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Testing common assumptions in studies of songbird nest success

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We studied Ovenbird *Seiurus aurocapilla* and Golden-winged Warbler *Vermivora chrysoptera* populations in northern Minnesota, USA, to test two common assumptions in studies of songbird nest success: (1) that the condition of an empty nest on or near its expected fledge date is an indicator of nest fate; and (2) that the presence of a fledgling or family group within a territory confirms a successful nest in that territory. We monitored the condition of nests and used radiotelemetry to monitor juveniles through the expected fledging date and early post-fledging period. Of nests that contained nestlings 1–2 days before the expected fledge date, fates were misidentified using nest condition alone for 9.5% of Ovenbird nests, but those misidentifications were made in both directions (succeeded or failed), yielding only a small bias in estimated nest success. However, 20% of Golden-winged Warbler nests were misidentified as successful using nest condition during the final visit interval, biasing the nest success estimate upward by 21–28% depending on the treatment of uncertain nest fates. Fledgling Ovenbirds from 58% of nests travelled beyond their natal territory within 24 h, rising to 98% after 5 days, and those fledglings travelled up to 390 m from nests within 10 days of fledging. Fledgling Golden-winged Warblers from 13% of nests travelled beyond their natal territory within 24 h, rising to 85% after 5 days, and those fledglings travelled up to 510 m from nests within 10 days of fledging. We conclude that nest condition and fledgling presence can be misleading indicators of nest fate, probably commonly biasing nest success estimates upward, and we recommend that these assumptions should be tested in additional species.

Keywords: fledgling, Golden-winged Warbler, Ovenbird, *Seiurus aurocapilla*, telemetry, *Vermivora chrysoptera*.

Estimates of songbird reproductive success, typically limited to nest data, are used to assess habitat quality (e.g. Weinberg & Roth 1998), model population dynamics (e.g. Podolski *et al.* 2007), identify source and sink populations (e.g. Donovan *et al.* 1995), and inform conservation and management plans (e.g. Woodworth 1999). Although songbird population growth may be generally more sensitive to adult annual survival and fledgling survival (Donovan & Thompson 2001, Streby & Andersen 2011), population growth is also sensitive to variation in nest success (Donovan *et al.* 1995), and nest success is the only directly estimated parameter in most studies of songbird reproductive success (Anders *et al.* 1997). Many population models account for re-nesting (birds nesting again after initial failure) and estimates of nest productivity (number of young produced per successful nest). All such studies require accurate field identification of whether each monitored nest succeeded or failed in producing young. However, observational studies of songbird nests often

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depend on several assumptions that potentially bias results. Here we address two such assumptions that are critical because they deal with the determination of whether nesting attempts succeeded or failed when fledging events were not observed.

First, it is often difficult to determine the fate of a nest that is found empty on or near the date young are expected to fledge. Nest-monitoring protocols recommend that nests be checked from a distance daily, starting the day before expected fledging (Ralph *et al.* 1993). However, daily checks are not always possible due to logistical constraints, inclement weather or disturbance risk, and it is difficult to ascertain the fate of an empty nest regardless of how often it was visited.

Excluding nests with uncertain fates from analyses can cause a downward bias in nest success estimates that assume constant daily survival (Manolis *et al.* 2000). Manolis *et al.* (2000) used simulation models to determine the most effective treatment of uncertain nest fates in estimation of nest success. They found the least bias when terminating exposure (number of days a nest is observed active) with the last observation the nest was active for nests with uncertain fates. However, some bias remains if the probability of failure during the final interval differs between nests with known or uncertain fates. If the signs of failure or success are more obvious (i.e. more easily determined), or more likely to be incorrectly identified during observations of empty nests, bias in the direction of the more easily determined fate will increase as a function of the proportion of uncertain fates in a dataset. In addition, if the probability of predation increases with nestling age, as theory and experimental evidence suggest (Haskell 1994, Martin *et al.* 2000, McDonald *et al.* 2009), even proper treatment of uncertain fates during analysis would underestimate failures and bias nest success estimates upward. Some studies exclude the final days of the nestling period altogether and include all nestlings alive within a few days of the expected fledging date as fledged young (e.g. Murphy 2007), which inherently assumes predation does not occur in the final days before fledging. As nestlings age, parental nest-visit frequency increases (Kluyver 1961), nestling vocalization type changes and volume increases (Khayutin 1985), and the reward to predators (i.e. nestling mass) increases, all of which can increase predation risk (Haskell 1994, Martin *et al.* 2000, McDonald *et al.* 2009). The common assumption that predation risk remains unchanged or is absent during the days immediately preceding fledging therefore contradicts the evidence. Datasets that exclude the final days of the nestling stage or those that include many uncertain fates may produce estimates of nest success biased upward.

Manolis *et al.* (2000) used the Mayfield (1961) method for estimating nest daily survival. This method requires the commonly unrealistic assumption that the exact day of nest failure is known (Heisey *et al.* 2007). Recently developed methods, including those in program MARK (Dinsmore *et al.* 2002) and generalized linear models (Shaffer 2004), incorporate the appropriate likelihood estimator for interval data. However, even the most robust statistical techniques are limited by the quality of the raw data, and all nest survival analyses share the assumption that nest fates are correctly determined (Johnson 2007). Many studies limit the number of nest fates classified as uncertain by examining nest condition for signs of success or failure as suggested by the BBIRD protocol (Martin *et al.* 1997). This 'Nest Condition' method uses a series of rules to make an educated guess about the fate of a nest that is empty on or near the expected fledging date. The rules differ among studies, but a typical summary follows. If a nest is empty prior to the expected fledge date, it is assumed to have failed. If a nest is empty on or after the expected fledge date and there are signs of disturbance to the nest-site (e.g. nest broken or destroyed, broken egg shells, feathers, dead young), the nest is assumed to have failed. If a nest is empty on or after the expected fledge date and there is no sign of predation or disturbance, or there are signs of nest success (e.g. rim of nest flattened, faeces on or near rim of nest), the nest is assumed successful. These rules have been used in studies that consequently report having no uncertain nest fates (e.g. Dalley *et al.* 2009) but their reliability is questionable. For example, Thompson *et al.* (1999) video-monitored songbird nests and found that many that were predated showed no disturbance or evidence of predation. Similarly, Stake *et al.* (2005) found that snake predation of songbird nests increases in frequency late in the nestling stage and usually does not disturb the nest, so could be misinterpreted as fledging. These observations suggest that the Nest Condition method may identify some failed nests as successful, and that treating uncertain nest fates with appropriate statistical considerations may be superior to identifying fates based on the condition of empty nests.

A second common assumption in studies of songbird nest success is that observing a fledgling or family group in a territory is reliable confirmation of a successful nest in that territory (e.g. Vickery *et al.* 1992a, Seagle & Sturtevant 2005). Many studies have circumvented the observation of nests by creating indices of reproductive activity (IRA) using observations during surveys and spot-mapping of territories (e.g. Vickery *et al.* 1992a). Proper application of an IRA requires observer knowledge of species-specific nesting phenology and other natural history characteristics (Vickery *et al.* 1992a). For example, an observation of an adult with food could be a sign of courtship feeding, feeding of an incubating mate, feeding of nestlings, feeding of fledglings, feeding of a brood parasite nestling or fledgling, carrying food to caching sites, or simply a prey item that requires extended handling time. Even if an observer has sufficient knowledge to interpret such activities during the nesting period, little is known about movement and habitat use for most songbird species during the post-fledging period (Anders *et al.* 1998). In particular, if fledglings move off their natal territory and into neighbouring territories soon after fledging, they could cause one to assume the nest in the neighbouring territory was successful. For example, the majority of Dickcissel *Spiza americana* (Berkeley *et al.* 2007) and Lark Bunting *Calamospiza melanocorys* (Yackel Adams *et al.* 2001) fledglings were > 100 m and > 250 m from nests, respectively, within the first week after fledging. The assumption that a fledgling or family group in a territory containing a nest that recently contained nestlings confirms fledging of that nest remains untested.

We studied a population of breeding Ovenbirds *Seiurus aurocapilla* in north-central Minnesota and a population of breeding Golden-winged Warblers *Vermivora chrysoptera* in north-western Minnesota, USA, and assessed whether: (1) the condition of an empty nest on or near its expected fledge date is a reliable indicator of nest fate; and (2) the presence of a fledgling or family group within a nesting territory is a reliable confirmation of a successful nesting attempt within that territory. We monitored conditions of nests and used radio-telemetry to monitor survival and movements of juvenile Ovenbirds and Golden-winged Warblers through expected fledging dates and the early post-fledging period. We expected the proportion of nest fates determined incorrectly by nest condition alone to be small but still potentially a source of bias. We further expected most fledglings to remain within or near nesting territories for at least a few days after fledging.

METHODS

Study area

We studied Ovenbirds during May–July 2007 and 2008 at two study sites in the Chippewa National Forest (CNF: 47°31′N, 94°16′W) in north-central Minnesota, and Golden-winged Warblers during May–July 2011 at Tamarac National Wildlife Refuge (Tamarac NWR: 47°02′N, 95°35′W) in north–western Minnesota. Both species are ground-nesting, primarily insectivorous Neotropical migratory wood warblers (Parulidae); Ovenbirds nest primarily in mature forest, and Golden-winged Warblers nest primarily in early successional forest and other open shrubby areas within a forested landscape. The CNF encompasses ~600 000 ha of Cass and Itasca Counties in the northern hardwood–coniferous forest transition zone. Mature forest stands, in which we studied nesting Ovenbirds, were over 50 years after harvest, more than 200 ha in area, ranged from mostly coniferous to mostly deciduous, and were primarily composed of Red Pine *Pinus resinosa*, Sugar Maple *Acer sacharum*, American Basswood *Tilia americana*, aspens *Populus* spp., birches *Betula* spp., White Pine *Pinus strobus* and Northern White-cedar *Thuja occidentalis*.

Tamarac NWR encompasses ~17 000 ha of primarily deciduous forest, interspersed with lakes, grasslands, shrubby wetlands and early-successional forest stands of various ages. Early-successional forest stands, in which we studied nesting Golden-winged Warblers, were 5–15 years after harvest, 10–30 ha in area, and were primarily composed of hazel *Corylus* spp., aspen, birch, sedges and forbs. We also monitored Golden-winged Warbler nests in shrubby wetlands that ranged from 3 to 20 ha and were dominated by alder *Alnus* spp., hazels, and Tamarack *Larix laricina*.

Nest monitoring

We searched for and monitored Ovenbird nests in eight 10-ha plots at each of two study sites. We randomly established each 10-ha nest-searching plot within mature-forest stands to minimize non-independence among nests and broods we monitored. We searched for and monitored Golden-winged Warbler nests in four early-successional forest stands and four shrubby wetlands during the 2011 breeding season. In addition, we captured female Golden-winged Warblers during May 2011, fitted them with radio-transmitters and monitored nests we found by tracking radio-marked females. For both species, we searched each plot every 4 days and visited nests at 4-day intervals. We made more frequent visits (every 1–2 days) during periods of egg-laying and expected hatching to predict the date of fledging. To reduce disturbance of nest-sites, we took different paths to and from nests during each visit, and we sometimes ($\sim$10% of observations) observed nests remotely (> 10 m from nests) with binoculars. We visited each nest 1–2 days before the expected fledging date, removed the nestlings and carried them in a soft cloth bag $\geq$ 10 m from the nest. We ringed all nestlings with numbered aluminium US Geological Survey rings, and attached a radio-transmitter to at least one nestling from each nest. We attached transmitters using a figure-eight harness designed for passerines (Rappole & Tipton 1991). The combined mass of transmitter and harness was 4.3–4.9% of nestling mass. We returned nestlings to their nest within 15 min, and only when no nest predators were seen or heard. We then monitored each nest daily from a distance of several metres until we observed that the nest was empty. Once a nesting attempt was finished, we closely inspected the condition of the nest-site using the Nest Condition method. After determining the fate of a nesting attempt using this method, we then determined the fate (dead or alive) and location of each radio-marked nestling/fledgling. We recorded locations of nests and fledglings using handheld GPS units (100 points averaged, accuracy usually under 5 m).

We fitted logistic exposure models to data we collected using three methods: (1) Telemetry; (2) Nest Condition; and (3) Manolis (Last Active-B in Manolis *et al.* 2000). In all three methods, nests that failed during laying, incubation or early in the nestling period were treated as failures. In the Telemetry method, we determined nest fates based on the fate and location of radio-marked nestlings (tracked after observing nest condition) immediately after the nest was observed empty. In the Nest Condition method, we assigned a fate of failed or successful to each of those nests based on the condition of the nest-site. However, we did not use fledgling activity near an empty nest as a sign of nest success, in contrast to Manolis (1999), because the validity of using fledgling activity as an indicator of nest success is addressed in the telemetry analysis.

Ovenbirds and Golden-winged Warblers in our study populations average a 4-day laying stage, a 12-day incubation stage, and an 8-day (Ovenbirds) and 9.5-day (Golden-winged Warblers) nestling stage, with 10–15% fledging a day earlier and 10–15% fledging a day later (H.M. Streby and D.E. Andersen unpubl. data). For the Nest Condition and Manolis methods, when a previously occupied nest was observed empty on or after the penultimate day of the nestling stage, we used the following rules to determine nest fates based on nest-site condition. If a nest was empty before the penultimate day of the nestling period (i.e. two or more days before the species-specific mean fledging age), we assumed the nesting attempt failed. If a nest was empty on or after the penultimate day and the nest-site was disturbed, we assumed the nesting attempt failed. If a nest was empty on or after the penultimate day and we found any sign of success, we assumed the nesting attempt succeeded. If a nest was empty on or after the penultimate day and the nest-site was not disturbed, we assumed nestlings successfully fledged from the nest (Nest Condition method) or the nest fate was uncertain (Manolis method). These nest-fate determination methods are consistent with the commonly applied BBIRD protocol (Martin *et al.* 1997).

Fledgling monitoring

We used ARC GIS 9.3 (use of trade names does not imply endorsement by either the US Geological Survey or the University of Minnesota) to measure distances from nests for each daily location of marked fledglings to determine if fledglings were inside or outside their natal territory. Although we did not measure territory sizes for Ovenbirds directly, we recorded 5–15 singing males and monitored 4–10 simultaneous nesting attempts per ha in some of our plots. Therefore, using conservative estimates of 4–10 territories/ha, we determined that Ovenbird territories range from 0.10 to 0.25 ha in this population; this is similar to other densely populated regions (e.g. Smith & Shugart

1987). We considered fledgling Ovenbirds to be outside their probable minimum (0.10 ha) and maximum (0.25 ha) territories if the distance between a fledgling and its nest was greater than the radius of a hypothetical exclusive circular territory of each size. Based on point counts, spot mapping, proximity of monitored nests and tracking of radio-marked adults, Golden-winged Warblers nested at *c.* one pair/ha on our study plots at Tamarac NWR (H.M. Streby, D.E. Andersen & J. P. Loegering unpubl. data). We considered fledgling Golden-winged Warblers to be outside their natal territory if the distance between a fledgling and its nest was greater than the radius of a hypothetical exclusive circular 1-ha territory.

Statistical analysis

For each species, we used PROC GENMOD in SAS (SAS Institute 2008) to fit logistic exposure models (Shaffer 2004) to data collected using each of the three methods (Telemetry, Nest Condition and Manolis). The candidate models we considered included a constant survival model and models including all combinations of nest initiation date, nest age and a quadratic term for nest age. We used Akaike's information criterion corrected for small sample size (AIC_C) to rank candidate models, and we report Akaike weights for each best supported model (Burnham & Anderson 2002). Because the Akaike weight of the best supported model was < 0.90 in most cases, we used model-averaged coefficients to calculate daily survival estimates (Burnam & Anderson 2002). We fitted values of daily survival from model-averaged coefficients to visually compare the models produced from each method.

RESULTS

Nest success

Ovenbirds

We monitored 184 Ovenbird nests, 116 (63%) of which contained nestlings during observations 1–2 days prior to their expected fledge date; 68 (37%) nests failed earlier in the nesting period. From the 116 nests that contained nestlings near the expected fledge date, we ringed 375 nestlings and attached transmitters to 130 nestlings. Transmitters fell off 11 nestlings in 11 nests. We found four of those fledged family groups, confirmed identities of ringed fledglings and re-attached transmitters. The fates of the remaining seven nests for which transmitters fell off nestlings were uncertain. Because there was no sign of failure at those seven nest locations, we considered them successful in the Nest Condition method, and uncertain in the Manolis and Telemetry methods.

Using the Telemetry method, we identified 18 failures, 91 successes and seven nests with uncertain fates for the 116 Ovenbird nests that contained nestlings 1–2 days before their expected fledge date. Using the Nest Condition method, we identified 17 failures and 99 successes in the same sample of nests. Of the 99 successful nests in the Nest Condition method, 80 were assumed successful only because there was no sign of failure. Therefore, for the Manolis method, we identified 17 failures, 19 successes and assigned 80 nests uncertain fates (Table 1).

Of fates determined by condition of the 116 nests active during the final visit interval, 11 (9.5%) were incorrectly identified: six as successful and five as failed. Using telemetry, we found dead nestlings (with and without transmitters) or parts of nestlings (i.e. feathers and ringed legs) under leaf litter < 1 m from each of these six undamaged nests. This suggests that predation probably occurred at the nest. Although it is possible that these birds were killed immediately after fledging, thus technically meeting the definition of a successful nest, they nonetheless clearly represent a failed reproductive attempt. In addition, using telemetry, we observed two nests found empty on day 6 after hatching, and three nests that were damaged or destroyed on day 7 or 8 after hatching, but family groups from these nests were subsequently observed (using telemetry) alive.

For all three methods, the best supported model of Ovenbird nest daily survival was the model including linear and quadratic terms for nest age, with Akaike weights of 0.80, 0.53 and 0.91 for the Telemetry, Nest Condition and Manolis methods, respectively. Because similar numbers of Ovenbird nest fates were incorrectly identified as successful and failed, the net bias caused by incorrectly identified fates was relatively small for the Nest Condition method (Fig. 1, Table 1). However, because the nest fates incorrectly identified as successful were considered uncertain in the Manolis method, that method was disproportionately affected by the nest fates incorrectly

Table 1. Estimates of Ovenbird and Golden-winged Warbler nest success from logistic exposure models (using model-averaged coefficients) fitted to data on 184 Ovenbird nests monitored during 2007–2008 in the Chippewa National Forest, Minnesota, and 53 Golden-winged Warbler nests monitored during 2011 at Tamarac National Wildlife Refuge, Minnesota. Each analysis was identical except for the three methods (Telemetry, Nest Condition and Manolis) used to determine fates of nests found empty on or near the expected fledge date.

Species	Method	No. failed (no. incorrect)	No. successful (no. incorrect)	No. uncertain	Nest success estimate[d]	Percentage difference in estimate
Ovenbird	Telemetry[a]	86	91	7	0.427	0
	Nest Condition[b]	85 (5)	99 (6)	0	0.448	+4.9
	Manolis[c]	85 (5)	19	80	0.384	−11.2
Golden-winged Warbler	Telemetry	29	24	0	0.392	0
	Nest Condition	23 (6)	30	0	0.501	+27.8
	Manolis	23	0	30	0.474	+20.9

[a]Nest fates determined by survival of nestlings and fledglings using radiotelemetry. [b]Nest fates determined by condition of nests found empty on or after expected fledge dates. [c]Nest fates determined as in Nest Condition method when predation was evident on nests found empty on or after expected fledge dates, fates of undisturbed empty nests considered uncertain, and exposure for uncertain fates terminated at the end of the last active interval (Last Active B from Manolis *et al.* 2000). [d]Standard Errors of estimates (not shown) were very similar within species, 0.040–0.045 for Ovenbirds and 0.138–0.164 for Golden-winged Warblers.

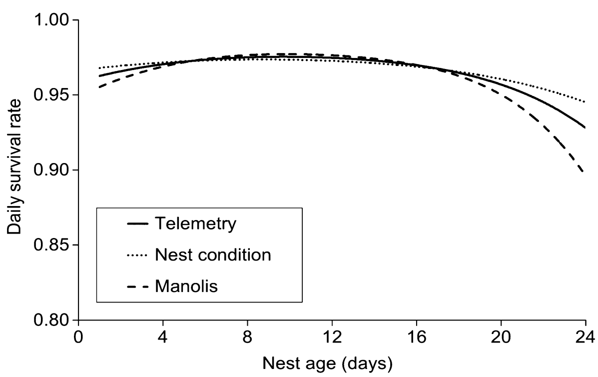

Figure 1. Fitted values from logistic exposure models (from model-averaged coefficients) for data on 184 Ovenbird nests for which fates were determined using three methods (Telemetry, Nest Condition and Manolis) when nests were found empty on or near expected fledge dates. The Manolis method underestimated daily survival because the sample of uncertain nest fates included a disproportionate number of successful nests, resulting from nest failures being more readily identified than nest successes.

determined as failed (Fig. 1) and produced a nest success estimate biased downward (Table 1).

Golden-winged Warblers

We monitored 53 Golden-winged Warbler nests, 30 of which contained nestlings during observations 1–2 days prior to their expected fledge date, whereas 23 (43%) nests failed earlier in the nesting period. From the 30 nests that contained nestlings close to the expected fledge date, we ringed 122 nestlings and attached transmitters to 47 nestlings.

Using the Telemetry method, we identified six failures and 24 successes for the 30 Golden-winged Warbler nests that contained nestlings 1–2 days before their expected fledge date. Using the Nest Condition method, we identified all 30 nests as successful because there was no sign of nest failure at any of those nests. Therefore, we identified all 30 of those nests as having uncertain fates in the Manolis method.

Of fates determined by condition of the 30 nests active during the final visit interval, six (20%) were incorrectly identified: all six failed with no sign of failure at the nest. As with Ovenbirds, using telemetry we found dead nestling Golden-winged Warblers, or parts of nestlings (i.e. feathers and ringed legs), under or on leaf litter < 4 m from each of these six undamaged nests. In addition, we tracked radio-tagged adult female Golden-winged Warblers from those nests and observed them foraging 200–400 m from the nest with no sign of feeding fledglings.

For the Telemetry method, the best-supported model of Golden-winged Warbler nest daily survival included linear and quadratic terms for nest age, with an Akaike weight of 0.60. For the Nest Condition and Manolis methods, the best-supported model included only a linear term for nest age, and had an Akaike weight of 0.48 and 0.57, respectively. Unlike our Ovenbird sample, all incorrectly identified nest fates for Golden-winged Warblers were failed nests that we identified as successful based on nest condition alone, biasing the estimates of nest success from Nest Condition and Manolis methods upward by 28 and 21%, respectively (Fig. 2, Table 1).

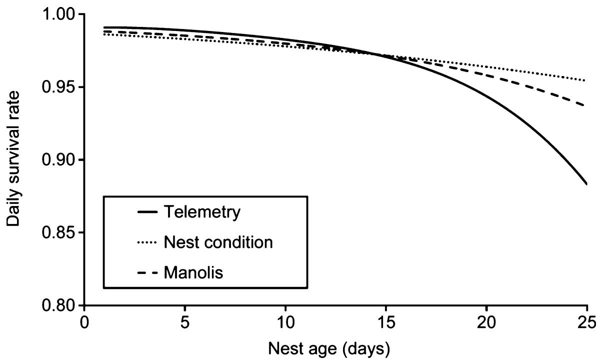

Figure 2. Fitted values from logistic exposure models (from model-averaged coefficients) for data on 53 Golden-winged Warbler nests for which fates were determined using three methods (Telemetry, Nest Condition and Manolis) when nests were found empty on or near expected fledge dates. The Nest Condition and Manolis methods greatly overestimated daily survival because six failed nests were incorrectly identified as successful using those methods.

Fledgling movements

Ovenbirds

We located fledgling Ovenbirds 3–108 m ($\bar{x}$ = 36 m, n = 89) from their nests within 24 h of fledging. This suggests that 58–74% of fledgling Ovenbirds were outside their presumed natal territory within 24 h, based on estimated territory sizes ranging from 0.10 to 0.25 ha (Fig. 3). We located fledgling Ovenbirds 37–174 m ($\bar{x}$ = 117 m, n = 61) from nests within 5 days of fledging and 86–390 m ($\bar{x}$ = 152 m, n = 41) within 10 days of fledging. This suggests that 98 and 100% of fledglings were outside assumed 0.25-ha natal territories within 5 and 10 days of fledging, respectively. We located 8, 17 and 32% of fledgling Ovenbirds outside of the 10-ha plot containing their nest ≤ 24 h, ≤ 5 days and ≤ 10 days after fledging, respectively.

Golden-winged Warblers

We located fledgling Golden-winged Warblers 8–66 m ($\bar{x}$ = 26 m, n = 16) from their nests within 24 h of fledging. This suggests that 13% of fledgling Golden-winged Warblers were outside of their presumed natal territory within 24 h of fledging (Fig. 4). We located fledgling Golden-winged Warblers 25–346 m ($\bar{x}$ = 156 m, n = 13) from nests within 5 days of fledging, and 126–510 m ($\bar{x}$ = 252 m, n = 12) within 10 days of fledging. This suggests that 85 and 100% of fledgling Golden-winged Warblers were outside 1-ha natal territories within 5 and 10 days of fledging, respectively. We located 6, 54 and 83% of fledgling Golden-winged Warblers outside our study plots ≤ 24 h, ≤ 5 days and ≤ 10 days after fledging, respectively.

DISCUSSION

In this study of Ovenbird and Golden-winged Warbler nest success, the use of radiotelemetry to monitor nestlings and fledglings reduced the number of uncertain nest fates, thus also reducing potential bias in nest success estimation. In addition, using radiotelemetry avoided bias from incorrectly determined fates (i.e. nests for which there was evidence of success or failure but where that

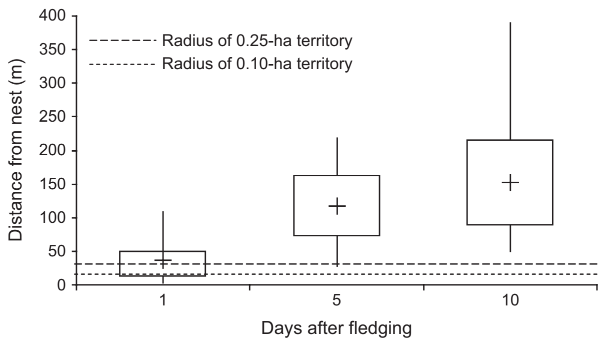

Figure 3. Distances moved from nests by fledgling Ovenbirds within 1 (n = 89), 5 (n = 61) and 10 (n = 41) days after fledging in the Chippewa National Forest, Minnesota. Plus signs, boxes and whiskers represent mean, SD and range, respectively. Dashed lines represent radii of estimated nesting territories of 0.10 and 0.25 ha.

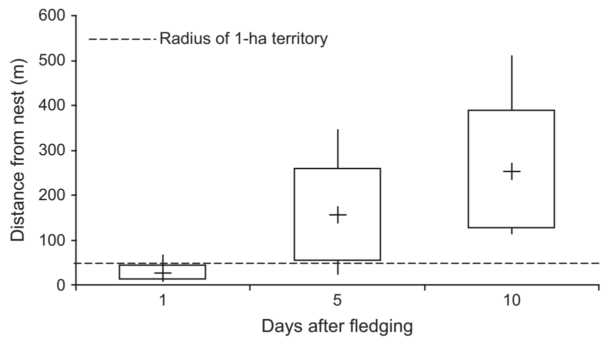

Figure 4. Distances moved from nests by fledgling Golden-winged Warblers within 1 (n = 16), 5 (n = 13) and 10 (n = 12) days after fledging in Tamarac National Wildlife Refuge, Minnesota. Plus signs, boxes and whiskers represent mean, SD and range, respectively. Dashed line represents the radius of an estimated nesting territory of 1.0 ha.

evidence was misleading) based on nest condition alone. Using radiotelemetry, we were able to determine fates of 96% of Ovenbird nests and 100% of Golden-winged Warbler nests, whereas only 57% of nest fates were known correctly without telemetry for each species.

Excluding nests with uncertain fates from nest success estimation is inappropriate (Manolis *et al.* 2000). Observation of the condition of empty nests is often used to determine otherwise uncertain nest fates (e.g. Dalley *et al.* 2009). However, in our study, nest fates were incorrectly determined using nest condition alone for 9.5% of Ovenbird nests and 20% of Golden-winged Warbler nests that contained nestlings near the expected fledge date. Because we did not radiotag all nestlings, it is possible that one or more of the Ovenbird nests for which we determined failure based on telemetry may have experienced partial fledging success. However, for all six Golden-winged Warbler nest failures determined from telemetry, we observed the radiotagged females foraging far from their nests (> 200 m) and not feeding fledglings.

The similarity in Ovenbird nest success estimates produced by the Nest Condition and Telemetry methods obscures the fact that the Nest Condition method included incorrectly identified nest fates. In this study, the Nest Condition method produced an estimate similar to that of the Telemetry method simply because nest successes and failures were similarly likely to be incorrectly assigned. If that were the case in all study populations, incorrectly identified fates in the Nest Condition method would cause little or no net bias in estimates of nest success. However, our estimates of Golden-winged Warbler nest success demonstrate the possible severity of the bias caused by incorrectly determined nest fates when all of those fates are incorrectly determined as either succeeded or failed. Studies of video-monitored nests suggest that incorrectly identified fates are likely to be unbalanced, with failed nests misdiagnosed as successful more often than successful nests are misdiagnosed as failed (Thompson *et al.* 1999, Stake *et al.* 2005), biasing nest success estimates upward as in both of our examples. Another potential problem highlighted by our study is the importance of data from the laying stage in analyses of nest success. We discovered > 50% of nests on or before the day the first egg was laid (H.M. Streby unpubl. data), and nest survival was lower during the laying stage than in any other period until the end of the nestling stage for Ovenbirds (Fig. 1) but not Golden-winged Warblers (Fig. 2). This suggests that excluding the laying stage from analysis can potentially bias nest success estimates upward even more than excluding only the end of the nestling stage.

One might speculate that our ringing and radio-tagging activities could have attracted predators to nests or made tagged birds more vulnerable to predation, thereby increasing predation in the final days of the nestling period. However, predation rates increased throughout the nestling stage for both species we studied, consistent with nests monitored by video (Stake *et al.* 2005) and with the hypothesis that nest predation increases as nestlings grow and with the increased activity of adults and nestlings (Haskell 1994, Martin *et al.* 2000, McDonald *et al.* 2009). Therefore, when all nestlings alive within a few days prior to fledging are considered fledged (e.g. Murphy 2007), the inherent assumption that predation is either absent or greatly reduced in the final days of the nestling stage is more precarious than our assumption that our activities did not increase predation rates. Importantly, terminating all nest observations at the last active visit ('Early Termination' in Manolis 2000) requires the similarly unsupported assumption that nest failure rates do not increase during the final 1 or 2 days of the nestling stage.

The potential pitfalls of right-censored data in survival analysis, including the consequences of falsely assuming that censoring does not impact survival estimates, have been discussed at length (e.g. Lagakos 1979). It is important to note that incorrectly determined fates cause bias only when either survival or mortality is more likely to be incorrectly identified. However, our Ovenbird example demonstrates that a very small imbalance in incorrectly identified fates can bias an estimate of nest success meaningfully even when the sample size is reasonably large. It is also important to note that imbalances in incorrectly identified fates cause bias, not imprecision, and therefore cannot be compensated for with increased sample size. In other words, samples of nests are likely to include a similar proportion and imbalance of incorrectly identified fates regardless of sample size. The percentage of successful or failed nests with incorrectly determined fates probably varies due to differences among species' nesting ecology, rules used to determine fates and predator groups, and our results demonstrate that these factors can have notable influences on nest success estimates. We cannot presume to know whether other nest success estimates based on the Nest Condition method include a net bias as small as our Ovenbird estimate or as large as our Golden-winged Warbler estimate. However, in many cases a very small range determines whether 95% confidence intervals overlap or statistical tests of differences between estimates are significant, and it is these sometimes small differences on which conclusions about treatment effects (e.g. Manolis *et al.* 2002) or whether populations are sources or sinks (e.g. Confer *et al.* 2010) depend.

We did not include observations of fledglings near a nest as a sign of its success, as is typical in methods not using telemetry (Martin *et al.* 1997). However, our observations of fledgling movements during telemetry work demonstrated the potential for additional bias in nest success estimates when assuming that fledglings near a nest came from that nest. Because most Ovenbirds and some Golden-winged Warblers travelled beyond presumed natal territories within 24 h of leaving the nest, presence of a fledgling or family group within a nesting territory is not confirmation of nest success in that territory for Ovenbirds or Golden-winged Warblers in our study populations. We observed fledglings up to 510 m from their nests within 10 days of fledging, even though fledglings may not appear capable of undertaking movements of that magnitude. Therefore, although an observation of a young fledgling or family group certainly indicates a successful nest, that successful nest may be anywhere within the surrounding 82 ha (in our study populations) if the observed bird fledged 10 days earlier. Ralph *et al.* (1993), Martin and Geupel (1993) and Martin *et al.* (1997) are commonly cited sources for nest-monitoring methodology and each caution that some species move up to 100 m within hours of fledging, and that fledglings from neighbouring territories may be attributed incorrectly to a nest territory. We reiterate that caution, and suggest that observations of fledglings should not be used as indicators of nest success unless fledglings can be individually identified and linked to their nests. If fledgling activity near a nest is used as a sign of success, nest success estimates are likely to be inflated, especially in areas of high nesting density. This effect may be smaller in populations or species with larger territories and less mobile fledglings. However, in a population of Lark Buntings with approximately one pair per hectare (Yackel Adams *et al.* 2006) broods moved 256 m (range 16–800 m) from their nests in the first 7 days after fledging (Yackel Adams *et al.* 2001), suggesting that our study populations are not extreme examples. Furthermore, we photographed development of fledgling Ovenbirds of known age throughout this study (H.M. Streby unpubl. data), and we determined that individual variation in development (especially during the first few days after fledging) limits accurate ageing of fledgling Ovenbirds to a range of 3–4 days. Thus age estimates of unmarked fledglings are unlikely to be useful for determining a range of potential proximity to the nest of origin.

Seagle and Sturtevant (2005) used territory density and post-fledging observations of adults and fledglings within territories to demonstrate that Ovenbird reproductive success is predicted by forest productivity. However, density is not a reliable indicator of habitat quality (Van Horne 1983, Vickery *et al.* 1992b) and our results demonstrated that observed fledglings may not have been produced within 10-ha study plots, and fledglings are more likely than not to be outside natal territories within 24 h of fledging. We suggest that Seagle and Sturtevant (2005) found that Ovenbird post-fledging habitat use, but not necessarily reproductive success, was predicted by forest productivity.

In conclusion, our results demonstrate that using radiotelemetry or other methods of individually identifying fledglings or family groups, rather than using nest condition, can improve accuracy of determination of nest fates, and improve nest success estimates. In the absence of individual identification of fledglings or family groups, our results suggest that treating all nests found empty on or near the expected fledge date, regardless of nest condition, as uncertain fates does not necessarily reduce bias as suggested by Manolis *et al.* (2000), because daily nest survival is rarely constant. In addition, radiotelemetry or other methods of individually identifying birds to confirm nest success within a territory or larger study area provides more accurate estimates of nest success than observations of birds from nests of unknown location. Without knowledge of species-specific post-fledging movements and habitat use, and considering the large movements made by fledglings of species that have been studied (e.g. Yackel Adams *et al.* 2001, Berkeley *et al.* 2007), an observation or capture of a fledgling or family group during the post-fledging period is evidence of no more than the use of the sampled area by that species during that period.

We acknowledge that radiotelemetry and other technology can be costly and time-consuming and may not be available for use in every study. However, due to the potential limitations of nest success studies conducted without such efforts, we suggest that telemetry, nest cameras or some other method should at least be used when possible to test whether their absence results in large bias (e.g. Golden-winged Warblers) in nest success estimates or relatively small bias (e.g. Ovenbirds). It is possible that the net bias caused by incorrectly identified nest fates is inconsequential for many species. Without testing that assumption, however, we are left to question the value of many affordable but potentially inaccurate studies compared with fewer costly but accurate ones.

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