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## Research

### Patterns of parental care and movement in divided broods of golden-winged warblers

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Post-fledging brood division is a poorly understood, yet widespread suite of avian behaviours that includes both division of parental care and spatial division of a brood. For most species, the differences in parental care between adult males and females and the behavioural mechanisms explaining spatial patterns of brood division are unknown. We studied brood division in golden-winged warblers *Vermivora chrysoptera* to describe the spatial and behavioural characteristics of brood division and assess hypotheses describing the potential benefits of brood division. Female golden-winged warblers are known to travel farther from their nests than males within the post-fledging period, although the mechanism resulting in this spatial pattern is unknown. From 2010 to 2012, we monitored radio-marked golden-winged warbler fledglings from fledging until independence from adult care at three sites in the western Great Lakes region of North America. We observed no significant differences in provisioning, parental attendance, daily distance traveled and fledgling begging between male- and female-reared sub-broods. We also did not observe a relationship between parental sex and fledgling sex or mass. However, female-reared sub-broods exhibited a unique period of relatively consistent directional movement on days 8–10 after fledging, which resulted in females traveling farther from the nests than males. Our observations were not fully consistent with any previously proposed hypotheses about the benefits of brood division. Brood division is a complex behaviour that may have a suite of benefits, including predation defense and provisioning efficiency, that are not fully understood.

Keywords: behaviour, brood division, North America, post-fledging period, radio telemetry, *Vermivora chrysoptera*

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## Introduction

Brood division is a taxonomically and geographically widespread, yet poorly documented or described avian behaviour that manifests as division of parental care and, for some species, spatial division of a brood. It has been documented in many different bird orders, including Strigiformes, Gruiformes, Passeriformes, Podicipediformes, Charadriiformes and Piciformes (Williamson 1946, Simmons 1974, Horsfall 1984, Linkhart and Reynolds 1987, Leedman and Magrath 2003, Cox 2011). Parental brood division is characterized by separation of parental care so that each adult provisions and defends a stable subset of the brood, forming two 'subfamilies' (Harper 1985, Leedman and Magrath 2003; hereafter we use the term 'sub-brood' to describe these units of division to avoid confusion with the taxonomic term 'subfamily' and to more accurately describe the object of division (i.e. the brood)). Spatial brood division is characterized by the separation of sub-broods in different locations, where they may be exposed to different conditions (e.g. food availability, predation pressure). There is considerable variation in how brood division is manifested, with some species demonstrating obligate brood division (McLaughlin and Montgomerie 1985, Tarwater and Brawn 2008, Raybuck et al. 2020), whereas in other species, only a portion of broods are divided (Harper 1985, Leedman and Magrath 2003). Similarly, timing of brood division varies among species, with most species dividing broods immediately after fledging (Nolan 1978, Smith and Merkt 1980, McLaughlin and Montgomerie 1985, Byle 1990, Anthonisen et al. 1997, Evans Ogden and Stutchbury 1997) but others dividing broods up to several weeks after fledging (Leedman and Magrath 2003).

In some multi-brooded species, divided broods recombine under the care of the male when the female begins incubation of a subsequent clutch of eggs (Weatherhead and McRae 1990, Evans Ogden and Stutchbury 1997). However, in other multi-brooded species, brood division occurs predominantly only in breeding attempts late in the season (Mills et al. 1980, Edwards 1985, Harper 1985, Zaias and Breitwisch 1989). Brood division can also be related to fledgling sex, with some species exhibiting a tendency to care for fledglings of the same or opposite sex from the parent (Harper 1985, Byle 1990, Vega et al. 2007) whereas other species exhibit no sex-related pattern in brood division (Price and Gibbs 1987, Evans Ogden and Stutchbury 1997, Wheelwright et al. 2003, Tarwater and Brawn 2008, Watson et al. 2012). Leedman and Magrath (2003) summarized potential evolutionary factors influencing parental brood division in birds and formulated eight hypotheses to explain the division of parental care, although no individual hypothesis has garnered extensive support (Table 1). One or more of these factors may influence evolution of brood division, and because the natural history of species that exhibit brood division differs considerably, it is unlikely that any single hypothesis describes the evolutionary factors shaping this behaviour for all species that undergo brood division.

Spatial brood division is poorly documented but has been reported in at least five species: prairie warblers *Setophaga discolor* (Nolan 1978), lapland longspurs *Calcarius lapponicus* (McLaughlin and Montgomerie 1985), hooded warblers *Setophaga citrina* (Evans Ogden and Stutchbury 1997, Rush and Stutchbury 2008), golden-winged warblers *Vermivora chrysoptera* (Peterson et al. 2016a), and in a small percentage of gray vireos *Vireo vicinior* (Fischer 2020). In each of these species, female-reared sub-broods travel farther from the nest and/or natal patch than male-reared sub-broods. The benefits to spatial brood division are unclear, but it has been suggested that spatial brood division could be related to male nest-site philopatry, reduction of full-brood predation, inbreeding avoidance or polygamy (McLaughlin and Montgomerie 1985, Evans Ogden and Stutchbury 1997, McNeil et al. 2019).

Golden-winged warblers are migratory songbirds that breed in northeastern and north-central North America and winter in Central America and northern South America (Confer et al. 2011; Kramer et al. 2018). Mean fledged brood size in this study population was four, with an average age of fledging of nine days (H. Streby unpubl.). Both parents of this single-brooded species care for nestlings and fledglings until independence ~25 days after fledging (Will 1986, Streby et al. 2014). During the dependent post-fledging period, golden-winged warblers often form crèches (i.e. loose flocks comprised of multiple broods) with fledglings of both other species and other non-related conspecific sub-broods (Will 1986, H. Streby, unpubl.). Brood division has been documented in golden-winged warblers (Will 1986), but the extent and characteristics of brood division are not known. Early in the post-fledging period, male- and female-reared sub-broods occur at similar distances from the nest; however, by the end of the post-fledging period, female-reared sub-broods travel almost three times as far from the nest as male-reared sub-broods, indicating a potential shift in parental behaviours at some point in the post-fledging period (Peterson et al. 2016a). The mechanism resulting in female-reared sub-broods traveling further from nests than male-reared sub-broods is currently unknown but could be the result of larger daily distances traveled, higher directionality or both. As in most species that divide broods, sex-based differences in parental care are currently unknown. However, Peterson et al. (2016a) reported that golden-winged warbler fledgling survival from day eight after fledging until independence was similar between both male- and female-reared sub-broods. Furthermore, despite considerably different space use between male- and female-reared sub-broods, both parents use areas with similar habitat characteristics throughout the post-fledging period and experience similar fledgling mortality rates (Peterson et al. 2016a).

We used radio telemetry to study brood division in three populations of golden-winged warblers to describe sex-based differences in parental care and movement patterns, and examine the influence of space use on parental care. To better understand the potential evolutionary basis of this behaviour, we also assess support for six of the existing hypotheses

Table 1. Assessment of support for expected observations for brood division hypotheses in golden-winged warblers in the western Great Lakes region of North America 2010–2012.

| Hypothesis                             | Prediction   | Observation   | Conclusion      |
|--|--|---|-----------------|
| Predation                              | 1) Brood and 2) sub-brood spatially divided, especially at most vulnerable age                 | Spatial division between sub-broods at the most vulnerable age was no stronger than division between broodmates within the same sub-brood. Spatial division occurred after day 8, when survival was high        | Partial support |
| Sibling competition                    | 1) Brood and 2) sub-brood spatially divided  | Sub-broodmates were spatially divided early in the post-fledging period, whereas broods were only spatially divided after age 10 days   | Partial support |
| Provisioning                           | Conspecific individuals from other sub-broods and broods avoided                               | Sub-broods associated with conspecifics within crèches  | No support      |
|  | Provisioning rates more even in divided broods than undivided broods                           | Not assessed, brood division was nearly obligate  | N/A             |
|  | Sub-broodmates closely associated with each other  | After day 10, sub-broodmates were closely associated with each other  | Partial support |
|  | Females travel farther from the nest, to more productive habitat                               | Females traveled farther from the nest, but there was no difference in habitat use (Peterson 2016a) and the movement was driven by active directionality from females rather than constrained movement by males | Partial support |
| Preferential care                      | Females have higher provisioning rates due to exploiting more productive post-fledging habitat | Provisioning observations were similar between parental sexes   | No support      |
|  | Males preferentially care for their own offspring  | Not directly assessed, however, caring for brown-headed cowbirds suggests males do not discern genetic relatedness  | No support      |
| Preferential care/<br>specialized care | Parents preferentially care for individuals of a specific sex                                  | We observed no correlation between adult sex and fledgling sex within sub-broods  | No support      |
| Adult conflict                         | Dominant sex cares for less needy fledglings or fitter fledglings                              | We observed no correlation between begging rate (i.e. needy fledglings) or nestling mass (i.e. fitter fledglings) and adult sex   | No support      |
|  | Dominant sex cares for fewer fledglings  | We observed no difference in the number of fledglings cared for by males and the number of fledglings cared for by females  | No support      |
| Fledgling choice                       | Dominant fledgling associated with the best provisioner  | Not directly assessed, however we observed similar provisioning rates between males and females. If the dominant fledgling selects the best provisioner, then provisioning is not a sex-based trait             | No support      |
|  | 1) Agonistic behaviour between fledglings 2) Uneven brood division                             | 1) We did not observe any agonistic behaviour between fledglings 2) We observed even brood division   | No support      |
| Social specialization                  | Provisioning efficiency increases over time  | Not assessed  | N/A             |

explaining the evolutionary benefits of dividing parental care. We hypothesized that 1) male and female fledgling care would be similar, as we observed no difference in fledgling mortality in a previous study (Peterson et al. 2016a), 2) the mechanism driving differing space use between male- and female-reared sub-broods would be increased directional movements by female golden-winged warblers during the post-fledging period and 3) that brood division would most likely be driven by predation risk, provisioning efficiency or both.

## Methods

### Study sites

From 2011 to 2012, we studied golden-winged warblers at Tamarac National Wildlife Refuge (NWR) in Becker County, Minnesota, USA (47.049°N, 95.583°W), Rice

Lake NWR in Aitkin County, Minnesota, USA (46.529°N, 93.338°W) and Sandilands Provincial Forest (PF) in south-eastern Manitoba, Canada (49.637°N, 96.247°W). We also performed a pilot study in 2010 at Tamarac NWR. All three study sites were located in the northern hardwood transition zone between boreal forest in the north and east and tall-grass prairie in the south and west (for detailed site description, Peterson et al. 2016b).

### Field methods

We used two methods for searching for golden-winged warbler nests: 1) systematic searching for nests and using adult behavioural cues (Martin and Geupel 1993) to locate nests and 2) radio-telemetry of adult female golden-winged warblers passively captured in mist-nets and marked with radio transmitters in the first three weeks of the breeding season (Streby et al. 2014, Peterson et al. 2015). We attached radio

transmitters with a figure-eight elastic harness (Rappole and Tipton 1991, Streby et al. 2015). Radio transmitters were ~4.1% of mean adult mass at time of attachment and had no measurable impact on productivity (Streby et al. 2013a). We recorded nest locations using handheld Global Positioning System (GPS) units (Garmin GPSMAP 76 or eTrex Venture HC) and achieved < 5 m accuracy by averaging 100 points at each location.

When nestlings were 6–9 days old (counting hatch day as day one), we measured nestling mass to the nearest 0.01 g using a digital scale, banded all nestlings with standard U.S. Geological Survey aluminum legbands, and attached a radio transmitter with a unique frequency (~4.6% of mean nestling mass) to 1–5 randomly selected nestlings using the same attachment method described for adults. We also attached radio transmitters to three brown-headed cowbird *Molothrus ater* (a brood parasite) nestlings from two nests. We used mist nets to capture, band and attach radio transmitters to 26 additional fledglings encountered during field activities (21% of all fledglings monitored). Given the ages of fledglings encountered during field activities, it is likely that these individuals were from unknown nests within the study patches or from nearby patches that were not searched for nests. We estimated the age of these captured fledglings based on observed plumage development of fledglings of a known age (i.e. those monitored from fledging).

We monitored 66 radio-marked 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. We located fledglings each morning, and monitored them using the ground-based telemetry methods described by Streby and Andersen (2013b). For each fledgling, we identified parental sex using plumage. After visually identifying the radio-marked fledgling, we recorded daily fledgling locations using handheld GPS units as we did for nest locations. For the purposes of analysis and clarity, we considered the location of the radio-marked fledgling to be representative of the sub-brood. Older fledglings were occasionally moving when tracked (e.g. foraging). In those instances, location was recorded as the first point the fledgling was observed. For each sub-brood, we derived minimum daily distance moved (i.e. the minimum distance between sub-brood locations on successive days), distance between fledglings (both those within the same sub-brood and those in different sub-broods) and daily change in azimuth (i.e. the change in direction a fledgling traveled between successive days), using ArcGIS 10.0 Geographic Information System (GIS) software.

In addition to recording fledgling location, in 2012 we also recorded parental and fledgling behaviour for a 5-min period following location of the fledglings via radio telemetry. Using these 5-min observation periods, we recorded induced begging observations (i.e. begging during interaction with the adult), unattended begging observations (i.e. begging with no adult present), adult attendance (i.e. whether the parent was present) and provisioning (i.e. whether the fledgling was fed by an adult). We did not observe any evidence of fledgling

disturbance due to observer presence, with the exception of a small number (< 10) of accidental disturbances of fledglings tracked in the first three days after fledging. The majority of adult females and ~10% of adult males were colour banded, so were easily differentiated from other conspecific adults. In sub-broods for which the adult was marked, we did not observe any interactions between the fledglings we monitored and any other conspecific adults. Therefore, we assumed that sub-broods for which adults were not marked also only interacted with their parents and not conspecific adults. We used throat and auricular plumage colouration to identify fledgling sex beginning at 14 days after fledging, when the preformative molt initiated (McNeil 2019).

## Statistical analyses

To avoid potential bias in our statistical tests due to non-independence of location for broods in which we monitored only one sub-brood, we used only broods for which we monitored both sub-broods from a known nest ( $n = 17$ ) in all statistical tests. As described above, we did not radio mark all fledglings from each brood due to logistical constraints. In addition, fledgling mortality was highest during the first few days after fledging from the nest (Streby et al. 2016), as is common among songbirds (Cox et al. 2014, Naef-Daenzer and Gruebler 2016), reducing the likelihood that both sub-broods were monitored, or even remained, after days 1–3. As the biological unit of interest is the sub-brood, we used mean sub-brood measurements for four sub-broods in which we monitored > 1 fledgling (12% of paired sub-broods).

After testing for statistical differences between paired sub-broods for each parameter, we described patterns over time using data from all 129 sub-broods, including 42 female-reared and 53 male-reared sub-broods for which we only monitored fledglings from one sub-brood. For seven sub-broods in which we monitored > 1 fledgling, we used the mean value for each response variable. We excluded two broods in which we did not observe evidence of brood division from analyses (1.7% of observed nests). All data are presented as mean  $\pm$  standard error.

## Sex-based differences in parental care

We assessed mean sub-brood size for each parental sex with a Student's t-test using a sample of 10 nests in which all fledglings were tracked. We tested for variation in fledgling sex selection by each parental sex using a  $\chi^2$  test. To avoid potential sex-specific capture biases, we used only fledglings that we marked as nestlings in this analysis. To assess whether adult selection of fledglings for their sub-brood was correlated with nestling mass, we used a paired Student's t-test to compare mean nestling mass at time of banding for paired sub-broods. We acknowledge that nestling mass may not be a reliable indicator of nestling condition (Streby et al. 2013b), but higher mass of one sub-brood would suggest that sub-brood had access to more food. Although mass measurements were not standardized by nestling age, we only used

pair-wise comparisons, so nestlings in each sub-brood were of the same age at the time of comparison. We assessed differences in male and female behaviour towards fledglings for four parameters (parental presence, provisioning, total begging and unattended begging) with linear mixed-effect models with the parameter of interest as the dependent variable, the interaction of parental sex and age as the independent variables, and brood as a random effect. We did not use year as a random effect for this analysis, as all but one paired sub-brood was monitored in 2012. We fit models using the 'lmer' function in the R package lme4 and assessed significance using 95% confidence intervals from the 'confint' function (<www.r-project.org>, Bates et al. 2015).

### Spatial brood division

As reported in Peterson (2016a), female-reared sub-broods traveled nearly three times farther from their nest than male-reared sub-broods, an observation which could be caused by either differing daily distance moved (i.e. females move greater daily distances than males) or differing directional movements (i.e. females direct movements away from nests), or both. We assessed differences in minimum daily distance moved between male- and female-reared sub-broods using a linear mixed-effect model with daily distance moved as the dependent variable, the interaction between parental sex and fledgling age as the independent variables, and brood as a random effect as described above. We used a Rayleigh test for circular uniformity (Durand and Greenwood 1958) to assess average azimuth (i.e. the mean direction traveled by a sub-brood from fledging until independence) for both male- and female-reared sub-broods by testing recorded daily average azimuths throughout the post-fledging period against a general alternative. To identify directionality of movements, we calculated daily change of azimuth from day 2 to 25 for each sub-brood (sample size ranged from 7 to 17 paired sub-broods, depending on how many broods were monitored on each day after fledging). This method results in a distribution of values between 0° and 180°, with random selection of directional movement producing an average daily change of azimuth of 90°, movement in similar directions to the previous day (i.e. moving away) producing an average daily change of azimuth < 90°, and movement in dissimilar directions to the previous day (i.e. turning back or maintaining an area of use) producing an average daily change of azimuth > 90°.

### Assessing brood division hypotheses

We assessed support for hypothesis explaining brood division by comparing our observations to 17 behaviours predicted by those hypotheses (Leedman and Magrath 2003; Table 1). For each prediction, we report our observations and whether our observations supported, partially supported or did not support hypotheses explaining brood division, or whether predictions from hypotheses were not applicable to golden-winged warblers.

## Results

### Sex-based differences in parental care

We observed brood division in 123 radio-marked fledglings (including those we marked after fledging from unknown nest locations), including 109 fledglings from 78 nests. We monitored two additional broods that did not exhibit brood division, but instead exhibited bi-parental care for fledglings (1.7% of nests). For fledglings observed  $\geq 14$  days after fledging, we identified the sex of 27 fledglings (65.9%) in female-reared sub-broods and of 32 fledglings (59.3%) in male-reared sub-broods. Females were equally likely to care for female offspring ( $n=15$ ) as they were for male offspring ( $n=12$ ;  $\chi^2=0.61$ ,  $df=1$ ,  $p=0.56$ ). Similarly, males equally cared for female ( $n=18$ ) and male ( $n=14$ ) offspring ( $\chi^2=0.41$ ,  $df=1$ ,  $p=0.48$ ). In broods marked as nestlings for which we monitored both sub-broods ( $n=17$ ), nestling mass was similar between male- ( $\bar{x}=7.33 \pm 0.14$ ) and female-reared ( $\bar{x}=7.15 \pm 0.19$ ) fledglings ( $t=-0.66$ ,  $p=0.26$ ). For 10 nests in which we tracked all fledglings, mean fledged brood size was  $4.60 \pm 0.22$ . Of 46 fledglings tracked, 42 had a known fate through independence, with four transmitter harness failures. We determine parental care for 17 fledglings (40%) that lived > 4 days. Mean sub-brood size for fledglings that survived > 3 days was similar between males ( $\bar{x}=0.90 \pm 0.23$ ) and females ( $\bar{x}=0.80 \pm 0.19$ ;  $t=0.70$ ,  $p=0.75$ ).

Adult and fledgling behaviours (i.e. provisioning, adult attendance and attended and unattended fledgling begging) were similar between paired male- and female-reared sub-broods (Table 2). In the larger sample of both paired and unpaired sub-broods, we observed no temporal trend in provisioning throughout the post-fledging period (Fig. 1A), although parental attendance for both male- and female-reared sub-broods declined steadily throughout the post-fledging period (Fig. 1B). Similarly, we found no difference between male- and female-reared sub-broods in unattended begging (Fig. 1C) or total begging (Fig. 1D).

### Spatial brood division

Fledglings in both male- and female-reared sub-broods exhibited similar minimum daily distances moved throughout the post-fledging period (Table 2). We observed two periods of relatively directional movement, or less change in direction between subsequent days than expected at random. On day three and four, both male- and female-reared sub-broods were relatively more likely to travel in a direction similar to what they had traveled on the previous day (Fig. 2B). On days 8–10 only female-reared sub-broods moved in relatively similar directions to the previous day. After this directional movement by female-reared sub-broods, both male- and female-reared sub-broods on average changed direction > 90° on a majority of days, suggesting maintenance of an area of use (Fig. 2B). Male-reared sub-broods changed direction > 90° on 13/15 days, and female-reared sub-broods changed direction > 90° on 9/15 days. Neither sex on average

Table 2. Linear mixed-effect model parameter estimates and 95% confidence intervals for parental behaviour estimates as a function of the interaction of parental sex and fledgling age, with brood as a random effect for golden-winged warblers in the western Great Lakes region of North America. Significant effects are indicated in bold.

| Dependent variable               | Independent variable | Estimate      | 95% confidence interval |
|----------------------------------|----------------------|---------------|-------------------------|
| Daily distance <sup>1</sup>      | Sex                  | 3.972         | -22.959 to 30.916       |
|                                  | <b>Age</b>           | <b>5.729</b>  | <b>4.176–7.288</b>      |
| Provisioning <sup>2</sup>        | Sex × Age            | -0.654        | -2.663 to 1.345         |
|                                  | Sex                  | -0.034        | -0.132 to 0.064         |
|                                  | Age                  | 0.004         | -0.001 to 0.010         |
| Parental attendance <sup>3</sup> | Sex × Age            | -0.002        | -0.009 to 0.006         |
|                                  | Sex                  | 0.006         | -0.145 to 0.158         |
|                                  | <b>Age</b>           | <b>-0.014</b> | <b>-0.231 to -0.006</b> |
| Unattended begging <sup>4</sup>  | Sex × Age            | -0.001        | -0.012 to 0.010         |
|                                  | Sex                  | -0.026        | -0.165 to 0.115         |
|                                  | Age                  | 0.006         | -0.002 to 0.014         |
| Total begging <sup>5</sup>       | Sex × Age            | 0.007         | -0.004 to 0.017         |
|                                  | Sex                  | 0.048         | -0.077 to 0.173         |
|                                  | <b>Age</b>           | <b>0.025</b>  | <b>0.018–0.032</b>      |
|                                  | Sex × Age            | -0.004        | -0.013 to 0.006         |

<sup>1</sup> Random effect variance: 1463; residual variance: 7084.

<sup>2</sup> Random effect variance: 0.002; residual variance: 0.088.

<sup>3</sup> Random effect variance: 0.012; residual variance: 0.209.

<sup>4</sup> Random effect variance: 0.012; residual variance: 0.175.

<sup>5</sup> Random effect variance: 0.005; residual variance: 0.140.

changed direction  $< 90^\circ$  after day 10. Neither male- ( $n = 25$ ,  $Z = 0.218$ ,  $p = 0.31$ ) nor female-reared sub-broods ( $n = 25$ ,  $Z = 0.243$ ,  $p = 0.23$ ) moved in a consistent direction over the entire post-fledging period. There was a relatively larger difference in directional movement patterns between male- and female-reared sub-broods than there was in minimum daily distance traveled (Fig. 2A and B).

### Sub-brood movement patterns

Early in the post-fledging period, sub-broods were diffusely spread in an overlapping area where fledglings occurred at similar distances from each other regardless of sub-brood association (Fig. 3). However, after the period of directional movement by female-reared sub-broods, sub-broods were more cohesive and sub-broodmates occurred closer to each other than they were to fledglings of the other sub-brood (Fig. 3). Sub-broodmates were frequently observed in the same shrub or tree after day 10. In 12 broods for which we tracked both sub-broods after day eight, we rarely observed sub-broods close ( $< 15$  m) to each other (9/68 days [13%];  $\bar{x} = 271.7 \pm 32.7$  m apart). However, in five broods, we observed sub-broods in close proximity ( $\bar{x} = 6.1 \pm 1.7$  m) to each other for a brief period ( $\bar{x} = 1.6 \pm 0.4$  days) after day 10. These sub-broods traveled an average of 135 m ( $\pm 13$  m) from the previous day's location when the brood reunited.

### Assessing brood division hypotheses

There was no clearly supported hypothesis for the benefits of brood division in golden-winged warblers, based on

comparing our observations to predictions from hypotheses explaining brood division. We found partial support for the predation, sibling competition and provisioning hypotheses and we did not observe support for the preferential care, specialized care, adult conflict and fledgling choice hypotheses (Table 1). We were unable to assess the social specialization hypothesis and one of the predicted observations of the provisioning hypothesis (Table 1). In 1233 records of fledgling behaviour during the post-fledging dependent period, we did not observe any agonistic actions of fledglings directed at broodmates, parents or other non-related fledglings (including golden-winged warblers and other species) within a crèche. It is unlikely that some assessment of genetic paternity plays a role in which chicks are selected to be cared for. As part of this study, we tracked brown-headed cowbirds ( $n = 3$ ) reared in two golden-winged warbler nests: one brown-headed cowbird that fledged with one golden-winged warbler, and two brown-headed cowbirds that fledged with one golden-winged warbler. In the first instance, we observed the male exclusively feeding the cowbird, whereas the female exclusively fed the golden-winged warbler. In the second group, we observed the female exclusively feeding the golden-winged warbler fledgling and the male exclusively feeding one of the cowbird fledglings, but both adults providing care to the second cowbird fledgling.

## Discussion

Brood division was the dominant strategy for post-fledging care in the three populations of golden-winged warblers we studied in the western Great Lakes region in North America. Brood division was also the dominant strategy for golden-winged warblers in Michigan, USA (Will 1986), Tennessee, USA (J. Lehman pers. comm.) and Pennsylvania, USA (McNeil et al. 2019), suggesting that this behaviour is widespread. We observed two instances of bi-parental care in this population, but did not record any distinct behavioural or brood/clutch differences for those two broods, so we cannot speculate why brood division did not occur. We observed similar parental behaviours for male and female golden-winged warblers, with the exception of movement patterns, and were able to reject many of the hypotheses for why this behaviour occurs in this species.

### Sex-based differences in parental care

Like most species, the differences in parental care between males and females within the context of brood division were unknown for golden-winged warblers. Similar to Byle (1990), we observed no meaningful difference between male and female provisioning. Although we did not directly assess differences in the quality of food delivered by each parent, Streby et al. (2013b) reported that the stomach contents of nearly all recovered fledgling golden-winged warblers in this population were similar, suggesting that food items provided by each parent were similar. We also did not observe a

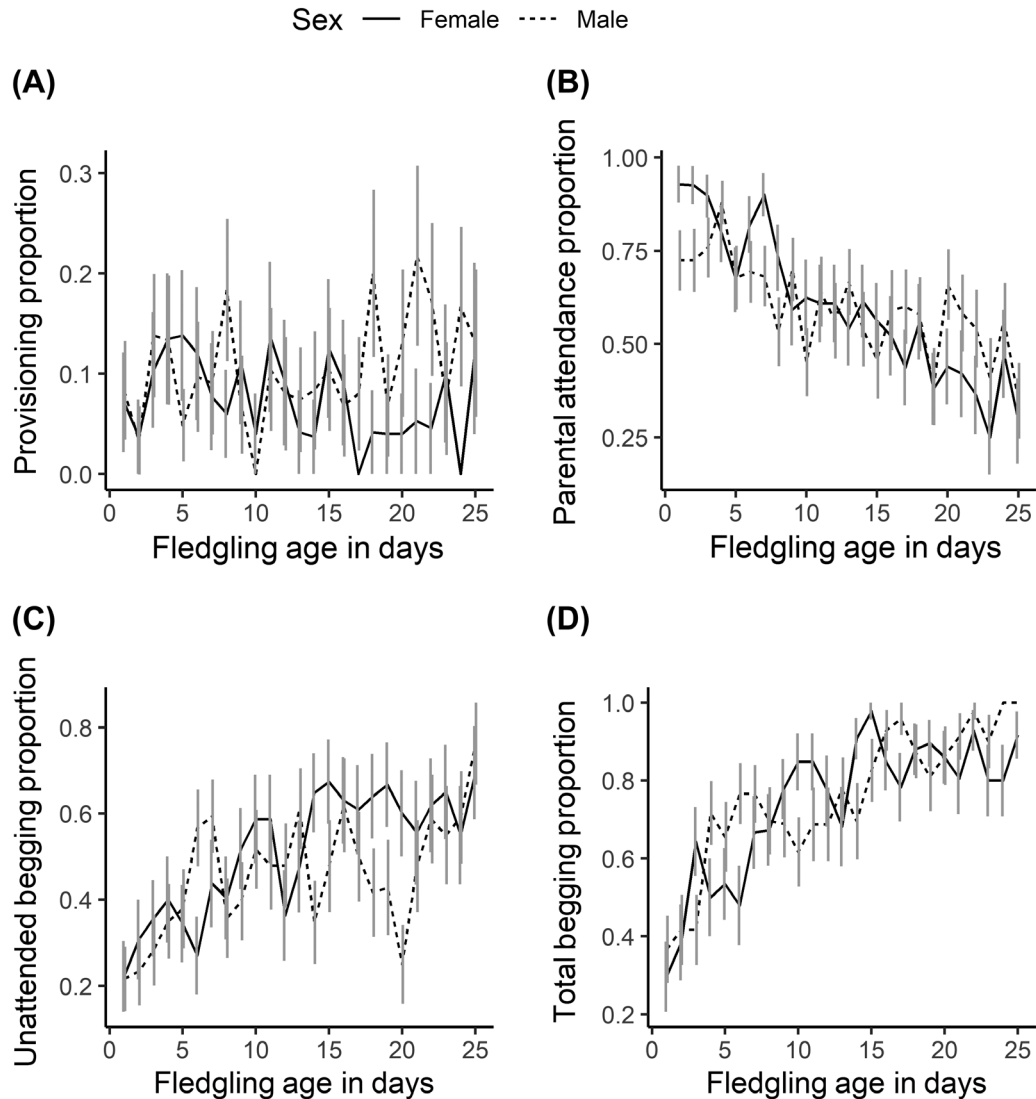


Figure 1. Daily trends in (A) provisioning (% of daily observation periods with adult provisioning), (B) parental attendance (% of daily observation periods with adult present), (C) unattended begging (% of daily observation periods with fledgling begging in the absence of the adult) and (D) total begging (% of daily observation periods with fledgling begging, including begging induced by adult) all by day after fledging in male-sub-brood and female-reared sub-broods in three populations of golden-winged warblers in the western Great Lakes region of North America 2012 (data presented as mean  $\pm$  SE).

difference in the amount of begging by fledglings in male- and female-reared sub-broods. Although parental attendance of fledglings does not equate to equally effective defense of fledglings, our observations of similar attendance in male- and female-reared sub-broods indicate that parents of each sex had similar opportunities to defend their fledglings. We note, however, that there is a potential bias in our study in that there may be a correlation between patterns of parental care and fledgling mortality. Although we did not observe any indication of differing behaviour when most fledglings were alive (days 1–3) nor any difference in fledgling mortality based on parental sex (Peterson et al. 2016a), we were unable to rule out the possibility that there is a relationship between parental behaviour and fledgling survival. It is possible that

some differences in parental behaviour were not detected due to our short, 5-minute observation window. Future research in brood division may be able to better quantify behaviours and prevent subject disturbance by employing longer observation periods.

### Spatial brood division

Although sub-brood spatial separation has been documented in at least four other species – prairie warblers (Nolan 1978), Lapland longspurs (McLaughlin and Montgomerie 1985), hooded warblers (Evans Ogden and Stutchbury 1997, Rush and Stutchbury 2008) and some gray vireos (Fischer 2020) – the mechanism for separation in these species was not

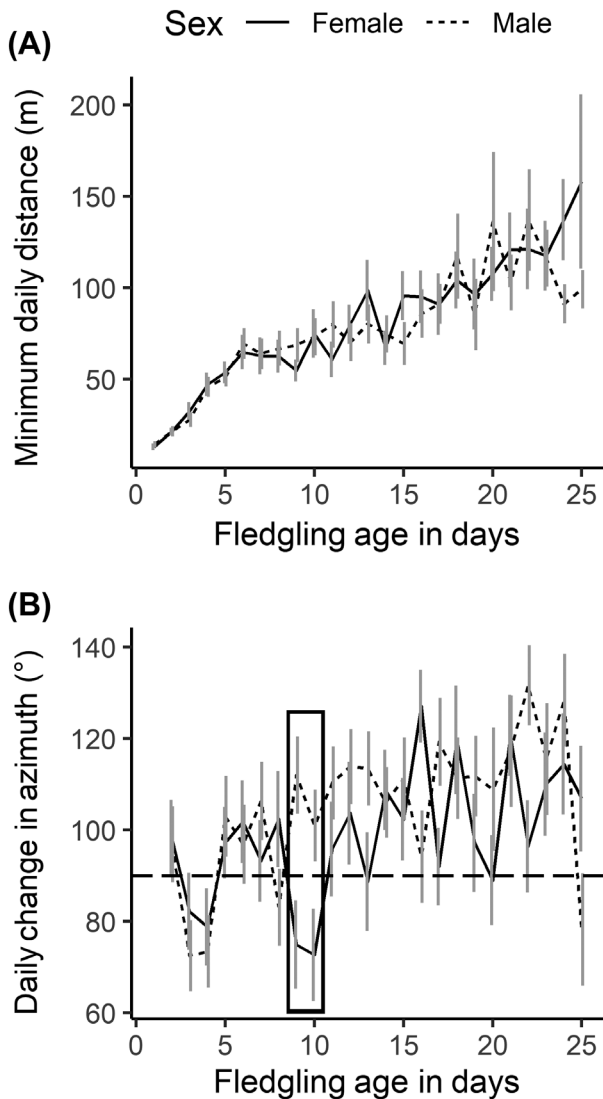


Figure 2. Trends in (A) minimum daily distance moved (m; distance between fledgling locations on subsequent days) and (B) daily change in azimuth (degrees) by day after fledging from nest in male- and female-reared sub-broods in three populations of golden-winged warblers in the western Great Lakes region of North America 2010–2012. Outlined area in (B) highlights period (days 8–10 after fledging) when female-reared sub-broods, but not male-reared sub-broods, showed apparent directionality in movements away from nests. All data presented as mean  $\pm$  SE.

documented. McLaughlin and Montgomerie (1985) hypothesized that territory fidelity in Lapland longspurs may be the reason that males stay close to the nest, although they did not provide any hypotheses as to the evolutionary benefit of this behaviour. The territory fidelity hypothesis predicts that female movements away from the nesting territory are unconstrained random movements that result in females eventually traveling farther from the nest (McLaughlin and Montgomerie 1985). We observed partial support for this hypothesis, as male-reared sub-broods appeared to change direction in a way that kept them close to the nest. However,

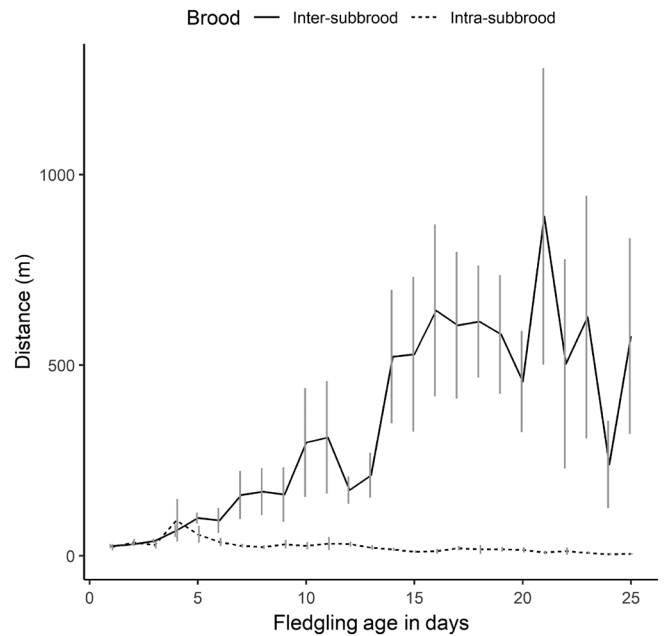


Figure 3. Distance between sub-broods (inter-sub-brood) and between sub-broodmates (intra-sub-brood) by day after fledging from the nest in three populations of golden-winged warblers in the western Great Lakes region of North America 2010–2012 (data presented as mean  $\pm$  SE).

we did not observe random movement in female-reared sub-broods, but rather a period of directional movement in female golden-winged warblers 8–10 days post-fledging. Because there was no difference between male- and female-reared sub-broods in minimum daily distance moved (Fig. 2A), spatial brood division in the populations of golden-winged warblers we studied occurred as a result of this directional movement by female-reared sub-broods (Fig. 2B). Following day 10 post-fledging, female- and male-reared sub-broods demonstrated no multi-day directionality (Fig. 2B). The non-directional movement of sub-broods throughout the remainder of the post-fledging period was characterized by movements  $> 90^\circ$  different in direction between successive days (Fig. 2B), which resulted in sub-broods remaining in the same general area, likely associated with appropriate brood-rearing habitat structure (Streby and Andersen 2013a).

After the period of directional movement by female-reared sub-broods, observed distances between sub-broodmates of either parental sex become smaller until individuals from the same sub-brood often occupied the same shrub or tree. Fledgling golden-winged warbler daily survival is high in the later portion of the post-fledging period (male  $\bar{x} = 0.989$ , 95% CI = 0.977–0.995, female  $\bar{x} = 0.987$ , 95% CI = 0.974–0.994; Peterson et al. 2016a), likely due to increased fledgling vagility and predator avoidance capability. The decreasing proximity between sub-broodmates as they age may be explained by a switch in priorities from avoiding multi-fledgling predation events to reducing parental effort by keeping fledglings together. In addition, close association among sub-broodmates may contribute to fledglings learning



to forage for themselves (a behaviour that increases around this age, McNeil 2019), with siblings able to observe each other's successful foraging behaviours and exploit foraging locations discovered by sub-broodmates or adults. It is unlikely that this association is due to migratory flocking, based on the timing of migration (mid-late-August) and that golden-winged warblers from the same breeding sites exhibit variation in timing and route-use during migration (Kramer et al. 2017).

### Assessing brood division hypotheses

Despite its prevalence, the evolutionary benefits of brood division are unclear, especially regarding differences in space use between male- and female-reared sub-broods. Our observations did not provide strong support for any of the hypotheses summarized by Leedman and Magrath (2003; Table 1). Several hypotheses describing the evolutionary mechanism causing brood division predict that fledglings are separated by some intrinsic or extrinsic characteristic (McLaughlin and Montgomerie 1985, Wheelwright et al. 2003). We observed no relationship between parental sex and fledgling sex, fledgling begging (i.e. neediness) or nestling mass. Although we did not assess paternity, parental care of brown-headed cowbird fledglings by both parents suggests that adults do not or cannot discern genetic relatedness to their fledglings. It is possible that fledglings select parents by some unknown factor rather than vice versa, but that mechanism is less likely given that fledging is often parent-induced and adults lead fledglings away from the nest. The majority of predation on fledgling golden-winged warblers occurred immediately after leaving the nest (Peterson et al. 2016a), a period in which the brood was diffusely spread, but spatial division between sub-broods was low (Fig. 3). This suggests that spatial brood division is not a response to predation pressure during the highest risk period. However, spatial brood division may not be feasible early in the post-fledging period in species that fledge relatively altricial young that are incapable of flight. We cannot reject predation as a potential cause of spatial brood division later in the post-fledging period, although predation rates were very low after broods were spatially divided. It is likely that separation of fledglings early in the post-fledging period increases survival by distributing predation risk across a larger area, but there was no indication that that early separation was related to brood division, but is instead an unrelated behaviour.

The benefit of females traveling farther from the nest than males is unclear. It is not related to ensuring post-fledging cover type availability, as both male- and female-reared golden-winged warbler sub-broods used the same cover types and the same microhabitats in the post-fledging period despite the significant difference in distances from the nest (Peterson et al. 2016a). It is also doubtful that this strategy is related to predation defense, as daily fledgling survival in this species was high late in the post-fledging period when spatial separation between male- and female-reared sub-broods was largest (Peterson et al. 2016a). It has been speculated that

this behaviour in golden-winged warblers may be related to polygamy (McNeil et al. 2019), with males moving shorter distances to attend to nests of additional mates. However, we observed no evidence of polygamy in colour-banded birds at our study sites, suggesting that spatial brood division is not limited only to populations with significant polygamy. It is also possible that females have low philopatry between years and use the post-fledging period to scout novel territories for the next breeding season, whereas males seek to maintain their current breeding territory. However, this behaviour is relatively unlikely in this species, as habitat use changes through the post-fledging period, and the location of individuals later in the post-fledging period does not represent likely breeding habitat (Peterson et al. 2016a).

It is likely that spatial brood division reduces conflict between parents when foraging simply by reducing the overlap in foraging area. If provisioning is a driver of spatial brood division, it could be related to the timing of primary productivity in North America (Sims et al. 2006). As resources become scarce later in the post-fledging period, competition between adults and increased spatial division would increase over time. This hypothesis could be tested latitudinally within similar habitats, as we would expect more separation between sub-broods in areas with shorter productivity windows and less separation in areas with near-constant productivity, such as in the tropics. However, this hypothesis is at odds with our observations of crèching, which suggest that intraspecific competition for space or other resources is not a driver of spatial brood division. The combined benefits of spatial brood division and flocking with conspecifics and heterospecifics may be as simple as reducing the probability of losing all offspring in a single event, even when mortality is rare, while gaining from group foraging and vigilance against predators. Indeed, some post-fledging mixed-species flocks joined by the fledglings we tracked contained dozens of birds and were often highly vocal upon our approach (Streby unpubl.).

A potential benefit of brood division that has not been extensively discussed is protection against the post-fledging effects of brood parasitism (Nolan 1978, Hoover and Reetz 2006, Peterson et al. 2012, Ridley and Thompson 2012). We tracked fledglings from two parasitized nests, one exhibited complete brood division and the other exhibited partial brood division. The nest that exhibited partial brood division was heavily parasitized, fledging one golden-winged warbler and two brown-headed cowbirds. It is possible that the increased demand of feeding cowbird fledglings causes parents to relax the exclusivity of their parental care. Although brood division has the potential to mitigate post-fledging effects of brood parasitism, it is likely that this fitness benefit is an exaptation of brood division and not an adaptation in response to brood parasitism, as there are many species that divide broods in the absence of brood parasites (e.g. flammulated owls *Otus flammeolus*, Linkhart and Reynolds 1987).

Given the widespread nature and variable characteristics of brood division among species, it is likely there are multiple and differing evolutionary benefits in different taxa. The patterns we observed may not be replicated across species,

especially with distantly related taxa. The patterns of movement in brood division may be highly dependent on the vagility and care requirements of fledglings, and could vary with species development and fledging timing. Our observations of golden-winged warblers did not provide strong support for any of the existing hypotheses describing the evolutionary benefits of brood division. However, its prevalence in birds suggests that there are strong evolutionary pressures driving the maintenance of this behaviour. Further study is needed to fully understand the evolutionary and ecological implications of this important behaviour.

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## Author contributions

**Sean M. Peterson:** Conceptualization (lead); Data curation (lead); Formal analysis (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead). **Henry M. Streby:** Conceptualization (supporting); Data curation (supporting); Funding acquisition (equal); Methodology (supporting); Project administration (equal); Supervision (supporting); Writing – review and editing (equal). **Gunnar R. Kramer:** Investigation (supporting); Project administration (supporting); Writing – review and editing (supporting). **Jared M. Feura:** Investigation (supporting); Project administration (supporting); Writing – review and editing (supporting). **David E. Andersen:** Conceptualization (supporting); Funding acquisition (equal); Methodology (supporting); Project administration (equal); Resources (lead); Supervision (equal); Writing – review and editing (equal).

## Transparent Peer Review

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## Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.3j9kd51m0>> (Peterson et al. 2022).

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