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Retirement investment theory explains patterns in songbird nest-site choice

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When opposing evolutionary selection pressures act on a behavioural trait, the result is often stabilizing selection for an intermediate optimal phenotype, with deviations from the predicted optimum attributed to tracking a moving target, development of behavioural syndromes or shifts in riskiness over an individual's lifetime. We investigated nest-site choice by female golden-winged warblers, and the selection pressures acting on that choice by two fitness components, nest success and fledgling survival. We observed strong and consistent opposing selection pressures on nest-site choice for maximizing these two fitness components, and an abrupt, within-season switch in the fitness component birds prioritize via nest-site choice, dependent on the time remaining for additional nesting attempts. We found that females consistently deviated from the predicted optimal behaviour when choosing nest sites because they can make multiple attempts at one fitness component, nest success, but only one attempt at the subsequent component, fledgling survival. Our results demonstrate a unique natural strategy for balancing opposing selection pressures to maximize total fitness. This time-dependent switch from high to low risk tolerance in nest-site choice maximizes songbird fitness in the same way a well-timed switch in human investor risk tolerance can maximize one's nest egg at retirement. Our results also provide strong evidence for the adaptive nature of songbird nest-site choice, which we suggest has been elusive primarily due to a lack of consideration for fledgling survival.

1. Introduction

Selection pressures acting on a single trait but in opposite directions can result in stabilizing selection for that trait [1–3]. It is not uncommon for selection pressures on individual components of fitness, for example survival of different life stages, to oppose each other [4–6], and the resulting stabilizing selection can optimize an individual's total fitness at the expense of failing to maximize particular components of fitness. When the trait of interest is a behavioural strategy, stabilizing selection can result in all individuals behaving in a similar way, with trait values centred around the optimum phenotype and little variation among individuals or over time [5]. However, theoretical and empirical studies have presented several hypotheses to explain why mean trait values might deviate from the optimum value predicted under pure stabilizing selection. First, environmental variation may cause selection pressures to vary over time, such that the optimal strategy is a moving target (the Red Queen hypothesis [7]). Second, syndromes may develop in which some individuals are consistently conservative in their behavioural strategies while others adopt a bolder, risk-taking strategy (disruptive selection [8–10]). Finally, individuals may change their behaviour over their lifetime, taking greater risks as they age because they have less to lose in terms of future reproductive output [11–14]. In the latter two examples, the population trait mean is centred around the optimum phenotype, but variation in trait values is due to variation

among individuals (behavioural syndromes) or within individuals over a lifetime (increased riskiness with age), even when opposing selection pressures are constant.

Predation is the primary cause of mortality for songbird nests and fledglings [15,16]. Therefore, minimizing risk of nest predation is probably a driver of nest-site choice in avian systems [17]. However, although some positive and negative relationships have been identified, most avian studies have found no relationship between nest-site choice and nest success [16,17], and it is often concluded that nesting habitat selection could be maladaptive in terms of nest success [18]. One explanation for these seemingly incongruous results is that selection for nest sites that optimize one trait, for example nest success, may be opposed by selection acting on other traits, as demonstrated in a variety of non-avian systems (reviewed in [19]). For example, phytophagous lichen moths lay eggs on the species of host plant with the highest nutritional value for late-instar larvae, thus favouring rapid growth of older larvae over high growth rates of early-instar larvae [20]. Similarly, female turtles adjust their nest-site choice to prioritize their own survival over that of their offspring when predation risk increases [6,21]. In some birds, nest sites are chosen to minimize physiological stress on [22–24] or predation risk to [18,25,26] the incubating adult. Although predation on nests and incubating adults is probably rarely independent, nest sites were chosen in all of these examples for reasons other than, or in addition to, maximizing nest or egg survival. Thus, studies attempting to identify nest-site choice variables that predict nest or egg survival in these cases would be likely to yield unclear results because selection for nest or egg survival was not the ultimate driver of nest-site choice.

Logistical constraints historically precluded most research on the fledgling stage (after young leave the nest but remain under adult care; also called the dependent post-fledging period) of songbird systems. However, over the past two decades radio-telemetry micro-technology has made studies of this important life stage feasible for songbirds of all sizes [27,28]. Telemetry studies of fledgling songbirds have demonstrated for many species that habitat used during the post-fledging period differs from that used for nesting [28–30], fledgling survival is typically low in the first few days off the nest [27,28,31], and fledgling survival is directly influenced by nest location [28–31]. These studies demonstrate that it is critical to include the fledgling stage when considering a species's reproductive ecology. Indeed, studies of other taxa have demonstrated that selection for survival of juvenile stages, analogous to the avian fledgling stage, drives nest-site choice (e.g. insects [32], fish [33], amphibians [34] and reptiles [35]). Therefore, we hypothesized that selection for fledgling survival might explain nest-site choice in avian systems as well.

Here, we investigated nest-site choice by female golden-winged warblers throughout the nesting season and examined the relative influences of nest success (i.e. the probability of a nest producing fledglings) and fledgling survival (i.e. the probability of fledglings surviving to complete independence from adult care) on nest-site choice. We considered the selection pressure imposed by predation on the nest and fledgling life stages, which correspond to two different components of an adult's reproductive fitness that must be balanced by females choosing nest sites. As discussed above, predation on adults attending the nest is also an important driver of nest-site choice in some species [25,26,36]. However, because predation on an adult not only results in a failed reproductive attempt, but also precludes all future reproduction [37], and because we observed no evidence of adult mortality at nests in our study, we assumed that adult survival produced negligible variation in nest-site choice in our study system, and we therefore focused only on nest success and fledgling survival. We predicted that the optimal nest site would represent an equal trade-off between opposing selection pressures (i.e. stabilizing selection) on nest success and fledgling survival.

2. Material and methods

We studied golden-winged warblers (*Vermivora chrysoptera*) at three sites in the region of the species's densest breeding populations, spanning approximately 400 km in Minnesota and Manitoba. Sites were Tamarac National Wildlife Refuge (NWR) and Rice Lake NWR in northern Minnesota, USA, and Sandilands Provincial Forest (PF) in southeastern Manitoba, Canada. All sites were generally characterized by a mature forest matrix interspersed with regenerating forest stands of various ages, upland and wetland shrublands, and forested wetlands. Golden-winged warblers used all of those cover types to some degree throughout the breeding season, but nesting was concentrated in the open upland and wetland shrublands, and in adjacent forest. Vegetation at all study sites was reflective of managed northern hardwood–coniferous forests of the region. Shrublands were dominated by shrubs, sedges, grasses, forbs and patches of trees more than 5 m tall, and often contained remnant individual or sparse clusters of mature trees. The upland shrublands were in early stages of regeneration after forest harvest. Some of the shrublands consisted of a mosaic of both upland and wetland areas. The forest surrounding each shrubland was characterized by canopy trees more than 10 m tall, a dense and patchy understorey and shrub-layer, and relatively sparse ground vegetation compared with the shrublands. The shrubland–forest edge was generally abrupt owing to its origin in forest harvest.

Golden-winged warblers are Neotropical migratory songbirds that winter in montane forests from Guatemala to central Venezuela, and breed across the Great Lakes region of the United States and Canada, and along the Appalachian Mountains. Males establish nesting territories, nearly all of which include forest edge and extend more than 40 m on either side of the edge, such that they include both forest and shrubland [38]. The edge, or boundary between forest and shrubland, was generally abrupt and clearly defined at our study sites owing to its origin in forest harvest. Females build small open-cup nests on or very near the ground, typically at the base of grasses, shrubs or stems of sapling trees less than 1 cm in diameter. The species's nesting ecology has been well studied [39]. However, the ecology of its post-fledging stage is virtually unknown, as is true of most passerines [29]. Golden-winged warblers, like many songbirds, are a multi-nesting, single-brooded species, which means they will renest after initial nest failure, but can or will only successfully raise one brood in a breeding season. In our study, individuals renested up to two times after initial nest failure. A typical successful reproductive attempt, from first egg laid to independence of all young, takes 48 days: 24 days from first egg to fledging young from the nest, and 24 days to raise fledglings to complete independence.

Potential and confirmed predators of golden-winged warbler eggs and nestlings at our study sites are mammals, including thirteen-lined ground squirrel (*Ictidomys tridecemlineatus*), eastern chipmunk (*Tamias striatus*), red squirrel (*Tamiasciurus hudsonicus*), striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*) and black bear (*Ursus americanus*), and reptiles, including plains garter snake (*Thamnophis radix*) and common garter snake (*Thamnophis sirtalis*). Fledgling golden-winged warblers are depredated

by the preceding predators as well as avian predators including American crow (*Corvus brachyrhynchos*), blue jay (*Cyanocitta cristata*), red-shouldered hawk (*Buteo lineatus*), broad-winged hawk (*Buteo platypterus*), sharp-shinned hawk (*Accipiter striatus*) and Cooper's hawk (*Accipiter cooperii*).

(a) Data collection

In 2011 and 2012, we used radio telemetry and standard nest-searching methods to locate golden-winged warbler nests. At each of the three study sites, we established four to eight study plots, each composed of a shrub-dominated upland, wetland or a mix of both, as well as the adjacent surrounding forest. After birds arrived from migration, but before most nesting began, we used mist nets to capture female golden-winged warblers. Each day, we placed 20–50 mist nets (each 12 × 2.5 m) throughout at least one study plot and captured birds passively for 3–7 h. We placed nets such that they bisected or paralleled edges and dense shrubby areas commonly used for foraging by warblers (Parulidae) during the pre-breeding period. We fitted a 0.39 g radiotransmitter (3.9–4.3% of body mass) to each captured female golden-winged warbler using a figure-eight harness design modified from Rappole & Tipton [40]. We monitored each female once or twice daily using standard ground-based telemetry methods until we identified her nest site during the building, laying or early incubation stage.

In addition to locating nests by radio-tracking females, from 15 May to 30 June, we searched for nests in each study plot on a 4-day cycle following standard nest-searching protocols [41]. We walked through each plot searching for nests in areas with vegetation structure typical of nest sites of the species [39] and by observing adult behavioural cues. We monitored each nest every 4 days and more often during late incubation to accurately document the hatching date and predict the fledging date. We also attached radiotransmitters to some females whose nests we found during nest-searching. In those cases, we flushed the bird from the nest into a mist net during incubation, radio-marked the bird and monitored it for the remainder of the nesting season. When a nest was depredated, we resumed daily tracking of the female until we found her subsequent nesting attempt, until the transmitter expired or until all known nests were no longer active, after which we assumed no new nests were initiated.

One to three days before the expected fledge date for each nest, we removed the entire brood of nestlings and carried it in a soft cloth bag more than 10 m from the nest. We ringed each nestling with a standard US Geological Survey aluminium legband and fitted transmitters to one to five (usually two) randomly selected nestlings before returning the entire brood to the nest within 15 min. After we attached transmitters to nestlings, we checked nests once or twice daily from a distance of more than 3 m to identify the day and approximate time of fledging. After fledglings left the nest, we located each radio-marked fledgling once daily using ground-based telemetry methods. We first used triangulation to estimate fledgling location, and then carefully approached the transmitter's location to achieve visual confirmation of fledgling fate (dead or alive) and cause of mortality.

We focused analysis on mortality caused by predation, and we censored from survival analysis the few nests that failed and fledglings that died from other causes. Specifically, we excluded nests that failed because females were depredated away from the nest (known from telemetry monitoring; $n = 6$) and fledglings that died due to apparent exposure ($n = 11$) during cold and wet nights. Exposure was a cause of mortality we observed primarily at Sandilands PF and that we assumed was related to the proximity of that site to the species's northern range limit, and not due to local nest-site choice. In addition, we excluded from survival analysis a nest ($n = 1$) and fledglings ($n = 3$) that drowned in an extreme flooding event at Rice Lake NWR, because drowning in the highest water level recorded since the establishment of the refuge in 1935 was probably not related to within-season nest-site choice.

Predation on adult songbirds attending nests is generally uncommon, and its occurrence is usually evident from the presence of adult feathers around a depredated nest [29]. Although we observed evidence of predation on six radio-marked adult females 10–145 m away from their nests, we observed no evidence of predation on females while attending their nest, indicating those mortalities were likely to be independent of nest location. We therefore assumed that female survival was either consistently unimportant in nest-site choice, or, more likely, it was consistently the highest priority, which should produce no discernible variation in nest-site choice. We consequently considered only selection pressures on nest survival and fledgling survival for analysis.

(b) Statistical analysis

We used the logistic exposure method [42] to model nest and fledgling daily survival. The logistic exposure method accounts for the fact that not all nests are found on the initiation date, and incorporates an appropriate likelihood estimator for interval data. In most nesting bird studies, it is necessary to estimate nest success from a model of nest daily survival because apparent success can be biased when not all nests are found on or before the day the first egg is laid [43]. In addition, modelling fledgling survival was necessary in our analysis because we could not track every fledgling from every brood owing to logistical constraints. We fitted nest survival models using PROC GENMOD [44], after initial models showed no effect of year or study site on either nest or fledgling survival. We fitted fledgling survival models in PROC NLMIXED to allow inclusion of a random effect for brood. In a preliminary model-ranking procedure, we used Akaike's information criterion corrected for small sample size (AICc [45]) to rank 14 (nest survival) and 26 (fledgling survival) models including null models, linear and curvilinear effects of nest distance to forest edge, and vegetation characteristics at nest and fledgling locations. The linear model of nest distance to edge was the best-supported model (lowest AICc [45]) for nest and fledgling survival (H. Streby 2011–2012, unpublished data). All other models had $\Delta\text{AICc} > 3.9$ and were therefore not considered competitive [45].

We assessed whether selection pressures were consistent throughout the breeding season by testing for an effect of the interaction between nest-site distance to edge and nest initiation date on both nest success and fledgling survival. We used Wald's χ^2 tests and *t*-tests to assess whether selection patterns (i.e. regression coefficients from daily survival models) were different from zero (i.e. significant) for the general linear models (GLMs) and mixed models, respectively. We calculated period survival, or the probability of a nest succeeding (nest success) or a fledgling surviving to independence from adult care, as daily survival raised to the power of 24, the number of days in each period. We estimated the number of young predicted to be produced (raised to independence from adult care) from a nest site as the product of the probability of nest success, the number of young produced from a successful nest and the probability of a fledgling surviving to independence from adult care. We then calculated relative total maternal fitness for a female that chooses a nest site at a particular distance to edge as the number of young predicted to be produced from each nest site divided by the mean number of young predicted to be produced from all nest sites.

Our models of nest success (figure 1*a*) and fledgling survival (figure 1*b*) illustrate selection patterns analogous to, but not mathematically equivalent to, selection gradients used in other

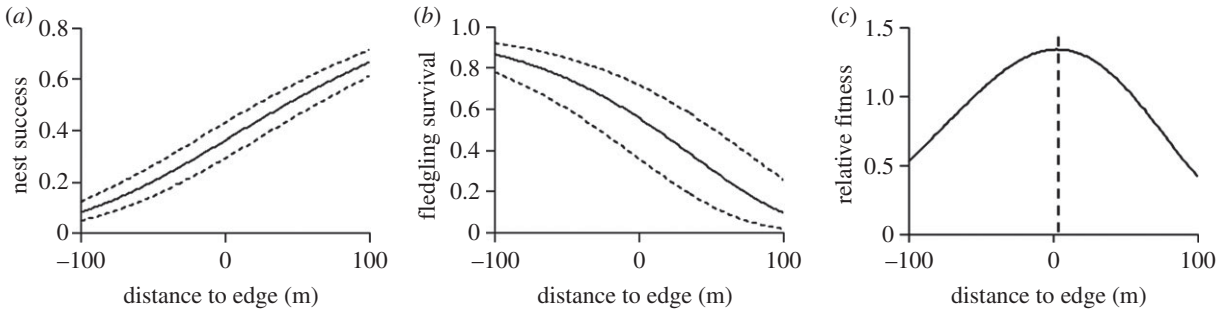

Figure 1. Opposing selection pressures on nest-site choice by female golden-winged warblers with respect to distance from forest edge. Negative distances are in mature forest and positive distances are in shrublands, with zero corresponding to the shrubland–forest edge. An even trade-off between (*a*) the probability of successfully fledging young from a nest and (*b*) the survival probability for fledglings that emerge from that nest results in (*c*) the prediction of stabilizing selection with nest sites close to the forest edge producing the highest relative maternal fitness. The vertical dotted line in (*c*) represents the nest location predicted to maximize relative total fitness, which occurs at +5 m from forest edge.

systems [46,47]. For reasons described above, calculating nest success and fledgling survival from models of nest and fledgling daily survival was necessary. Therefore, calculation of traditional selection gradients was not possible. However, we calculated approximate selection gradients as $1/\hat{W}$ [46], where $\hat{W}$ was mean maternal fitness from our models for each fitness component, to place the patterns of selection we observed in context with similar studies.

We examined the relationship between nest-site distance to forest edge and nest initiation date using linear and quadratic general linear models and a general additive model (GAM) in program R. We ranked the GLMs and GAM using AICc. A GLM with the strongest support (lowest AICc) would indicate a linear or curvilinear relationship between nest-site distance to edge and nest initiation date, and suggest a gradual change in nest-site choice priorities throughout the season. A GAM with strong support may indicate a temporal threshold in nest-site choice, suggesting an abrupt strategy switch as opposed to a gradual change. We used the inflection point of the GAM to separate early and late nesting attempts (figure 2). The inflection point was identified visually and consistently as the same value by seven independent observers. Repeating this analysis with the similar method of piecewise regression produced identical results (H. Streby 2013, unpublished data), but we chose the GAM *a priori* for its superior performance in, among other things, fitting complex curvilinear relationships [48]. We used a Student's *t*-test to compare mean distance from forest edge for early- and late-season nest sites. To avoid bias in nest-site distance to edge associated with standard nest-searching methods (S. Peterson 2010–2012, unpublished data), we included only nests ($n = 95$) found by radio-tracking adult females ($n = 110$) in comparisons of early and late nest-site locations. Those 95 nests included all nests found by radio-tracking females, regardless of nest fate. Owing to the limited battery life of the transmitters (approx. 30 days), and because renesting only occurs after nest failure, we monitored consecutive nesting attempts found using radio telemetry for only 15 females, and six of those renests were initiated during the early nesting period. We used a paired *t*-test to compare mean distance from forest edge for early- and late-season nests for the nine females for which we monitored consecutive nesting attempts initiated during the early and late season. We report regression coefficients ± s.e. We considered all tests significant at $\alpha = 0.05$.

3. Results

We monitored 226 nests and 198 fledglings. Overall, nest sites were distributed approximately normally with respect to edges, with more than 95% of nests placed within 100 m of either side of the edge. Regardless of nest location, golden-winged warblers usually moved their fledglings into forest within 10 days of leaving the nest, or kept them there if the nest was in forest. As is common among songbirds [29], most (85%) fledgling mortality occurred within the first week after leaving the nest.

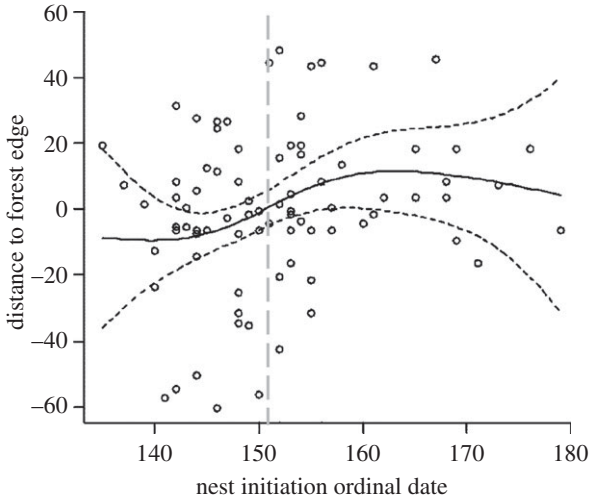

Figure 2. Locations of golden-winged warbler nests initiated throughout the breeding season in the western Great Lakes region, USA. All nests in this analysis ($n = 95$) were found using radio telemetry to track females, removing potential human searching bias. The inflection point (vertical dotted line, ordinal date 151) in the GAM indicates the date of an apparent strategy switch in nest-site choice, whereby nests initiated before that date were close to or in forest and nests initiated on or after that date were generally in shrublands. GAM is presented with 95% CI.

Our models indicated that nest survival did not differ among study sites ($\chi^2 = 0.04$, d.f. = 2, $p = 0.838$) or between years ($\chi^2 = 0.10$, d.f. = 1, $p = 0.755$), and that fledgling survival did not differ among study sites ($t = -0.44$, d.f. = 93, $p = 0.664$) or between years ($t = -0.23$, d.f. = 93, $p = 0.821$). Consistent among sites and years, the selection pattern for nest sites with respect to distance to forest edge was positive (regression coefficient = 0.0093 ± 0.0037) and significant for nest daily survival ($\chi^2 = 6.35$, d.f. = 1, $p = 0.012$), and was negative (regression coefficient = −0.0160 ± 0.0079) and significant for fledgling daily survival ($t = -2.03$, d.f. = 93, $p = 0.045$). These regression coefficients are for models of nest and fledgling daily survival, and are not equivalent to selection gradients [46]. Approximate selection gradients calculated from our models of nest success ($\beta = 0.65$) and

fledgling survival ($\beta = 0.45$) are similar to those from studies on phenotypic traits [49]. The selection patterns we observed illustrate strong opposing selection pressures on nest-site choice for maximizing nest success and maximizing fledgling survival (figure 1*a*,*b*). Mean fledged brood size was 4.2 (± 0.09), which varied slightly among years and sites, but not with respect to nest-site distance to forest edge ($F_{1,93} = 0.18$, $p = 0.668$). Multiplying the probability of successfully nesting by 4.2 (fledglings from a successful nest) and then by the probability of survival to independence for fledglings from nest sites at particular distances from edge, and dividing by the mean total fitness for all nest sites, resulted in highest predicted relative total fitness for females nesting +5 m from forest edge (figure 1*c*).

We found no effect of a nest-site distance to edge × nest initiation date interaction on either nest success ($\chi^2 = 0.08$, d.f. = 1, $p = 0.777$) or fledgling survival ($t = 0.71$, d.f. = 93, $p = 0.480$), indicating that the opposing selection pressures on nest-site choice persisted throughout the breeding season. Therefore, any temporal change in nest-site choice with respect to distance to forest edge probably represents either a gradual change or an abrupt switch in the relative prioritization of selection pressures by the birds. The GAM outperformed the linear and quadratic GLMs (ΔAICc linear = 2.54, ΔAICc quadratic = 2.06, ΔAICc null model = 7.30) for explaining nest-site distance to edge over time with a good fit to the data (GAM approximate fit of smoothed terms, $F = 2.11$, $p = 0.08$), and the shape of the GAM indicated a short-term switch in nest-site choice instead of a gradual change throughout the season (figure 2). The ΔAICc values for the GLMs suggested that they received some support, but the GAM was superior. The inflection point in the GAM was at ordinal day 151, which we considered the estimated switching point. Early nest sites (initiated before day 151) and late nest sites (initiated on or after day 151) were in significantly different locations relative to forest edge ($t = 2.71$, d.f. = 93, $p = 0.008$), with early nests in locations that prioritized fledgling survival over nest success and later nests in locations that prioritized nest success over fledgling survival (figure 3). Although the estimated switching point was day 151, there was variation around that estimate, suggesting the switch may have occurred slightly before or after that date. Moving the switching date forward or backward by 1 or 2 days resulted in similarly significant differences in early and late nest locations (all $p < 0.03$), indicating the switch could have occurred during or across this short period.

The behavioural switch we observed is consistent with time limitation caused by the impending end of the nesting season. The latest nest we observed was initiated on ordinal day 179 (28 June), suggesting that ordinal day 179 is the approximate limit for initiating new nests. The maximum time between subsequent nesting attempts is 28 days if a nest fails on the day before nestlings fledge (nest-cycle day 23) and the next nest is initiated 5 days later (typical from our observations). Therefore, approximately 28 days before ordinal day 179 is the last day a nest can be initiated with certainty that there is time remaining for renesting if that nest fails. In other words, any nest initiated on or after day 151 is likely to be a female's last nesting attempt of the season. Importantly, the switch in nest-site choice we observed was related to a specific time in the nesting season rather than to the number of previous nesting attempts made by a female. Depending on when a nest fails in the 24-day nesting cycle, the final nesting attempt of the season could be a second or a third nest attempt

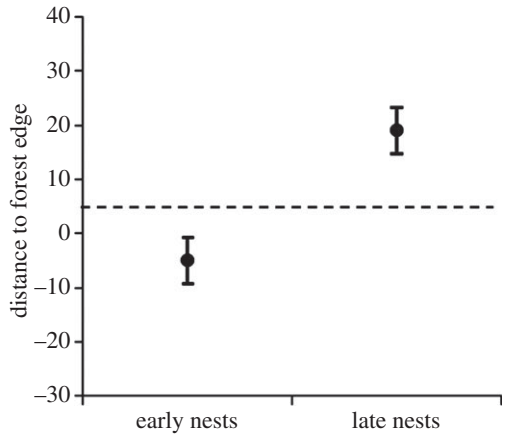

Figure 3. Nest sites (mean ± s.e.) chosen by golden-winged warblers before (early nests) and after (late nests) a risk-tolerance threshold related to the time limitation of the breeding season. Instead of choosing nest sites that optimally balanced opposing selection pressures (dotted line; reproduced from figure 1*c*), early nest sites were in locations that prioritized fledgling survival over nest success, whereas later nest sites were in locations that prioritized nest success over fledgling survival. This significant shift in nest-site choice suggests that individuals risk early nest failure in exchange for greater potential fledgling survival to maximize total maternal fitness, but make relatively conservative choices after early nests fail and time to renest becomes limited, to increase the probability of salvaging moderate total maternal fitness.

for females in our study population. Using radio telemetry, we identified two subsequent nest sites, one initiated before and one initiated after the switching date, for nine individual females. Early nest sites chosen by those females ($\bar{x} = -6 \pm 5$ m from edge) were in significantly different locations relative to edge ($t = 2.34$, d.f. = 8, $p = 0.047$) than their later nest sites ($\bar{x} = 23 \pm 12$ m from edge), confirming that the switch in nest-site choice we observed occurred within individuals and was not indicative of multiple strategies, or syndromes, among individuals. None of these females initiated a nest within 2 days of day 151, so moving the switching date forward or backward 1 or 2 days did not affect this result.

4. Discussion

Golden-winged warblers consistently deviated from the predicted optimal behaviour when choosing nest sites because they could make multiple attempts at one fitness component, nest success, but only one attempt at the subsequent component, fledgling survival. We observed positive selection for nest success with respect to distance to forest edge and negative selection for the survival of fledglings from those same nest locations. That is, nest success was highest in shrublands and lowest in forest, while fledgling survival was lowest from nests in shrublands and highest from nests in forest. Both life stages experienced intermediate survival near edges. These relationships, analogous to selection gradients, illustrate strong opposing selective pressures on nest-site choice for maximizing nest success and maximizing fledgling survival, with the greatest relative total fitness predicted for females that chose nest sites close to forest edge. The opposing selection pressures on nest-site choice persisted throughout the breeding season, but, importantly, females did not balance

these selection pressures evenly throughout the season. Early nest sites were farther into forest, thereby prioritizing fledgling survival, whereas later nest sites were farther away from forest, thereby prioritizing nest success, compared with what was predicted assuming pure stabilizing selection resulting from evenly balancing opposing selection pressures on nest success and fledgling survival.

The within-season switch in nest-site choice was not concurrent with any apparent phenological shift in vegetation structure or food availability. Golden-winged warblers arrived on our study sites during leaf out of trees and shrubs, and vegetation gradually developed throughout the nesting season. There was no apparent change in vegetation structure that co-occurred with the shift in nest-site choice. Golden-winged warblers at our study sites preyed upon leaf-dwelling invertebrates, especially leafroller caterpillars (*Archips* spp.). There was no apparent change in foraging locations used by radio-marked females throughout the nesting season, although they tended to follow a daily pattern of foraging farther from their nest later in the day throughout the nesting season (H. Streby 2010–2012, unpublished data). Therefore, there was no apparent spatial shift in food availability to correspond with the shift in nest-site choice. Additionally, plant phenology, and thus that of leaf-dwelling invertebrates, was more than one week earlier in 2012 than in 2011 across our study sites, and was a few days later at Sandilands PF than at the Minnesota sites in both years. However, the timing of the shift in nest-site choice was consistent among sites and years, indicating its relation to the end of the nesting season regardless of when the nesting season began. There was variation around the estimated switching point in the GAM, suggesting that the switching point may have occurred slightly before or after day 151, or could have occurred over a few days around day 151. We suspect at least some of this variation is due to females taking 5 days between a failed nesting attempt and the initiation of a subsequent nest. This delay between nesting attempts could give the impression of a multi-day period of switching even if the true switching point was on a single day. Regardless of the switch occurring over one day or over a few days, our results indicate that the switch was brief and significant with respect to distance to edge.

The opposing selection pressures were consistent throughout the season; therefore, the switch in the fitness component females prioritized was not consistent with the optimal nest site being a moving target the birds were attempting to track [7]. In addition, the switch in nest-site choice occurred within individuals, which is not consistent with the presence of behavioural syndromes among individuals [8]. Instead, the switch in nest-site choice was consistent with a risk-tolerance threshold, or a switch in the relative prioritization of two fitness components in response to a change in time limitation. Given a successful nest, a female's total reproductive fitness depends entirely on fledgling survival and is represented by the selection pattern illustrated in figure 1*b*. Consequently, there is minimal fitness cost to risking nest failure early in the season, when time to renest is not limited, for the reward of maximizing fledgling survival and thereby maximizing total fitness. But if early nests fail and time to renest becomes limited, the fitness benefit switches to the prioritization of nest success because potential fledgling survival is unimportant if the final nesting attempt fails to produce fledglings.

The period within which nest-site choice switched was brief and occurred 28 days before the last observed nest initiation date. The longest period between consecutive nest initiation dates for this species is 28 days, which corresponds to a nest that fails on the 23rd and final day before fledging plus the typical 5-day period between nest failure and renest initiation. The 28-day threshold for switching nest-site choice to prioritize nest success over fledgling survival thus coincides with the date after which an initiated nest is likely to be an individual's final nest of the season.

We emphasize that the strategy of switching between nest sites with high to low nest predation risk within a season is not inconsistent with strategies in which risky behaviour increases over an individual's lifetime [12]. In such systems, the risk to total fitness is that of adult mortality, which is traded off with some parameter of reproduction such that older animals become more risky with their own lives for the potential reward of reduced risk to their current nest or offspring [11,14]. In our study system, the fitness trade-off is between success of the nest and survival of the fledglings that might emerge from that nest, and the risk-tolerance threshold is associated with adult females facing a time-limited breeding season. Therefore, a switch in priorities between fledgling survival and nest success should be expected during every breeding season, and should occur regardless of a breeding female's age.

Our observation of a risk-tolerance threshold in songbird nest-site choice in response to the time limitation of the breeding season represents a novel perspective on parental investment theory [50]. Traditionally, predictions based on parental investment theory pertain to the quantity or proportion of energy adults allocate to reproduction based on the age, quantity or quality of offspring [50]. Our study demonstrates an additional component of parental investment, wherein adults change the physical location of their energetic investment in reproduction, rather than the amount of investment, to maximize their total fitness. This risk-tolerance threshold is analogous to human retirement investment theory, wherein individuals investing early in their careers can afford to seek greater returns by choosing higher-risk investment options because they have time to recoup losses and even start over if they lose their entire investment [51]. By contrast, individuals time-limited by impending retirement have a lower risk tolerance and instead should make conservative investment choices to ensure modest returns while avoiding great losses. The relationship between time to retirement and investor risk tolerance is non-linear [51], as observed in our study, suggesting that there may be a threshold during which switching from a high- to low-risk strategy is optimal for humans as well. Departures from such a financial strategy, on average, result in a less than optimal nest-egg at retirement. Similarly, departures from the strategy of switching nest locations during the breeding season are likely to result in lower annual and lifetime fitness for songbirds, suggesting that the switching behaviour we observed is adaptive.

Choice of nest site affects a variety of fitness components across multiple life stages in oviparous animals [37], and trade-offs are regularly observed when selection pressures between individual fitness components or on different life stages are in opposition [35,52]. However, when individual fitness components or life stages are studied in isolation, rather than examining all components of an individual's total fitness, the resulting correlations between nest-site choice and proxies for fitness are likely to be incongruous

[16] and yield incomplete conclusions regarding the reasons for and consequences of nest-site choice. Evidence for the adaptive nature of nest-site choice has so far been elusive in bird studies [15,16], but we believe results similar to those found here will be observed in additional avian systems as more studies consider the contribution of fledgling survival to total fitness, and therefore the influence of fledgling survival on nest-site choice.

We collected data following Protocol no. 1004A80575, approved by the University of Minnesota Institutional Animal Care and Use Committee.

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Data accessibility. These data are a product of research conducted by a US federal government employee and they are therefore in the public domain. They are stored and accessible through the Minnesota Cooperative Fish and Wildlife Research Unit.

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