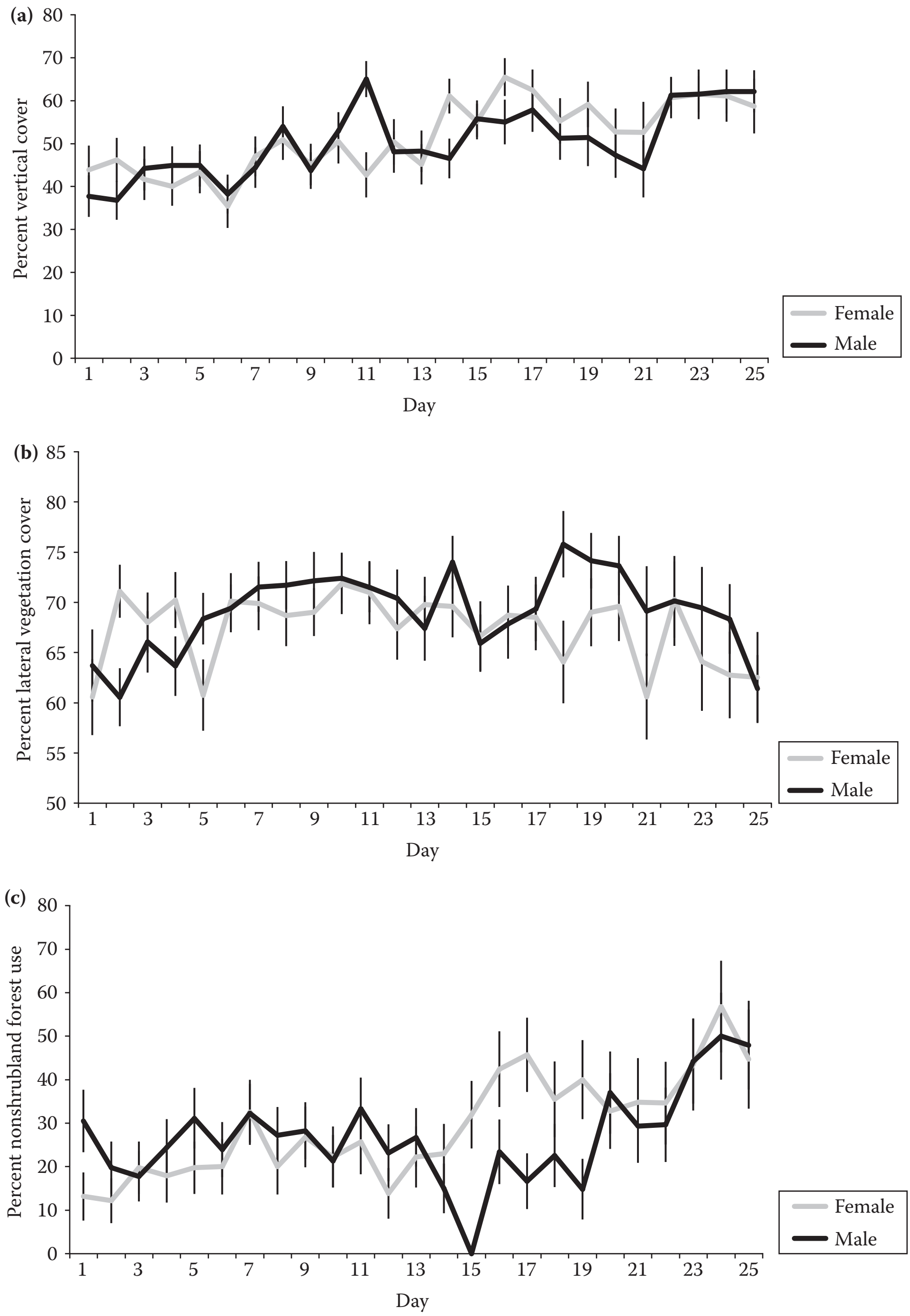

Figure 10.2. Daily trends of (a) vertical cover, (b) lateral vegetation cover, and (c) nonshrubland forest use in male-reared sub-broods and female-reared sub-broods. *(Continued)*

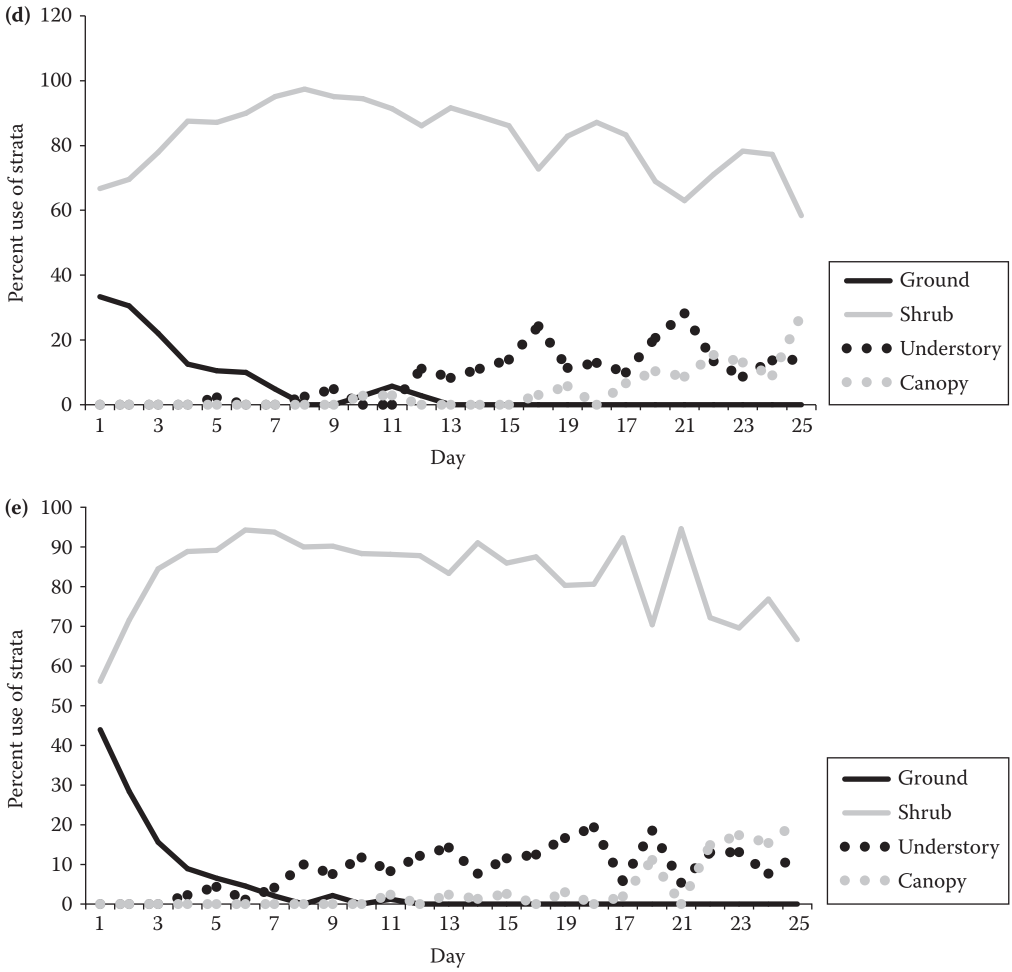

Figure 10.2. (*Continued*) Daily trends of strata use in (d) male-reared sub-broods and (e) female-reared sub-broods in three populations of Golden-winged Warblers in the western Great Lakes region 2010–2012 (data presented as mean ± SE; SE omitted from (d) and (e) for clarity).

(A. M. Roth et al., unpubl. plan). If we had not accounted for sex-related brood division in our study, we would have reported that broods move 201 m away from the natal patch edge and likely confirmed the current scale of management. However, both of these measurements significantly underestimate the extent of postfledging habitat used by female-reared sub-broods, which on average traveled 330 m from the natal patch edge before fledglings were independent from adult care.

To effectively manage breeding habitat of Golden-winged Warblers, it may be necessary to incorporate considerations for brood division and the different spatial scales used by male- and female-reared sub-broods during the postfledging period. Ignoring differential space use by male and female Golden-winged Warblers during the postfledging period may result in negative consequences for half the potential production of young to independence. We did not directly assess the consequences of failing to provide brood-rearing habitat at the spatial scaled used by female-reared sub-broods. However, landscapes that do not provide brood-rearing cover types at that spatial scale may provide lower quality habitat, and therefore productivity may be lower in such landscapes. Fledgling survival is a key component of full season productivity (Streby and Andersen 2011), and current recommendations underestimate the spatial scale of management needed to incorporate postfledging cover-type use (A. M. Roth et al., unpubl. plan). To provide adequate postfledging habitat for Golden-winged Warblers, mature forest or sapling-dominated clear-cuts should be maintained in close proximity to natal patches.

Habitat use of female-reared sub-broods is similar to habitat use of male-reared sub-broods throughout the postfledging period and managing for postfledging habitat from the edge of the natal patch to the scale that females use space will likely provide adequate habitat for both sub-broods, even as they move away from the natal patch. Current management recommendations need to be revised to consider cover types beyond what has been considered to be Golden-winged Warbler breeding habitat such as mature forest and sapling-dominated forest (Confer et al. 2011). Portions of the landscape not previously considered to be used by Golden-winged Warblers such as mature forest >244 m from shrublands may need to be reclassified as postfledging habitat and incorporated into management planning. Managing for postfledging cover types up to 700 m from a managed shrubland would provide postfledging habitat for 95% of the broods we monitored in our study.

Habitat characteristics at locations used by broods during the postfledging period likely influence survival (Streby and Andersen 2013a; Chapter 8, this volume). We observed no difference in survival between male- and female-reared sub-broods in the late postfledging period. Furthermore, although we did not directly test for differences in survival between male- and female-reared sub-broods in the early postfledging period, our observations that space use and vegetation characteristics at sub-brood locations were similar during this period suggest that predation pressures and, by extension, survival were likely also similar in male- and female-reared sub-broods. These observations suggest that both sexes are equally capable of rearing broods. Identification of parental care in our study populations often required multiple observations over several days. If the fledglings cared for by either parent were subjected to greater predation rates than fledglings cared for by the other parent during the early postfledging period, we would expect fewer fledglings observed under the care of that parental sex during the late postfledging period. Instead, we observed an equal proportion of parental care in males and females in this population (Peterson 2014), supporting the conclusions that predation pressures and survival rates were similar throughout the early postfledging period for both male- and female-reared sub-broods.

Last, our observations of differences in space use between male and female parents may influence mate choice and breeding habitat use. The mechanism of mate choice by female songbirds remains unclear, but mate choice in some species may be influenced more by territory quality than by male physical characteristics (Sirkiä and Laaksonen 2009, Temeles and Kress 2010, Hasegawa et al. 2012). We suggest that female Golden-winged Warblers likely use multiple criteria for choosing a breeding territory and mate, including male quality, potential nest success, and potential fledgling survival, all of which influence nest-site choice (Streby et al. 2014). Under such circumstances, many unoccupied areas that appear to humans structurally suitable as breeding territories may be unoccupied because they are not surrounded by adequate postfledging habitat at a scale used by females to rear their sub-broods. In addition, female-based postfledging habitat requirements may play a role in males remaining unpaired on seemingly suitable song territories. Managing at the territory scale, defined based on singing males, may be inadequate if females choose mates and associated breeding territories based on a much larger area or quality of adjacent habitats.

ACKNOWLEDGMENTS

We thank H. Saloka, P. Blackburn, W. Brininger, W. Faber, W. Ford, J. Loegering, M. McDowell, and R. Vallender for equipment and logistical support. We thank L. Arnold, S. Barlow, D. Bradshaw, J. Bruggman, R. Carr, M. Dawson, L. Deets, J. Feura, A. Fish, R. Franta, C. Gesmundo, A. Jensen, M. Johnson, G. Kramer, J. Lehman, T. McAllister, D. McNeil, E. Pokrivka, R. Poole, A. Rehmann, J. Refsnider, R. Refsnider, N. Seeger, E. Sinnot, and B. Vernasco for assistance with field data collection, D. Johnson for assistance with statistical analyses, L. Schofield, J. Loegering, and P. Wood for constructive comments on this manuscript, and two anonymous referees for comments improving the manuscript. Field data were collected during a project funded by the U.S. Fish and Wildlife Service, U.S. Geological Survey, and Minnesota Department of Natural Resources through Research Work Order no. 87 at the Minnesota Cooperative Fish and

Wildlife Research Unit. We collected data following Protocol #1004A80575, approved by the University of Minnesota Institutional Animal Care and Use Committee. Use of trade names does not imply endorsement by the U.S. Geological Survey, University of Minnesota, or any other organization supporting this research.

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