

POPULATION DYNAMICS OF A MIGRANT SONGBIRD:
DO WE NEED TO MONITOR THE ENTIRE BREEDING SEASON?

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The undersigned, appointed by the Dean of the Graduate School, have examined the dissertation entitled

POPULATION DYNAMICS OF A MIGRANT SONGBIRD:
DO WE NEED TO MONITOR THE ENTIRE BREEDING SEASON?

presented by ROBIN HIRSCH-JACOBSON

a candidate for the degree of DOCTOR OF PHILOSOPHY

and hereby certify that in their opinion it is worthy of acceptance.

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ABSTRACT

In Missouri, long-distance migrant songbirds can have relatively long breeding seasons, extending all the way into September for some species. Early models that assessed population status throughout the Midwest determined that forest fragments were population sinks for migrant songbirds. However, these models did not incorporate field data from the entire breeding season, with data collection stopping well before the birds finished breeding. Although newer models have recently been developed to account for longer breeding seasons, for the most part the data used in the models are still only from a subset of the breeding season.

I investigated the breeding of an interior forest, long distance migrant bird, the Acadian Flycatcher (*Empidonax virescens*), in Mid-Missouri to test whether seasonal fecundity is sufficiently high to support viable populations. I evaluated if the inclusion of the late season nests enabled these populations to have higher seasonal fecundity than predicted from a standard field season. However, seasonal fecundity can be difficult data to collect, so I also developed three individual-based models to predict seasonal fecundity, and compared the results of these models with the field data. I also looked at whether a reneest attempt was influenced by the fate of the previous nest attempt.

I found that 89% of females successfully raised at least one brood and 28% of females successfully raised two broods. Acadian Flycatcher females produced at least 37% more female offspring than the standard models

predicted. This results in a population that is nearly stable, as opposed to our current perception that they are a population sink.

The individual-based model that most successfully predicted empirically-derived seasonal fecundity included temporal variation in rates of daily nest survival. This underscores the importance of getting complete data from the entire breeding season, as the model that simply used a point estimate to determine rates of daily nest survival did not perform as well. All three individual-based models predicted observed seasonal fecundity with higher accuracy than any previous individual-based model.

After a failed nest attempt, birds built their next nest higher and further away than after a successful nest attempt. A nesting attempt was also slightly more likely to succeed, though this change was not significant.

This study only looked at the Acadian Flycatcher but the benefits of renesting late into the season should apply to other Mid Missouri long distance migrants as well. The individual-based model can also be adapted to other species and can help us better understand their demography. It is important to note that not all species nest into September. Many cease breeding in July and therefore it is not safe to assume that seasonal fecundity is underestimated for all migrant songbirds. It is critical that large tract of contiguous forests remain.

Chapter 1

THE DEMOGRAPHIC IMPORTANCE OF LATE-SEASON NESTS

ABSTRACT

Interior forest migrant songbirds are thought to be population sinks throughout fragmented Midwest forests. However, we know that the type of models used to predict annual fecundity tend to provide low estimates. Additionally, there is little support for the theory that these populations are receiving any significant rescue effect from populations in more contiguous habitat. We followed Acadian Flycatcher (*Empidonax vireescens*) females throughout the entire breeding season to determine how many young they fledged, as well as how many times they renested, and the percent of females that successfully raised two broods. We hypothesized that traditional models would underestimate the number of young fledged, and that populations of Acadian Flycatchers would be more stable than predicted by traditional models. We found that 89% of Acadian Flycatcher females eventually raised at least one brood. In total, 28% of females raised two broods. Traditional models underestimated annual fecundity by 37%. With standard estimates of adult and juvenile survival, population models predict these populations to be stable, as opposed to population sinks. To obtain accurate estimates of annual fecundity, it is important to follow multiple-brooded songbirds throughout the course of the entire breeding season. Estimates of fecundity derived from a subset of the breeding season can be inaccurate and lead to incorrect management recommendations. It is important to note, that

many birds do not nest late into the breeding season, and that forest habitat does need to be of a minimum size and quality to have a population of breeding migrant songbirds.

INTRODUCTION

Habitat fragmentation throughout the Midwest has resulted in increased rates of nest predation and increased rates of nest parasitism for forest songbirds (Robinson et al. 1995). Consequently, many songbirds in forest fragments have low rates of nest success, which led to the hypothesis that fragmented Midwest forests are population sinks for migrant songbirds (Pulliam 1988, Donovan et al. 1995, Fauth 2000). To determine source-sink status, early studies determined nest success using Mayfield (1961) which also allowed seasonal fecundity to be predicted (Donovan et al. 1995, Fauth 2000). The use of nest success estimates, with or without the inclusion of additional demographic parameters often does not provide accurate predictions of seasonal fecundity as nest success is only weakly correlated with productivity (Dececco et al. 2000, Murray 2000, Thompson et al. 2001, Underwood and Roth 2002). Using nest success data alone to estimate seasonal fecundity tends to underestimate fecundity (Anders and Marshall 2005).

Modeling seasonal fecundity is an integral component for determining songbird population viability (Pulliam 1988). Therefore, it is important to have accurate estimates of fecundity. Methods to estimate seasonal fecundity have evolved over the last fifteen years to account for clutch size, number of re-nesting attempts, multiple broods, and the length of the breeding season (Mayfield 1961,

Pease and Grzybowski 1995, Farnsworth et al. 2001, Grzybowski and Pease 2005). Additionally, logistic exposure (Shaffer 2004) or program MARK (Dinsmore and Dinsmore 2003) allows nest survival to be modeled as a function of covariates. The math behind nest success estimates is not different, so without the inclusion of covariates, Mayfield and logistic exposure will provide similar estimates (Lloyd and Tewksbury 2007). The most accurate method to determine seasonal fecundity is to monitor the nesting activity of breeding pairs throughout the breeding season (Anders and Marshall 2005) as it vastly reduces error associated with modeling clutch size, the number of renesting attempts, and the frequency of multiple broods. It is also important to follow birds throughout the entire season because nest success is often not constant throughout the season (Small et al. 2007, Fisher and Wiebe 2006, Shustack and Rodewald 2010, Hirsch-Jacobson et al. *in review*), which could lead to a biased estimate of nest success. Even an unbiased model to predict seasonal fecundity will be biased if the estimate of nest success is biased (Grzybowski and Pease 2005).

We currently recognize the shortcomings of the methods used to assess the status of Midwest forest songbirds, yet we still consider songbird populations in Missouri fragmented forests as population sinks. These populations are not thought to reproduce at replacement rate, and subsequently they stay afloat due to immigration and dispersal from birds in contiguous habitat (Donovan et al. 1995).

Because nest success tends to underestimate fecundity in areas with high rates of nest failure (Anders and Marshall 2005, Grzybowski and Pease 2005), it

is possible that seasonal fecundity has been underestimated in fragmented forests. Therefore, we hypothesize that they are only population sinks in perception because of inadequate modeling of seasonal fecundity. Even birds that winter in the tropics can have long breeding seasons in the Midwest; for example, Wood Thrush (*Hylocichla mustelina*) can breed from late April to early September (Fink 2003). A long breeding season allows more nesting opportunities and consequently more chances for a female to get off at least one successful clutch. Length of the breeding season has been incorporated in various models to estimate seasonal fecundity (Powell et al. 1999, Farnsworth et al. 2001, Mattsson and Cooper 2007) but it is clear that renesting attempts may have been underestimated when creating the source-sink models (Donovan et al. 1995).

Another benefit of having a long nesting season, other than simply having more time to nest, is that nest success is not constant throughout a breeding season (Norris 1993, Verhulst et al. 1995, Fisher and Wiebe 2006, Small et al. 2007, Wilson et al. 2009, Benson et al. 2010, Shustack and Rodewald 2010, Hirsch-Jacobson et al. *in review*). Breeding throughout a greater period of time increases the chance a bird has an active nest when a nest has the highest chance of success. Additionally, in the Midwest, Acadian Flycatchers (*Empidonax virescens*) have higher rates of nest success later in the season (Shustack and Rodewald 2010, Hirsch-Jacobson et al. *in review*). Studies of other species have also shown that nest success can vary with predator activity

(Sperry et al. 2008), and that predation risk can vary seasonally (Benson et al. 2010).

We investigated the breeding of an interior forest, long distant migrant bird, the Acadian Flycatcher, in Mid-Missouri to test whether we currently underestimate fecundity. We hypothesized that the models that shape our current view underestimated seasonal fecundity and that these populations produce more young annually than the models will predict, which affects the need for a rescue effect in fragmented forests (Brown and Kodric-Brown 1977).

METHODS

Study Sites

We studied breeding biology of the Acadian Flycatcher from 2007 – 2009 in Boone, Callaway, Howard, and Randolph counties in central Missouri. We selected the Acadian Flycatcher, because it is an abundant, territorial species, which breeds from late May through August. The four study sites (Hungry Mother Conservation Area, Rudolph Bennitt Conservation Area, Whetstone Creek Conservation Area are all owned by the Missouri Department of Conservation, and Baskett Wildlife Research and Education Center which is owned by MU) were located in mature oak-hickory forest. These sites were similar in structure and topography, and large enough to contain a sufficient number of Acadian Flycatchers (Table 1). Hungry Mother Conservation Area is characterized by steep slopes, which limit forestry and management. Rudolph Bennitt Conservation Area is managed for wildlife through timber stand improvement and row crops. It is also used for recreation, with a 24-hectare

lake, a shooting range, and a network of horse trails. Whetstone Creek Conservation Area has forest blocks surrounded by old fields, ponds, and cropland. Baskett Wildlife Research and Education Center is a research and education center with forest that has not been logged or burned in over 80 years.

Field Methods

We found and monitored nests from when the Acadian Flycatchers started nesting in late May until they ceased breeding. At the start of the season, we found nests opportunistically using parental behavior. Most nests were found by observing a female with nesting material, or following a female until she returned to a nest with eggs to incubate. Nests were checked every 1-4 days following Martin and Guepel (1993). When possible, we used a mirror pole to determine the contents of the nest during laying (to determine when it was a complete clutch) and to determine hatch day. Otherwise, we monitored nests by observing the female on the nest, observing her return to the nest, observing the number of eggs through the bottom of the nest, or by counting the number of bills hanging over the side of the nest.

Once a nest fledged or failed, we looked for the reneest attempt on the territory. Search efforts were concentrated on getting complete breeding season histories for individual females. Females become less vocal (Hirsch-Jacobson unpub. data) throughout the season, and subsequently nests become progressively more difficult to find. During the second half of the breeding season, we restricted nest searching to females for which we had relatively complete breeding season records, and that did not have an active nest. For the

targeted females, we cannot be sure every nest attempt was found, but we are sure every fledged nest was found for each of our target territories. We are fairly sure that subsequent nesting attempts were appropriately assigned to the correct female as Whitehead and Taylor (2002) found very little movement of breeding adult Acadian Flycatchers within years.

A nest was considered fledged if we found the fledglings, or saw parents delivering food to a location other than the nest. Nests where there was no evidence of fledglings were considered failed, even if timing suggested a fledged nest. We considered the number of young fledged as the number of fledglings we found, not the number of nestlings during the previous nest check.

Statistical Analyses

We calculated the average number of nest attempts and young fledged for each female. We used the logistic exposure method (Shaffer 2004) to estimate how nest survival varied by date. SAS (SAS Institute 2004) was used for all statistical tests. Period survival was calculated by taking the estimate of daily nest survival raised to the average length of the nesting cycle of 31 days (3 laying, 14 incubation, and 14 nestling).

We estimated fecundity using the same method used as Donovan et al. (1995). We used nest success generated from the logistic exposure and raised it to the power of 30 (the length of the nesting cycle) to obtain period survival. We assumed 13.6% of birds would attempt a second brood, the maximum reported rate of attempted double broods for the Acadian Flycatcher (Whitehead and Taylor 2002). We assumed each bird would reneest 2 times after a failed nest

attempt to remain consistent with the approach in Donovan et al. (1995). We assumed nestlings had a 50:50 sex ratio, as has been seen in a population of closely related Willow Flycatchers (*Empidonax traillii*) (Paxton et al. 2002). We compared predicted estimates of seasonal fecundity to observed seasonal fecundity.

We ran a sensitivity analysis to determine what rate of juvenile survival we would need for a stable population ($\lambda = 1$). We held adult survival fixed at .5, .6, and .7, and used both estimated and observed fecundities. This was computed using a simple 2-stage matrix. To generate the error bars we ran the same model using the 95% confidence interval from the predicted seasonal fecundity.

RESULTS

We found 284 Acadian Flycatcher nests from 137 territories (Table 2). Mean clutch size was 2.80 ± 0.051 (mean \pm SD, $n = 173$). In total, 137 of the 284 nests (48%) successfully fledged at least one young. We had complete data (all fledged nests, and most nesting attempts) for 107 of the 137 territories, with the 30 incomplete territories representing females we did not follow throughout the entire season. In the first year, we did not visit Hungry Mother Conservation Area through the entire breeding season, so none of these territories had complete history. Additionally, in subsequent years, we would find as many territories as we could at the start of the year. Once nests began to fledge and fail, we did not have enough time to find renests for every territory. In order to have complete season data for most of the territories, we eliminated some of the territories we monitored.

The average successful nest fledged 1.94 ± 0.64 ($n = 137$) young and, assuming a 50:50 brood sex ration, the average successful nest fledged 0.97 female young. For the territories in which we had full breeding history, the mean number of nesting attempts was 2.29 ± 0.57 , and 94 of the territories (89%) successfully fledged at least one brood. Thirty females (28%) successfully raised a second brood. This is considerably higher than the previously published rate where 13.6% of Acadian Flycatchers attempted a second brood (Whitehead and Taylor 2002).

Using the logistic exposure method, we found an overall daily survival rate of 0.974 and a period survival rate of 48.6%. Daily rates of nest survival increased throughout the season, ranging from 0.954 (95% CI: 0.935 – 0.967) to 0.989 (95% CI: 0.981 – 0.994). This resulted in a period survival that ranged from 23% (95% CI: 13% – 36%) to 71% (95% CI: 55% – 82%) (Figure 1).

Estimating seasonal fecundity using the model in Donovan et al. (1995) suggested females fledged 0.82 (95% CI: 0.75 – 0.87) female young per year. Females actually fledged 1.12 females per year, a difference of 37% (Figure 2). The sensitivity analysis shows how populations can be stable with considerably lower annual survival rates when looking at observed fecundity as opposed to predicted fecundity (Figure 3).

DISCUSSION

In small Missouri forest fragments, most migrant songbirds are absent, have populations consisting of only males, or are at low enough densities that demographic stochasticity may preclude having a sustainable population (Van

Horn et al. 1995). This supports the idea of a minimum area of occurrence and some of the marginal populations may rely on rescue from other populations within the region (Ambuel and Temple 1983, Blake and Karr 1984, Robbins et al. 1989, Wenny et al. 1993). However, for the forest fragments large enough to have a larger number of breeding pairs of migrant songbirds, we may have underestimated seasonal fecundity (Donovan et al. 1995), at least if the Acadian Flycatcher is representative of other migrant forest songbirds. Because measured productivity is 37% more than conventional methods would have predicted, it is possible that these populations are stable, or at worst declining slowly. Therefore, these populations are not as reliant on rescue from populations from the contiguous forest as currently believed, and it is possible that these populations are independently stable.

Observed fecundity is actually a conservative estimate. Thirty of 137 fledged nests had only one fledgling attributed to them. At our sites, it was rare for an Acadian Flycatcher to fledge only one young, even though we recorded 22% of all successful nests to have fledged just one offspring. This is because we determined the number of young fledged by the number of fledglings found. This decision was made because we preferred having our estimates biased low, as opposed to presenting a potentially inflated number of young fledged as would have been the case if we went with last known nest contents. Therefore, seasonal fecundity is most likely higher than reported, and this widens the difference between what was predicted and observed.

This increase in fecundity is largely because both 89% of females eventually had at least one successful nest, and 28% of females successfully raised two broods. Early in the breeding season, period nest survival is estimated at 23% and in the first month of the breeding season, many nests fail. However, in much of the Midwest, for many migrant songbirds, the breeding season continues into September, as seen by Fink (2003) for Wood Thrush, and Morris (2005) for Indigo Buntings (*Passerina cyanea*). This allows multiple opportunities to reneest throughout the season, and more opportunity to attempt second broods. Recognizing that birds have higher nest success late in the season and continue breeding if they have not yet successfully fledged a nest makes it possible that these populations are stable and continue to persist without support from populations in contiguous habitat. However, Acadian Flycatchers that successfully fledged a nest did not breed as late into the summer as a bird that was yet to successfully fledge a nest (Hirsch-Jacobson unpub. data). Temporally variable rates of nest success, high rates of double brooding, and a length of breeding season that is dependent on whether a female has already successfully raised a brood illustrates the importance of following birds throughout the entire season to measure seasonal fecundity. Many of the current models that estimate seasonal fecundity can do so accurately (Farnsworth et al. 2001, Grzybowski and Pease 2005) if the demographics of the species are well understood. This demographic information requires following females throughout an entire breeding season.

There are no good estimates of annual survival for adult or juvenile Acadian Flycatchers or any other members of the genus *Empidonax*. This makes it impossible to determine if this population is a source or a sink. What the sensitivity analysis (Figure 3) shows is that observed seasonal fecundity requires lower rates of annual survival in order to have a stable population compared to the estimated seasonal fecundity. If we assume an adult survival of 0.62 and a juvenile survival of 0.31, numbers typically used as survival estimates for migrant songbirds (Temple and Cary 1988, Howe et al. 1991, Thompson 1993, Donovan et al. 1995), then λ is predicted to be 0.98 for observed fecundity and 0.90 for the predicted fecundity. When looking at population growth over time this is a big difference as the population would be predicted to decline annually by 10% when in reality it is near stable, especially because the number of observed females fledged per female is a conservative estimate.

There are potential costs to nesting later in the breeding season. Breeding is energetically demanding for the parents (Drent and Daan 1980), and a longer breeding season takes a higher toll on a bird's body condition. Potential costs of reproduction are reduced annual survival (Linden and Møller 1989, Graves 1991, Roff 1992, Verhulst et al. 1995, Nilsson and Svensson 1996, Hemborg 1999, Dhondt 2001) and reduced future reproductive success (Gustafsson and Sutherland 1988, Nilsson and Svensson 1996, Wiggins et al. 1998). Nesting late leaves the parents with less time to molt and prepare for migration. However, at least Wood Thrush shorten the duration of molt the later they initiate molting (Vega Rivera et al. 1998). Some of these costs to parents

may be less of an issue in fragmented forests. Indigo Buntings recover body condition more quickly in fragmented sites than they do in contiguous forest sites (Morris 2005).

There are potential costs to the offspring as well. Young fledged later in the season are often smaller (Morton et al. 2009), and size has been correlated with future fecundity (Lindström 1999, Metcalfe and Monaghan 2001). In a population of Great Tits (*Parus major*), males fledged later in the season had reduced fecundity the following breeding season (Visser and Verboven 1999). Therefore, young that fledge later may be less fit than young that fledged earlier. Additionally, young fledged later in the season have less time to prepare for migration. Again, this may not be much of a problem if birds in fragmented landscapes are able to increase their body condition quickly (Morris 2005). One drawback to having fledged early in the season is that there is more time for mortality to occur. This is also probably not much of an issue as post-fledging mortality is generally highest during the first week after fledgling (Anders et al. 1997, Fink 2003 Naef-Daenzer et al. 2001, Cohen and Lindell 2004, Rush and Stutchbury 2008, Ausprey and Rodewald 2011).

Over a quarter (28%) of territories fledged multiple broods. This is surprising, as the highest published rate of attempted double broods in Acadian Flycatchers is 13.6% (Whitehead and Taylor 2002). Because this is an attempted rate, clearly fewer than 13% of parents successfully raised a second brood. It is unclear why rates of double brooding are so much higher in Missouri fragmented forests, but it is clear that the ability for over a quarter of the breeding

birds to produce a second brood significantly contributes to their overall fecundity and their ability to have a stable population. This could be in part because of the available post-breeding habitat and the ease at which parents recover their body condition even if they extend the breeding season. However, in Indiana the birds in the interior forests had higher rates of double brooding whereas the birds on the exterior of the forest had extremely low rates with only 2.5% of birds attempting to double brood (Whitehead and Taylor 2002).

There are clear benefits to breeding late into the season. By breeding through August nearly every female was able to fledge at least one brood. Late season nests may be especially important in areas where there is high nest predation throughout most of the season, with the mortality rates decreasing near the end of the season as observed in fragmented forest habitat. Therefore, migrant forest songbirds such as Wood Thrush and Indigo Bunting with high rates of nest predation but lengthy breeding seasons may also not require rescue from contiguous forests. Preliminary stable isotope data suggests that there is not a substantial rescue from contiguous forest habitat (Faaborg unpub. data). Success rates on these larger fragments may be sufficient to rescue smaller populations in smaller fragments that cannot produce enough young even with multiple nesting attempts.

Not all bird species nest late into the summer. For example, Ovenbirds (*Seiurus aurocapilla*) stop nesting in July and therefore their population growth rates are similar to what would be projected simply using nest success data (Porneluzi and Faaborg 1999). The Louisiana Waterthrush (*Seiurus motacilla*)

also does not breed late into the season and double brooding is extremely rare (Mulvihill et al. 2009). The Louisiana Waterthrush that did attempt a second brood delayed molting by up to 3 weeks (Mulvihill et al. 2009). This delay in molt can have a significant cost, especially for a species that is one of the earliest to arrive on the wintering grounds (Ridgely and Gwynne 1989, Stiles and Skutch 1989) and competes for wintering territories (Mulvihill et al. 2009). In higher latitudes, birds have shorter breeding seasons and may not have the opportunity to keep reneesting or to double brood as many times as the birds in our study. In these shorter breeding seasons, arrival date on the breeding grounds may be a more important factor than frequency of double broods and reneesting attempts (Norris et al. 2004, Smith and Moore 2005).

CONCLUSION

Acadian Flycatchers were more productive than previous methods of estimating fecundity for migrant songbirds in a forest fragment would predict. This difference is not trivial and may have significant impacts on how we view population viability of migrant songbirds in fragmented forests. If we truly are underestimating fecundity for other species as well, like the Wood Thrush, then we may be undervaluing fragmented forest habitat. Two issues must be considered when advocating the increased value of fragmented forests for migrant songbirds. Migrant birds have disappeared from forests that are too small or too low in quality; sites do need to be of a minimum size and quality to maintain a stable population. In addition, not all birds breed late into the summer. For these birds, their populations may indeed be doing as poorly as the

earlier models indicate. Therefore, it is critical that large, contiguous tracts of forest remain, and we must be aware that managers could affect fragment size and cause local extinction.

REFERENCES

- Anders, A. D., D. C. Dearborn, J. Faaborg, and R. T. Frank, III. 1997. Juvenile survival in a population of neotropical migrant birds. *Conservation Biology* **11**:698-707.
- Anders, A. D., and M. R. Marshall. 2005. Increasing the accuracy of productivity and survival estimates in assessing landbird population status. *Conservation Biology* **19**:66-74.
- Ausprey, I. J., and A. D. Rodewald. 2011. Postfledging survivorship and habitat selection across a rural-to-urban landscape gradient. *The Auk* **128**:293-302.
- Benson, T. J., J. D. Brown, and J. C. Bednarz. 2010. Identifying predators clarifies predictors of nest success in a temperate passerine. *Journal of Animal Ecology* **79**:225-234.
- Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: Effect of immigration on extinction. *Ecology* **58**: 445-449.
- Cohen, E. B., C. A. Lindell, and P. C. Stouffer. 2004. Survival, habitat use, and movements of fledgling White-Throated Robins (*Turdus assimilis*) in a Costa Rican agricultural landscape. *The Auk* **121**:404-414.
- Dececco, J. A., M. R. Marshall, A. B. Williams, G. A. Gale, and R. J. Cooper. 2000. Comparative seasonal fecundity of four neotropical migrants in middle appalachia. *The Condor* **102**:653-663.
- Dhondt, A. A. 2001. Trade-offs between reproduction and survival in tits. *Ardea* **89**:155-166.

- Dinsmore, S. J., and J. J. Dinsmore. 2003. Modeling avian nest survival in program mark. *Studies in Avian Biology* **34**: 73-83.
- Donovan, T. M., F. R. Thompson III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. *Conservation Biology* **9**:1380-1395.
- Drent, R. H., and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* **68**:225-252.
- Farnsworth, G. L., T. R. Simons, and J. Brawn. 2001. How many baskets? Clutch sizes that maximize annual fecundity of multiple-brooded birds. *The Auk* **118**:973-982.
- Fauth, P. T. 2000. Reproductive success of Wood Thrushes in forest fragments in Northern Indiana. *The Auk* **117**:194-204.
- Fink, M. L. 2003. Post-fledgling Ecology of Juvenile Wood Thrush in Fragmented and Contiguous Landscapes. PhD. University of Missouri, Columbia.
- Fisher, R., and K. Wiebe. 2006. Nest site attributes and temporal patterns of northern flicker nest loss: effects of predation and competition. *Oecologia* **147**:744-753.
- Graves, J. 1991. Comments on the sample sizes used to test the effect of experimental brood enlargement on adult survival. *The Auk* **108**:967-969.
- Grzybowski, J. A., and C. M. Pease. 2005. Renesting determines seasonal fecundity in songbirds: What do we know? What should we assume? *Auk* **122**:280-292.

- Gustafsson, L., and W. J. Sutherland. 1988. The costs of reproduction in the collared flycatcher (*Ficedula albicollis*). *Nature* **335**:813-815.
- Hemborg, C. 1999. Sexual differences in moult–breeding overlap and female reproductive costs in pied flycatchers, (*Ficedula hypoleuca*). *Journal of Animal Ecology* **68**:429-436.
- Hirsch-Jacobson, R., W. A. Cox, E., Tewes, F. R. Thompson III, J. Faaborg. *In review*. Parents or predators: examining intraseasonal variation in nest survival for a migratory passerine.
- Howe, R. W., G. J. Davis, and V. Mosca. 1991. The demographic significance of "sink" populations. *Biological Conservation* **57**:239-255.
- Linden, M., and A. P. Møller. 1989. Cost of reproduction and covariation of life history traits in birds. *Trends in Ecology & Evolution* **4**:367-371.
- Lindström, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology & Evolution* **14**:343-348.
- Lloyd, J., and J. J. Tewksbury. 2007. Analyzing avian nest survival in forests and grasslands: a comparison of the Mayfield and logistic-exposure methods. *Studies in Avian Biology* **34**:96-104.
- Martin, T. E., and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* **64**:507-519.
- Mattsson, B. J., and R. J. Cooper. 2007. Which life-history components determine breeding productivity for individual songbirds? A case study of the Louisiana Waterthrush (*Seiurus motacilla*). *The Auk* **124**:1186-1200.

- Mayfield, H. 1961. Nesting success calculated from exposure. *The Wilson Bulletin* **73**:255-261.
- Metcalfe, N. B., and P. Monaghan. 2001. Compensation for a bad start: grow now, pay later? *Trends in Ecology & Evolution* **16**:254-260.
- Morris, D. L. 2005. Effects of Forest Fragmentation on Reproductive Effort And Productivity of Indigo Buntings (*Passerina Cyanea*). University of Missouri, Columbia.
- Morton, M. L., M. E. Pereyra, J. D. Crandall, E. A. MacDougall-Shackleton, and T. P. Hahn. 2009. Reproductive effort and return rates in the mountain White-crowned Sparrow. *The Condor* **106**:131-138.
- Murray, B. G. 2000. Measuring annual reproductive success in birds. *The Condor* **102**:470-473.
- Naef-Daenzer, B., F. Widmer, and M. Nuber. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* **70**:730-738.
- Nilsson, J.-A., and E. Svensson. 1996. The cost of reproduction: A new link between current reproductive effort and future reproductive success. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **263**:711-714.
- Norris, K. 1993. Seasonal variation in the reproductive success of Blue Tits: An experimental study. *Journal of Animal Ecology* **62**:287-294.
- Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate

- breeding grounds in a migratory bird. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **271**:59-64.
- Paxton, E. H., M. K. Sogge, T. D. McCarthey, and P. Keim. 2002. Nestling sex ratio in the Southwestern Willow Flycatcher. *The Condor* **104**:877-881.
- Pease, C. M., and J. A. Grzybowski. 1995. Assessing the consequences of brood parasitism and nest predation on seasonal fecundity in passerine birds. *The Auk* **112**:343-363.
- Porneluzi, P. A., and J. Faaborg. 1999. Season-long fecundity, survival, and viability of Ovenbirds in fragmented and unfragmented landscapes. *Conservation Biology* **13**:1151-1161.
- Powell, L. A., M. J. Conroy, D. G. Krementz, and D. L. Jason. 1999. A model to predict breeding-season productivity for multibrooded songbirds. *The Auk* **116**:1001-1008.
- Pulliam, H. R. 1988. Sources, Sinks, and population regulation. *The American Naturalist* **132**:652-661.
- Ridgely, R. S., and J. A. Gwynne. 1989. *A guide to the birds of Panama, with Costa Rica, Nicaragua, and Honduras* 2nd ed. Princeton University Press, Princeton, NJ.
- Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* **267**:1987-1990.
- Roff, D. A. 1992. *The evolution of life histories: theory and analysis*. Chapman & Hall, New York.

- Rush, S. A., and B. J. M. Stutchbury. 2008. Survival of fledgling Hooded Warblers (*Wilsonia citrina*) in small and large forest fragments. *The Auk* **125**:183-191.
- SAS Institute. 2004. SAS/STAT user's guide. Version 9.1. SAS Institute, Inc., Cary, NC.
- Shaffer, T. L. 2004. A unified approach to analyzing nest success. *Auk* **121**:526-540.
- Shustack, D. P., and A. D. Rodewald. 2010. Attenuated nesting Season of the Acadian Flycatcher (*Empidonax vireescens*) in urban forests. *The Auk* **127**:421-429.
- Small, S. L., F. R. Thompson III, G. R. Geupel, and J. Faaborg. 2007. Spotted Towhee population dynamics in a riparian restoration context. *The Condor* **109**:721-732.
- Smith, R. J., and F. R. Moore. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. *Behavioral Ecology and Sociobiology* **57**:231-239.
- Sperry, J. H., R. G. Peak, D. A. Cimprich, and P. J. Weatherhead. 2008. Snake activity affects seasonal variation in nest predation risk for birds. *Journal of Avian Biology* **39**:379-383.
- Stiles, F. G., and A. F. Skutch. 1989. A guide to the birds of Costa Rica. Comstock, Ithaca, NY.
- Temple, S. A., and J. R. Cary. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conservation Biology* **2**:340-347.

- Thompson, B. C., G. E. Knadle, D. L. Brubaker, and K. S. Brubaker. 2001. Nest success is not an adequate comparative estimate of avian reproduction. *Journal of Field Ornithology* **72**:527-536.
- Thompson III, F. R. 1993. Simulated responses of a forest-interior bird population to forest management options in central hardwood forests of the United States. *Conservation Biology* **7**:325-333.
- Underwood, T. J., and R. R. Roth. 2002. Demographic variables are poor indicators of Wood Thrush productivity. *Condor* **104**:92-102.
- Van Horn, M. A., R. M. Gentry, and J. Faaborg. 1995. Patterns of Ovenbird (*Seiurus aurocapillus*) pairing success in Missouri forest tracts. *Auk* **112**:98-106.
- Vega Rivera, J. H., W. J. McShea, J. H. Rappole, and C. A. Haas. 1998. Pattern and chronology of prebasic molt for the Wood Thrush and its relation to reproduction and migration departure. *Wilson Bulletin* **110**:384-392.
- Verhulst, S., J. H. van Balen, and J. M. Tinbergen. 1995. Seasonal decline in reproductive success of the Great Tit: Variation in time or quality? *Ecology* **76**:2392-2403.
- Visser, M. E., and N. Verboven. 1999. Long-term fitness effects of fledging date in Great Tits. *Oikos* **85**:445-450.
- Whitehead, Donald R. and Terry Taylor. 2002. Acadian Flycatcher (*Empidonax virescens*), *The Birds of North America Online* (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu/bna/species/614>

Wiggins, D. A., T. Part, and L. Gustafsson. 1998. Timing of breeding and reproductive costs in Collared Flycatchers. *Auk* **115**:1063–1067.

Wilson, S., K. Martin, and S. J. Hannon. 2009. Nest survival patterns in Willow Ptarmigan: influence of time, nesting stage, and female characteristics. *The Condor* **109**:377-388.

FIGURE LEGENDS

FIGURE 1. Daily nest survival rates for Acadian Flycatchers as a function of date. Survival increases from .954 early in the summer to .989 at the end of the summer.

FIGURE 2. The observed and the predicted number of females fledged per Acadian Flycatcher adult female. The predicted was calculated using nest success data and assumptions about the number of renesting attempts and the frequency of double brooding. The error bars are based on variation in nest success. The observed bar represents the number of fledglings found assuming a brood sex ration of 50:50.

FIGURE 3. A sensitivity analysis where adult survival in Acadian Flycatchers was held fixed at 0.5, 0.6, and 0.7. The model determined the required juvenile survival to have a stable population ($\lambda = 1$) at the predicted and observed fecundities.

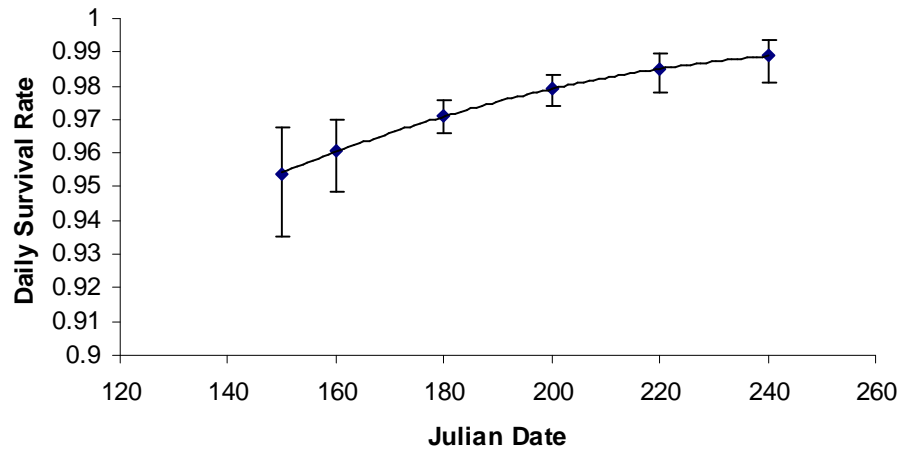


FIGURE 1.

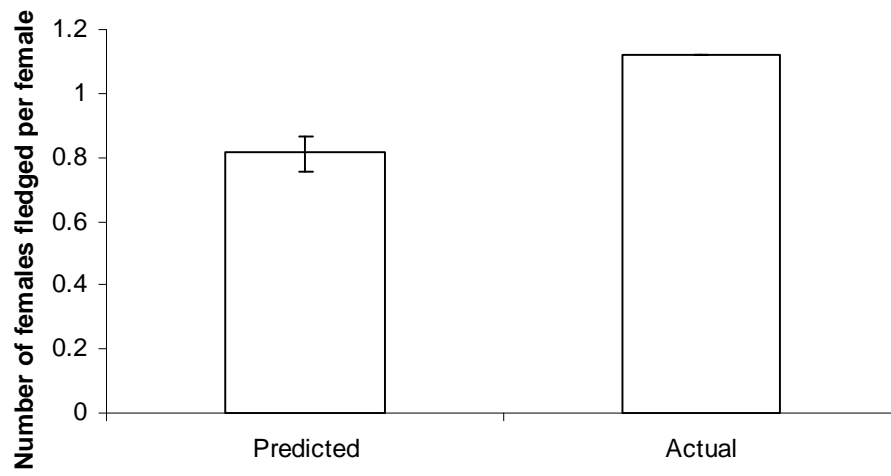


FIGURE 2.

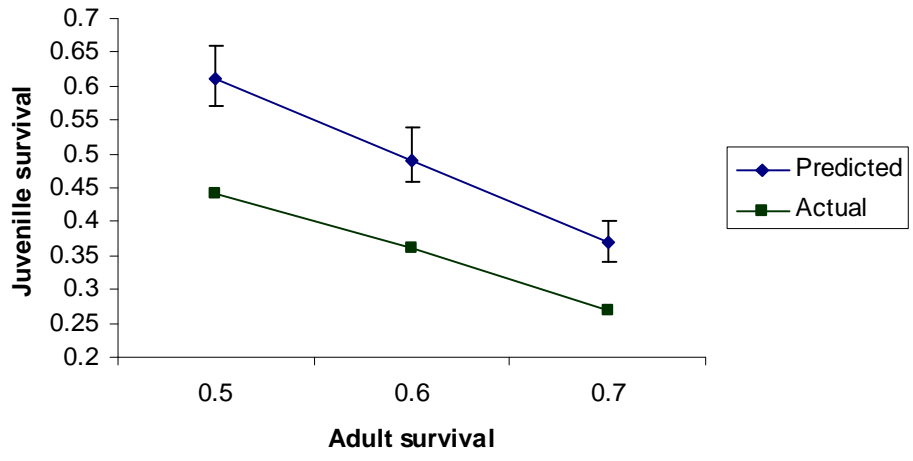


FIGURE 3.

Table 1. Study sites with GPS locations, overall site size, and amount of area that is forested.

Site name and Coordinates	Size (ha)	Forest area (ha)
Baskett Wildlife Area (38° 44'N, 92° 12'W)	917	Most
Rudolph Bennitt Conservation Area (39° 15'N, 92° 28'W)	1446	1146
Whetstone Creek Conservation Area (38°57'N, 91°43'W)	2082	1123
Hungry Mother Conservation Area (39°14'N, 92°33'W)	110	92

TABLE 2. The number of nests and territories of Acadian Flycatchers found at each site for each year.

	2007		2008		2009	
	# of nests	# of territories	# of nests	# of territories	# of nests	# of territories
Baskett	20	10	29	14	37	18
Whetstone	14	10	32	15	31	15
Bennitt	24	12	36	14	22	11
Hungry Mother	XXX	XXX	23	10	16	8

Chapter 2

AN INDIVIDUAL-BASED MODEL TO PREDICT ANNUAL FECUNDITY FOR THE ACADIAN FLYCATCHER: THE IMPORTANCE OF TEMPORAL VARIATION IN DAILY NEST SURVIVAL

ABSTRACT

Seasonal productivity, an important life-history parameter in many animals, is a common parameter used to model their population growth. Most models that predict seasonal fecundity include nest success as one of the demographic parameters. These different models have had various successes, with many of the models seriously under or overestimating productivity. An individual-based model allows there to be stochasticity for each female in a population, and provides the chance to incorporate this variability into estimates of productivity. We built three separate individual-based models of varying complexity to determine the importance of the demographic parameters in predicting productivity, number of nest attempts, and frequency of double broods of the Acadian Flycatcher (*Empidonax vireescens*). The model also limited the breeding season by length, not by a static number of nesting attempts. We hypothesized that these models would accurately predict fecundity, and that increasing complexity would not significantly improve the estimates. We found that the model that included temporal variability in daily nest survival proved the most accurate estimate of productivity, overestimating productivity by less than 1%. We believe that this model is an improvement over most of the models that attempt productivity. To test this model further, it should be modified to predict productivity for other species, in other regions and habitats. If it performs well in

other scenarios, than it could be a powerful tool to predict songbird productivity accurately. Additionally, this model has other potential utilities, which include investigating the importance of population size on long-term population viability.

INTRODUCTION

Seasonal productivity, an important life-history parameter in many animals, is a common parameter used to model their population growth (Pulliam 1988). The most accurate method to determine seasonal fecundity is to follow female birds throughout the entire breeding season, and observe the number of young they fledge (Anders and Marshall 2005, Hirsch-Jacobson *in prep*). In many studies, it is not possible to track females this intensively (Powell and Knutson 2006) as the scale of the project may be too large (Donovan et al. 1995), or birds may make long distance movements between nest attempts (Lang et al. 2002), making it difficult to find renesting attempts without transmitters.

Because it is a challenge to obtain seasonal fecundity from field data, a number of studies have come up with models to estimate seasonal productivity (Pease and Grzybowski 1995, Powell et al. 1999, Farnsworth et al. 2001, Mattsson and Cooper 2007, Etterson et al. 2009). These models require estimates of nest survival and number of young per successful nest; for multi-brooded songbirds estimates of the number of renesting attempts are also required (Thompson et al. 2001). The frequency of double broods also must be included in models to avoid underestimating seasonal productivity (Nagy and Holmes 2004, Nagy et al. 2005) or overestimating it by assuming all birds in a population will attempt a double brood if possible (Donovan et al. 1995, Burke

and Nol 2000, Dececco et al. 2000). To use the modeled estimates of productivity in population growth models, which is often a goal, it is important they include variance estimates (Conroy et al. 1995).

The number of nesting attempts a female will make is rarely known and modeling a fixed number of nesting attempts results in biased estimates of season productivity (Grzybowski and Pease 2005). To account for this bias, Grzybowski and Pease (2005) recommend building a model with a restricted breeding season length rather than an explicit number of re-nest attempts. The only way to know accurately the length is to determine it empirically by following birds throughout the entire breeding season. Otherwise, an estimate of season length leads to a biased prediction, as a shorter or longer estimated breeding season will lead to an under or overestimate of seasonal productivity respectively.

Some studies have used individual-based models to predict seasonal fecundity (Powell et al. 1999, Powell and Knutson 2006, Mattsson and Cooper 2007). An individual-based model can include variability between individuals, as well as temporal variation in breeding parameters. To date, no studies have incorporated temporal variation in an individual-based model to predict avian productivity. However, we know that breeding parameters can vary temporally (Thompson 2007). For example, clutch size (Crick et al. 1993), cowbird parasitism rates (Scott 1963), and nest success (Norris 1993, Verhulst et al. 1995, Fisher and Wiebe 2006, Small et al. 2007, Wilson et al. 2009, Benson et

al. 2010, Shustack and Rodewald 2010, Hirsch-Jacobson et al. *in review*) have all been found to have seasonal variation in passerines.

Models tend to underestimate seasonal fecundity when rates of nest mortality are high (Anders and Marshall 2005, Grzybowski and Pease 2005). This might not hold true if seasonal variation in nest success is included in the models. Acadian Flycatchers (*Empidonax virescens*) in Missouri forests continue nesting through the summer, where it has been recorded that 89% of the females eventually successfully raised at least one brood (Hirsch-Jacobson *in prep*). This is in large part because rates of nest success are higher at the end of the season than the beginning (Shustack and Rodewald 2010, Hirsch-Jacobson et al. *in review*).

A model that predicts seasonal fecundity might contain breeding parameters that are difficult to estimate and can vary temporally. To create a model with high predictive capability, all of the parameters and temporal variability would be included, if they can be accurately estimated. However, not only will this rarely be logistically possible, it will also result in a model that will be difficult to understand (Grimm and Railsback 2005) and too specialized to apply to other populations or species (Burnham and Anderson 1998). On the other hand, a model that incorporates fewer parameters will require fewer data and may have wider inference, but may have low predictive power.

Our objective was to build multiple individual-based models to test how changing the complexity in breeding parameters affected the models' predictions. For this study, we used a population of Acadian Flycatchers in Missouri to

generate the empirical data and test the efficacy of the models. We hypothesized that increased complexity in the models would result in higher predictive power, and that at least one of the models would still perform respectably at a simplified level.

METHODS

Study Sites

We studied breeding biology of the Acadian Flycatcher from 2007 – 2009 in Boone, Callaway, Howard, and Randolph counties in central Missouri. We selected the Acadian Flycatcher, because it is an abundant, territorial species, which breeds from late May through August. The four study sites (Hungry Mother Conservation Area, Rudolph Bennitt Conservation Area, Whetstone Creek Conservation Area are all owned by the Missouri Department of Conservation, and Baskett Wildlife Research and Education Center that is owned by MU) were located in mature oak-hickory forest. These sites were similar in structure and topography, and large enough to contain a sufficient number of Acadian Flycatchers (Table 1). Hungry Mother Conservation Area is characterized by steep slopes, which limit forestry and management. Rudolph Bennitt Conservation Area is managed for wildlife through timber stand improvement and row crops. It is also used for recreation, with a 24-hectare lake, a shooting range, and a network of horse trails. Whetstone Creek Conservation Area has forest blocks surrounded by old fields, ponds, and cropland. Baskett Wildlife Research and Education Center is a research and education center with forest that has not been logged or burned in over 80 years.

Field Methods

We found and monitored nests from when the Acadian Flycatchers started nesting in late May until they ceased breeding. At the start of the season, we found nests opportunistically using parental behavior. Most nests were found by observing a female with nesting material, or following a female until she returned to a nest with eggs to incubate. Nests were checked every 1-4 days following Martin and Guepel (1993). When possible, we used a mirror pole to determine the contents of the nest during laying (to determine when it was a complete clutch) and to determine hatch day. Otherwise, we monitored nests by observing the female on the nest, observing her return to the nest, observing the number of eggs through the bottom of the nest, or by counting the number of bills hanging over the side of the nest.

Once a nest fledged or failed, we looked for the re-nest attempt on the territory. Search efforts were concentrated on getting complete breeding season histories for individual females. Females become less vocal (Hirsch-Jacobson unpub. data) throughout the season, and subsequently nests become progressively more difficult to find. During the second half of the breeding season, we restricted nest searching to females for which we had relatively complete breeding season records, and that did not have an active nest. For the targeted females, we cannot be sure every nest attempt was found, but we are sure every fledged nest was found for each of our target territories. We are confident that subsequent nesting attempts were appropriately assigned to the

correct female as Whitehead and Taylor (2002) found very little movement of breeding adult Acadian Flycatchers within years in Indiana.

A nest was considered fledged if we found the fledglings, or saw parents delivering food to a location other than the nest. Nests where there was no evidence of fledglings were considered failed, even if timing of nest observations suggested a fledged nest. We considered the number of young fledged as the number of fledglings we found, not the number of nestlings recorded during the final nest check.

Model Structure

We developed multiple individual-based models to predict seasonal productivity of the Acadian Flycatcher using MATLAB (MATLAB® 2010). The models simulated the breeding season for an individual female (Figure 1). Females were restricted to a maximum of two successful broods, but were not restricted by a maximum number of nesting attempts. The breeding season length was simulated from 40 – 90 days at iterations of 5 days. The true breeding season lies safely in this range. From the natural population, less than 5% of females who had fledged a successful nest initiated another nest attempt after 15 July (Hirsch-Jacobson unpub. data). Therefore the model restricted females from attempting a second brood if it was later than 15 July (day 48 in the model).

In the model, nest construction took three days (Hirsch-Jacobson pers obs), one egg was laid per day, the nesting cycle was 28 days long (Whitehead and Taylor 2002), and females took one day to initiate a re-nest attempt (Hirsch-Jacobson unpub data). To date, individual-based models that predict seasonal

fecundity estimate the mean number of young fledged with a distribution generated by the variance around the mean (Powell et al. 1999, Powell and Knutson 2006, Mattsson and Cooper 2007). We modeled the number of young fledged in two different ways. In Model 1, we simply used 1.94 young fledged per successful nest, which was the observed mean value for this population (Hirsch-Jacobson *in prep*; the difference in the three models can be seen in Figure 1). In Model 2, instead of using a distribution around the mean number of young fledged per successful nest, we used the actual observed distribution. We felt this was more realistic in that a nest cannot fledge part of a young. In this population of Acadian Flycatchers, 25% of successful nests fledged one young, 58% fledged two, and the remaining 17% fledged three young. We also hoped to include seasonal variation in the number of young fledged, but clutch size in this population of Acadian Flycatchers does not vary seasonally (Hirsch-Jacobson et al. *in review*) so there was no variation to incorporate. In the model, the potential number of young fledged was determined before laying, and was used as the clutch size, with one egg being laid per day. In our study, partial predation was uncommon (Hirsch-Jacobson unpub. data), so we did not have a good estimate for it; therefore it was not included in the models.

Each day the nest was active, the nest had a probability of survival. If it survived, the nest remained active, and continued to the next day. If it survived for 28 days after the clutch was completed, it was considered fledged. In models 1 and 2, we used a daily survival probability of 0.974, which was the point estimate of daily nest survival generated from empirical data (Hirsch-Jacobson et

al. *in review*). For Model 3, we incorporated seasonal variability in nest survival.

Daily nest survival (DNS) was calculated with this equation:

$$\text{DNS} = -0.000003*((\text{SD}+149)^2)+0.0015*((\text{SD}+149))+0.7932.$$

This equation was generated from the same population of Acadian Flycatchers (Hirsch-Jacobson *in prep*), where SD represents the date in the model. Model 3 used the same distribution for the number of young fledged as model 2.

Analysis

We simulated the breeding season for 1000 females for each individual-based model. We assumed nestlings had a 50:50 sex ratio, as has been seen in a population of closely related Willow Flycatchers (*Empidonax traillii*) (Paxton et al. 2002). The output for each model was the mean number of nesting attempts per female, the number of females fledged per female, and the standard deviation and standard error for both. The model also determined the number of females that successfully raised two broods. These values were then compared to the observed values from field data from a population of Acadian Flycatchers (Hirsch-Jacobson *in prep*). The model-predicted values for the number of nesting attempts and the number of females fledged per female were compared to the observed values with a Kruskal-Wallis test. If the test was significant, we then ran a pairwise analysis between each model and the observed value, using a Bonferroni correction to account for multiple pairwise tests. The model-predicted values for the frequency of double broods were compared to the

observed values using logistic regression. The Kruskal-Wallis tests and the logistic regression were performed in SAS (SAS Institute 2004).

RESULTS

Empirical data showed the mean number of females fledged per female was 1.12 ± 0.70 , the mean number of nesting attempts was 2.29 ± 0.57 , and 28% of females successfully raised a second brood (Hirsch-Jacobson *in prep*). In the field, we observed that less than 5% of female Acadian Flycatchers that failed to fledge a brood continued to initiate nest attempts for more than 56 days after their first attempt. The predictions from the three models were compared to the above data.

For a simulated season length of 55 days, there was a significant difference between the observed data and the models estimates of the number of females fledged per female ($F_{3, 3103} = 5.59$, $P = 0.008$). All three model predictions were not different from the real data (Model 1: $F_{1, 1105} = 1.25$, $P = 0.26$, Model 2: $F_{1, 1105} = 1.25$, $P = 0.076$, and Model 3: $F_{1, 1105} = 0.033$, $P = 0.85$). We ran a *post hoc* pairwise test between Model 2 and 3, the lowest and highest predictions) to see if the differences between these models drove the initial significant result. Model 2 and 3 were significantly different ($F_{1, 1998} = 13.26$, $P < 0.0003$). We did not run all pairwise tests because each model simulated 1000 females, and with this sample size, all models were likely to be significantly different from each other. All three models overestimated the mean number of females fledged per female compared to the field data (1.12), with Model 3 being the closest, predicting 1.14 ± 0.79 females fledged per female (Figure 2).

There was a significant difference between the observed data and the models predictions of the number of nesting attempts per female ($F_{3, 3103} = 36.19$, $P < 0.0001$). All three models were significantly different from the real data (Model 1: $F_{1, 1105} = 18.986$, $P < 0.0001$, Model 2: $F_{1, 1105} = 21.33$, $P < 0.0001$, and Model 3: $F_{1, 1105} = 50.42$, $P < 0.0001$). All of the models predicted a higher mean number of nesting attempts per female compared to the field data. Model 2 was the closest to the observed value (2.29), with a prediction of 2.61 ± 0.81 number of nesting attempts per female, although Model 1 had essentially the same prediction (Figure 3).

There was a significant difference between the observed data and the models predictions of the frequency of double broods ($\chi^2_3 = 23.03$, $P < 0.0001$). The only model that did not statistically differ from the real data was Model 2 ($\chi^2_1 = 1.86$, $P = 0.173$). Model 2 most closely predicted the observed frequency of double broods (28%) with a prediction of 30.2% (Observed: 28%, Model 1: 33.2%, Model 3: 23.9%). As the simulated season length increased, so did the predicted number of females fledged per female (Figure 4).

DISCUSSION

The three individual-based models built in this study were similarly structured and used the same dataset, but incorporated the variation in the data differently. Changes in the way the number of young fledged per nest and daily nest survival rates were incorporated had a significant effect on the models' predictions. Interestingly, there was not a model that performed better across all three tested predictions when compared to the field data. Model 3 closely predicted the

empirically derived mean number of females fledged per female, but compared to the other models it did not predict the empirically derived mean number of nesting attempts or the rate of successful double broods as well.

We simulated a breeding season length of 55 days, as that was close to the empirical data for breeding season length. Model 3, when compared to the field data, overestimated the mean number of females fledged per female by only 0.016 fledglings or 1%. Models 1 and 2 overestimated the number of fledged young by 6% and 13% respectively (Figure 1). All three of these models performed well. A similar study used an individual-based model to predict seasonal fecundity of a population of Louisiana Waterthrush (*Seiurus motacilla*), with the model underestimating seasonal productivity by 19% (Mattsson and Cooper 2007). The difference between Model 3 (1.13 young) and Model 2 (1.26 young) is biologically significant. If we assume adult survival is 0.62 and juvenile survival is 0.31 (Temple and Cary 1988, Howe et al. 1991, Thompson 1993, Donovan et al. 1995) model three predicts a slowly declining population ($\lambda = 0.98$) versus a slowly increasing population ($\lambda = 1.01$) that is predicted by model one.

All three models significantly overestimated the mean number of nesting attempts per female compared to the field data (Figure 3). This is not surprising and the model predictions may be closer to reality than the empirical data. In the field, not every nesting attempt was found. We are confident every fledged nest was documented, but there were certainly nesting attempts that failed before we found them. Models 1 and 2 had nearly identical predictions, whereas Model 3

had a larger prediction than the field data. This can be explained by the inclusion of seasonal variation in daily nest survival, which led to high rates of nest mortality early in the simulated breeding season. Presumably, more nests in Model 3 failed early, which resulted in a higher mean number of nesting attempts per female.

When compared to field data, Model 3 underestimated the number of females who successfully raised two broods by over 4%. Seasonal variation in daily nest survival was fit to a linear equation. In reality, a quadratic equation may be more accurate. Very early in the season, daily nest survival is relatively high (Hirsch-Jacobson unpub. data). Shortly after the wave of first nests hatch, there is a spike in nest mortality. If daily nest survival was fit to a quadratic model, this simulated early success might result in more fledged first nest attempts in Model 3. This should also result in a lower, more accurate estimate due to the mean number of nesting attempts per female.

It is no surprise that the number of females fledged per female is predicted to increase as season length increases (Figure 4). A longer season leaves more opportunities to renest, and more time to fledge offspring. Powell et al. (1999) found that variation in season length was not as important to fecundity as other breeding parameters such as nesting success and adult and juvenile survival. Even though an increase in breeding season length may not be as important as other parameters in the number of young produced, season length is still an important demographic factor. This may be especially true for short breeding season as the models show season length has the most effect on the number of

young fledged for short breeding seasons (Figure 4). According to model three, a 10-day increase in the breeding season from 45 to 55 days, increases λ by 2%. In a population of American Redstarts (*Setophaga ruticilla*), which have a relatively short breeding season females that arrived earlier, and therefore had a longer breeding season, fledged more young than females that arrived later in the season (Norris et al. 2004). Acadian flycatchers in an urban setting had an attenuated breeding season compared to birds in a rural setting, and the urban birds fledged fewer young than did the rural birds (Shustack and Rodewald 2010).

One needs data from the complete breeding season to get estimates of the number of young fledged per nest, seasonal variation in daily nest survival, the length of the breeding season, and whether females who are yet to fledge young will nest later into the season (compared to females who previously successfully raised a brood). It can be logistically difficult to collect field data at this level of detail (Pease and Grzybowski 1995). However, to accurately model fecundity it is critical to have unbiased estimates of these parameters (Pease and Grzybowski 1995).

Our models did not include measures of juvenile or adult survival in spite of the fact that they are an important component of seasonal fecundity (Powell et al. 1999, Mattsson and Cooper 2007). Currently there are no usable estimates of adult breeding season survival of Acadian Flycatchers, although adult mortality during the breeding season may be negligible. From our field observations, it was extremely rare for a female to disappear in the middle of the breeding

season (Hirsch-Jacobson pers obs), and when they did we could not identify whether the bird moved or died. In a population of Black-throated Blue Warbler (*Dendroica caerulescens*) adult survival through a breeding season was estimated at 0.99 (Silllett and Holmes 2002). Undoubtedly, there is a higher rate of juvenile mortality than adult mortality in the breeding season. A recent study shows that 84% of Acadian Flycatcher fledglings survived for their first 21 days (Ausprey and Rodewald 2011). The inclusion of post-fledgling data would allow fecundity estimates to extend past the direct breeding season, and provide a more complete picture of Acadian Flycatcher breeding life history.

CONCLUSION

The individual-based model (model three) that most closely predicted measured seasonal productivity included seasonal variation in daily nest survival, which we believe underscores the importance of getting complete data from the entire breeding season. Most of the parameters included in these models are relatively easy to calculate, though time intensive to collect. To date, this model has only been tested on one species, the Acadian Flycatcher. To test the strength and utility of the model, it needs to be applied to a variety of species in different habitats. The way the model is structured, it can easily be modified for any species, as well as modified to include temporal variation in any breeding parameter. A more applied utility of the model is that it can examine how demographic stochasticity influences the stability of small populations. We believe individual-based models can be a powerful tool in predicting and

understanding seasonal productivity, but they require data from the entire breeding season to make accurate, meaningful predictions.

REFERENCES

- Anders, A. D., and M. R. Marshall. 2005. Increasing the accuracy of productivity and survival estimates in assessing landbird population status. *Conservation Biology* **19**:66-74.
- Ausprey, I. J., and A. D. Rodewald. 2011. Postfledging survivorship and habitat selection across a rural-to-urban landscape gradient. *The Auk* **128**:293-302.
- Benson, T. J., J. D. Brown, and J. C. Bednarz. 2010. Identifying predators clarifies predictors of nest success in a temperate passerine. *Journal of Animal Ecology* **79**:225-234.
- Burke, D. M., and E. Nol. 2000. Landscape and fragmentation size effects on reproductive success of forest-breeding birds in Ontario. *Ecological Applications* **10**:1749-1761.
- Burnham, K. P., and D. R. Anderson. 1998. Model selection and multimodel inference. A practical information theoretic approach, Second edition. Springer-Verlag, New York.
- Conroy, M. J., Y. Cohen, F. C. James, Y. G. Matsinos, and B. A. Maurer. 1995. Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. *Ecological Applications* **5**:17-19.
- Crick, H. Q. P., D. W. Gibbons, and R. D. Magrath. 1993. Seasonal changes in clutch size in British birds. *Journal of Animal Ecology* **62**:263-273.

- Dececco, J. A., M. R. Marshall, A. B. Williams, G. A. Gale, and R. J. Cooper. 2000. Comparative seasonal fecundity of four neotropical migrants in middle appalachia. *The Condor* **102**:653-663.
- Donovan, T. M., F. R. Thompson III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. *Conservation Biology* **9**:1380-1395.
- Etterson, M. A., R. S. Bennett, E. L. Kershner, and J. W. Walk. 2009. Markov chain estimation of avian seasonal fecundity. *Ecological Applications* **19**:622-630.
- Farnsworth, G. L., T. R. Simons, and J. Brawn. 2001. How many baskets? Clutch sizes that maximize annual fecundity of multiple-brooded birds. *The Auk* **118**:973-982.
- Fisher, R., and K. Wiebe. 2006. Nest site attributes and temporal patterns of northern flicker nest loss: effects of predation and competition. *Oecologia* **147**:744-753.
- Grimm, V., and S. F. Railsback. 2005. Individual-based modeling and ecology. Princeton University Press, Princeton.
- Grzybowski, J. A., and C. M. Pease. 2005. Renesting determines seasonal fecundity in songbirds: What do we know? What should we assume? *Auk* **122**:280-292.
- Hirsch-Jacobson, R., W. A. Cox, E., Tewes, F. R. Thompson III, J. Faaborg. *In review*. Parents or predators: examining intraseasonal variation in nest survival for a migratory passerine.

- Howe, R. W., G. J. Davis, and V. Mosca. 1991. The demographic significance of "sink" populations. *Biological Conservation* **57**:239-255.
- Lang, J. D., L. A. Powell, D. G. Krementz, M. J. Conroy, and T. Grubb. 2002. Wood Thrush movements and habitat use: effects of forest management for Red-Cockaded Woodpeckers. *The Auk* **119**:109-124.
- Martin, T. E., and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* **64**:507-519.
- MATLAB® 2010. Version R2010a. The MathWorks, Natick, MA.
- Mattsson, B. J., and R. J. Cooper. 2007. Which life-history components determine breeding productivity for individual songbirds? A case study of the Louisiana Waterthrush (*Seiurus motacilla*). *The Auk* **124**:1186-1200.
- Nagy, L. R., and R. T. Holmes. 2004. Factors influencing fecundity in migratory songbirds: is nest predation the most important? *Journal of Avian Biology* **35**:487-491.
- Nagy, L. R., R. T. Holmes, and P. C. Stouffer. 2005. To double-brood or not? Individual variation in the reproductive effort in Black-throated Blue Warblers (*Dendroica caerulescens*). *The Auk* **122**:902-914.
- Norris, K. 1993. Seasonal variation in the reproductive success of Blue Tits: an experimental study. *Journal of Animal Ecology* **62**:287-294.
- Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate

- breeding grounds in a migratory bird. Proceedings of the Royal Society of London. Series B: Biological Sciences **271**:59-64.
- Paxton, E. H., M. K. Sogge, T. D. McCarthey, and P. Keim. 2002. Nestling sex ratio in the Southwestern Willow Flycatcher. The Condor **104**:877-881.
- Pease, C. M., and J. A. Grzybowski. 1995. Assessing the consequences of brood parasitism and nest predation on seasonal fecundity in passerine birds. The Auk **112**:343-363.
- Powell, L. A., M. J. Conroy, D. G. Krentz, and D. L. Jason. 1999. A model to predict breeding-season productivity for multibrooded songbirds. The Auk **116**:1001-1008.
- Powell, L. A., and M. G. Knutson. 2006. A productivity model for parasitized, multibrooded songbirds. The Condor **108**:292-300.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. The American Naturalist **132**:652-661.
- SAS Institute. 2004. SAS/STAT user's guide. Version 9.1. SAS Institute, Inc., Cary, NC.
- Scott, D. M. 1963. Changes in the reproductive activity of the Brown-headed Cowbird within the breeding season. The Wilson Bulletin **75**:123-129.
- Shustack, D. P., and A. D. Rodewald. 2010. Attenuated nesting season of the Acadian Flycatcher (*Empidonax virescens*) in urban forests. The Auk **127**:421-429.

- Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* **71**:296-308.
- Small, S. L., F. R. Thompson III, G. R. Geupel, and J. Faaborg. 2007. Spotted Towhee population dynamics in a riparian restoration context. *The Condor* **109**:721-732.
- Temple, S. A., and J. R. Cary. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conservation Biology* **2**:340-347.
- Thompson, B. C., G. E. Knadle, D. L. Brubaker, and K. S. Brubaker. 2001. Nest success is not an adequate comparative estimate of avian reproduction. *Journal of Field Ornithology* **72**:527-536.
- Thompson III, F. R. 1993. Simulated responses of a forest-interior bird population to forest management options in central hardwood forests of the United States. *Conservation Biology* **7**:325-333.
- Thompson III, F. R. 2007. Factors affecting nest predation on forest songbirds in North America. *Ibis* **149**:98-109.
- Verhulst, S., J. H. van Balen, and J. M. Tinbergen. 1995. Seasonal decline in reproductive success of the Great Tit: variation in time or quality? *Ecology* **76**:2392-2403.
- Whitehead, Donald R. and Terry Taylor. 2002. Acadian Flycatcher (*Empidonax virescens*), *The Birds of North America Online* (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu/bna/species/614>

Wilson, S., K. Martin, and S. J. Hannon. 2009. Nest survival patterns in Willow Ptarmigan: influence of time, nesting stage, and female characteristics. *The Condor* **109**:377-388.

FIGURE LEGENDS

FIGURE 1. A flow chart representing the path of a female Acadian Flycatcher through the individual-based model. Clutch size and daily nest survival rates were not modeled the same way in all three models, though the overall structure remained the same.

FIGURE 2. The number of female young fledged per female for observed data as well as all three models. Standard errors are presented with error bars.

FIGURE 3. The number of nesting attempts per female for observed data as well as all three models. Standard errors are presented with error bars.

FIGURE 4. The predicted number of females fledged per female for all three models for a range of season lengths. The typical length of a breeding season for this population of Acadian Flycatchers was 56 days. Standard errors are presented with error bars.

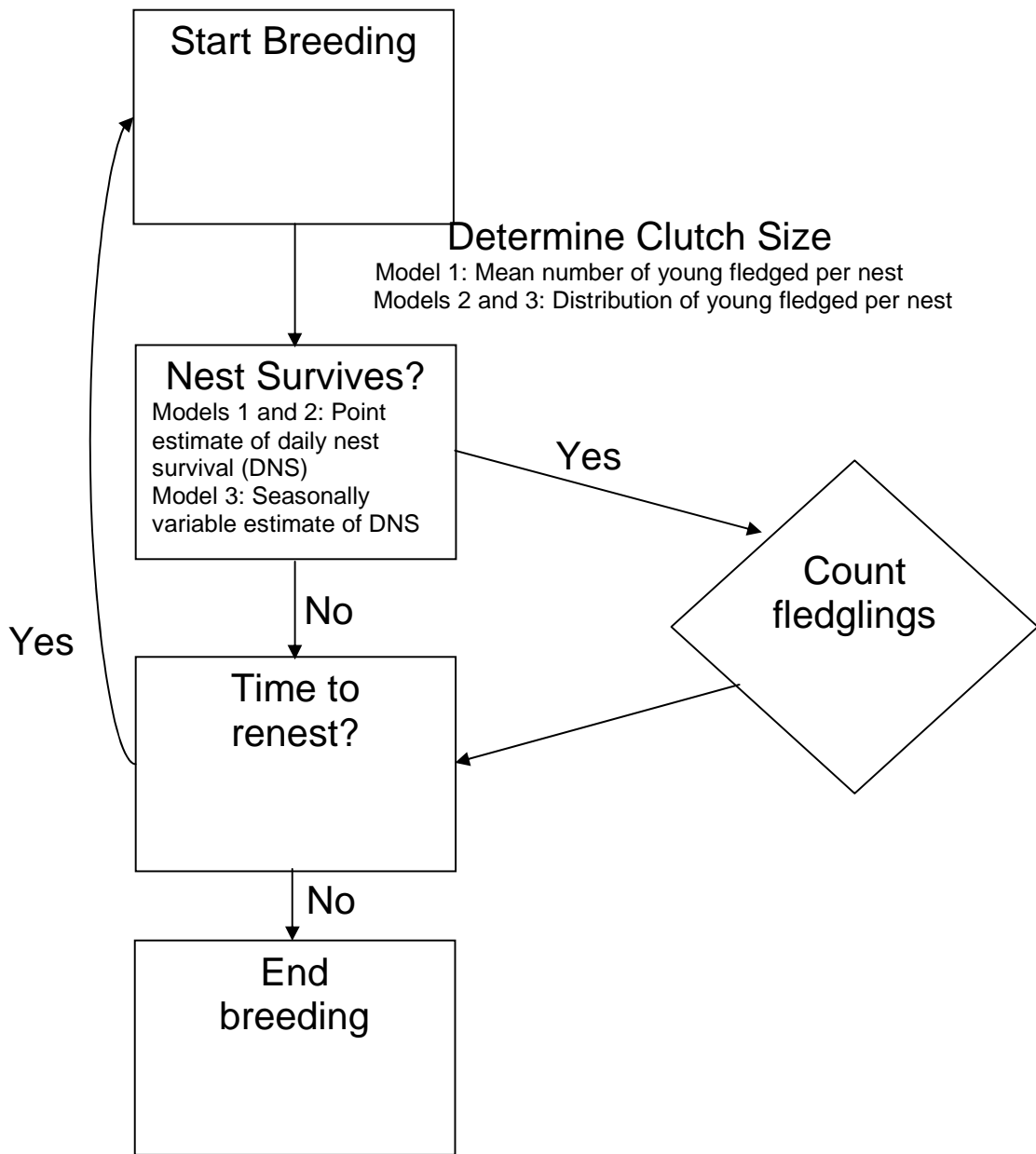


FIGURE 1.

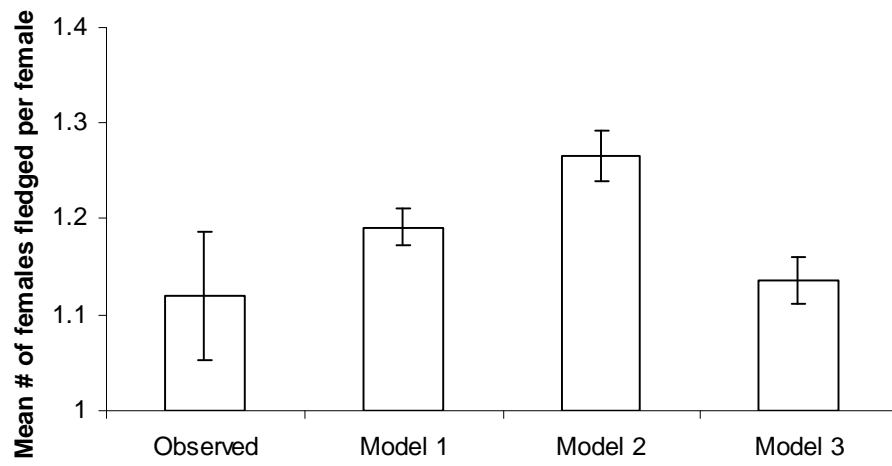


FIGURE 2.

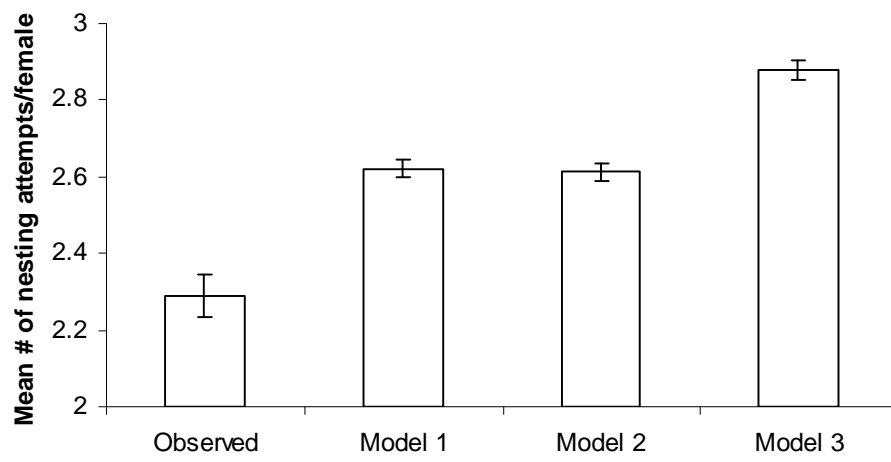


FIGURE 3.

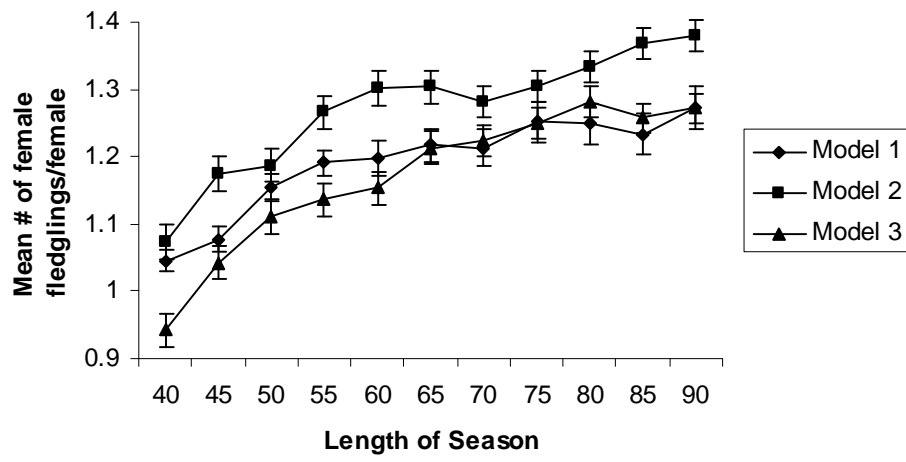


FIGURE 4.

Table 1. Study sites with GPS locations, overall site size, and amount of area that is forested.

Site name and Coordinates	Size (ha)	Forest area (ha)
Baskett Wildlife Area (38° 44'N, 92° 12'W)	917	Most
Rudolph Bennitt Conservation Area (39° 15'N, 92° 28'W)	1446	1146
Whetstone Creek Conservation Area (38°57'N, 91°43'W)	2082	1123
Hungry Mother Conservation Area (39°14'N, 92°33'W)	110	92

Chapter 3

ACADIAN FLYCATCHERS EMPLOY THE “WIN-STAY, LOSE-SWITCH” STRATEGY WITH REGARD TO NEST PLACEMENT

ABSTRACT

Songbirds have the ability to select their nest site. Though they do have some evolutionary constraints, cup nesters generally have a large number of suitable locations within a territory to build a nest. Nest placement can influence nest success, therefore a nest should be placed in a location that minimizes risk of failure. The primary cause of nest mortality for songbird is predation. We examined how previous nest fate affected the nest placement of subsequent nest attempts of the Acadian Flycatcher (*Empidonax virescens*). We hypothesized that the Acadian Flycatchers would employ the “win-stay, lose-switch” strategy and change nest placement after a failed nest attempt, but stay in a similar location following a successful nest attempt. We looked at the distance between nest attempts, as well as the increase in nest height between nest attempts. We also tested if daily nest survival is different following a fledged or a failed nest. We found that after a failed nest attempt, subsequent nests are built higher in the substrate, whereas as following a successful nest attempt, the nest height does not change. Acadian Flycatchers moved greater distances following a failed nest attempt compared to a fledged nest attempt. There was no difference in daily nest survival based on previous nest fate. This shows that Acadian Flycatchers, can show behavioral plasticity in nest placement, and respond when a nest attempt fails. They clearly use the “win-stay, lose-switch” strategy in an effort to minimize future risk of predation.

INTRODUCTION

The selection of nest sites can have profound influence on the reproductive output of an individual bird (Martin and Roper 1988, Martin 1993, Chalfoun and Martin 2009). Most habitat selection components are innate (Hildén 1965) but birds can also exhibit behavioral plasticity when selecting habitat (Greig-Smith 1982, Martin and Martin 2001). Plasticity in nest site selection can reduce the risk of nest predation (Martin 1993, Chalfoun and Martin 2009) which is important as nest predation is the primary cause of reproductive failure (Ricklefs 1969, Martin 1993, Chalfoun and Martin 2009) and a critical factor in the demography of songbirds (Donovan and Thompson 2001).

Birds can assess predation risk and have been found to build more concealed nests (Forstmeier and Weiss 2004, Eggers et al. 2006, Peluc et al. 2008) and reduce visitation rates (Ghalambor and Martin 2000, Ghalambor and Martin 2002, Chalfoun and Martin 2010b) in response to experimentally increased perceived predation risk. The truest assessment of nest predation risk may be after the completion of a nesting attempt, once the nest has either failed or fledged. The “win-stay, lose-switch” strategy states that a bird should change nest location and nest site characteristics after a failed nest while nesting in a similar location with similar properties after a successful nesting attempt (Nowak and Sigmund 1993, Switzer 1993).

Birds can employ the “win-stay, lose-switch” in a variety of ways. They can change nest location as well as other nest site characteristics, and these changes can occur both between breeding seasons or within a breeding season.

Plasticity in nest site characteristics has been seen both in response to perceived predation risk (Marzluff 1988, Eggers et al. 2006, Peluc et al. 2008) and in response to the fate of the previous nest attempt (Chalfoun and Martin 2010a). Studies show that birds move greater distances between nest sites after a failed nest both between years (Greenwood and Harvey 1982, Greig-Smith 1982, Dow and Fredga 1983, Schroeder and Robb 2003) as well as within years (Howlett and Stutchbury 1997, Chalfoun and Martin 2010a, but see Lang et al. 2002). Within-year movement can be across long distances, with Wood Thrush (*Hylocichla mustelina*) pairs moving up to 17 km, although 80% of the Wood Thrush moved less than 1 km between nesting attempts (Lang et al. 2002).

From an evolutionary standpoint, changes in nest site characteristics in response to a failed nest should be in a direction that increases nest success. For example, a nest built higher off the ground can reduce the risk of predation (Burhans et al. 2002). In a population of Brewer's Sparrows (*Spizella breweri*), if the previous nest fledged, daily nest survival was higher when the subsequent nest site was similar to the successful attempt (Chalfoun and Martin 2010a). After a failed attempt, daily nest survival increased as pairs increased the difference in nest site characteristics between nest attempts (Chalfoun and Martin 2010a).

We examined whether the Acadian Flycatcher (*Empidonax virescens*), a migrant songbird, exhibited behavioral plasticity in response to nest predation. We hypothesized that birds would increase nest height and moved subsequent nests farther distances after a failed nest attempt than a successful nest attempt.

For birds utilizing a “win-stay, lose-switch” strategy, we expected to see higher nests and more movement after failed nest attempts than after successful ones. Additionally, some individuals could be more productive with regard to nest placement. Therefore we hypothesized that daily nest success is greater for nests following a successful nest than a failed nest by the same female.

METHODS

Study Sites

We studied breeding biology of the Acadian Flycatcher from 2007 – 2009 in Boone, Callaway, Howard, and Randolph counties in central Missouri. We selected the Acadian Flycatcher because it is an abundant, territorial species, which breeds from late May through August. The Acadian Flycatcher is also a good species for studying re-nest attempts as they are territorial and pairs appear to remain together on a territory throughout the breeding season (Whitehead and Taylor 2002). The four study sites (Hungry Mother Conservation Area, Rudolph Bennitt Conservation Area, Whetstone Creek Conservation Area are all owned by the Missouri Department of Conservation, and Baskett Wildlife Research and Education Center is owned by University of Missouri) supported mature oak-hickory forest. These sites were similar in forest structure and topography, and each contained at least 20 pairs of Acadian Flycatchers (Table 1). Hungry Mother Conservation Area is characterized by steep slopes, which limit forestry and management. Rudolph Bennitt Conservation Area is managed for wildlife through timber stand improvement and row crops. It is also used for recreation, with a 24-hectare lake, a shooting range, and a network of horse trails.

Whetstone Creek Conservation Area has forest blocks surrounded by old fields, ponds, and cropland. Baskett Wildlife Research and Education Center is a research and education center with forest that has not been logged or burned in over 80 years.

Field Methods

We found and monitored nests from when Acadian Flycatchers started nesting in late May until they ceased breeding. At the start of the season, we found nests opportunistically by using parental behavior. Most nests were found by observing a female with nesting material, or following a female until she returned to a nest with eggs to incubate. Nests were checked every 1-4 days following Martin and Guepel (1993). When possible, we used a mirror pole to determine the contents of the nest during laying (to determine when it had a complete clutch) and to determine hatch day. Otherwise, we monitored nests by observing the female on the nest, observing her return to the nest, observing the number of eggs through the bottom of the nest, or by seeing nestlings in the nest. Clutch size is usually 3 (Hirsch-Jacobson et al. *in review*) which made counting young easy.

Once a nest fledged or failed, we looked for the reneest attempt on the territory. Search efforts concentrated on getting complete breeding season histories for individual females. Reneest attempts were classified by the fate of the previous nest attempt, either fledged or failed. Females become less vocal throughout the season (Hirsch-Jacobson unpub. data), and subsequently nests become progressively more difficult to find. We are confident most if not all

subsequent nesting attempts were appropriately assigned to the correct female as Whitehead and Taylor (2002) found very little movement of breeding adult Acadian Flycatchers within years.

A nest was considered fledged if we found the fledglings, or saw parents delivering food to a location other than the nest. Nests where there was no evidence of fledglings were considered failed, even if timing suggested a fledged nest. This was a conservative estimate of nest success as it is possible a few nests fledged where we were unable to locate the fledglings. We measured nest height with an electronic clinometer and the distance between nests with a measuring tape.

Statistical Analyses

We used a generalized linear mixed model for normally distributed data to test if nest height increased more after a failed nest attempt than after a successful one (Proc Mixed, SAS version 9.x, Cary, N.C.). We included site and previous nest fate as fixed effects, and territory and year were included as random effects. We included site as a fixed effect to control for this factor while evaluating the effect of previous nest fate. We included territory and year as random effects to account for possible correlated responses within territories and years. We used the change in nest height as opposed to the absolute nest height. We also tested to see if the distance moved between nest attempts differed after a successful or failed nest attempt. We used the same mixed model as we did for nest height, except we replaced change in height with distance from the previous nest attempt.

To evaluate our hypothesis that daily nest success would be greater for nests following a successful nest than a failed nest we used a logistic exposure model (Shaffer 2004) programmed in Proc genmod (SAS version 9.x, Cary, N.C.). We included a type III analysis within the model to test the significance of the covariates. We also controlled for site, year, and territory in this model. SAS (SAS Institute 2004) was used for all statistical tests.

RESULTS

We found and monitored 297 Acadian Flycatcher nests. We were able to analyze 128 renests from 103 territories; 91 nests followed a failed nest attempt and 37 nests followed a fledged nest attempt (Table 2). For all nests, the average nest height was $5.86 \text{ m} \pm 2.87$ (mean \pm standard deviation) and for all pairs of nests, the average distance moved between nest attempts was $44 \text{ m} \pm 27$.

We excluded 17 nests from the nest height analysis due to observer error in 2008 at Baskett Wildlife Research and Education Center. Both year and location were unimportant factors. Nest height increased more after a failed nest than a fledged nest ($F_{1,21} = 4.35$, $P = 0.049$, $n = 111$). Nest height increased by an average of $0.37 \text{ m} \pm 1.07$ (mean \pm standard error) if the previous nest fledged and nest height increased by an average of $3.19 \text{ m} \pm 0.78$ if the previous nest failed (Figure 1).

A nest was built farther from the previous nest attempt if the previous nest failed ($F_{1,25} = 20.21$, $P = 0.0001$, $n = 128$). Both year and location were unimportant factors. After a fledged nest, females renested on average $28 \text{ m} \pm$

4.07 from the previous nest attempt. After a failed nest, females renested on average $49 \text{ m} \pm 2.86$ away from the previous nest attempt (Figure 2).

Daily nest survival did not differ following a successful nest attempt compared to a failed one ($X^2_1 = 0.96$, $P = 0.3268$, $n = 930$). After a failed nest, estimated daily nest survival was 0.987 (95% CI: 0.979 – 0.992) compared to a daily nest survival of 0.991 (95% CI: 0.981 – 0.996) after a fledged nest (Figure 3).

DISCUSSION

Acadian Flycatchers seem to be employing the “win-stay, lose-switch” strategy. After a nest attempt failed, they increased the height at which they built their next nest, whereas after a successful nest attempt, they did not change the mean nest height at all (Figure 1). For this to be evolutionarily adaptive, this change in nest height should result in a decreased risk of nest predation and therefore an increase in nest success. Higher nest placement is associated with increased rates of nests success in some species (Peluc et al. 2008, Burhans et al. 2010), including a population of Acadian Flycatchers in Arkansas (Wilson and Cooper 1998). However, from the Mid Missouri population of Acadian Flycatchers, nest height was not correlated with nest success (Hirsch-Jacobson et al. *in review*). It is possible that the advantage gained from higher nests was too small of an effect size to be detected in the study, or perhaps this behavioral plasticity is conserved throughout the species, but does not provide a reproductive benefit in this particular habitat. In this population of Acadian Flycatchers, Barred Owls (*Strix varia*), Blue Jays (*Cyanocitta cristata*), and Broad-winged Hawks (*Buteo*

platypterus) are the primary nest predators (Hirsch-Jacobson et al. *in review*).

Avian nest predators are not expected to be affected by nest height as much as terrestrial predators (Schmidt 1999), which could explain why higher nests do not result in increased nest success. It is also possible that higher nests are correlated with a habitat characteristic that we did not measure such as nest concealment, which may be driving this increase in nest height.

Acadian Flycatchers moved significantly longer distances for a re-nest attempt after a failed nest than a fledged nest (Figure 2). This increase in movement should also be evolutionarily adaptive for this behavioral plasticity to persist. We did not directly test if there was a reproductive advantage to within-season dispersal in this population, so we cannot effectively assess its effectiveness. However, other species have been found to increase distance moved after failed nests (Jackson et al. 1989, Powell and Frasch 2000, Catlin and Rosenberg 2008). For Brewer's Sparrows where their previous nest failed, daily nest survival increased as a single measure of ecological differences (changes in nest patch height and potential nest shrub density) increased between nest attempts (Chalfoun and Martin 2010a). Increased movement after a failed nest might be evolutionary adaptive if it enables the pair to leave the predator's home range (Powell and Frasch 2000). However, only two Acadian Flycatchers moved more than 110 meters between nest attempts, which would likely remain within the breeding home range of the primary nest predators, raptors and corvids. Given that Acadian Flycatchers average territory size

ranges from 0.97-1.63 ha (Mumford 1964, Walkinshaw 1966, Whitehead and Taylor 2002) movements of nests are constrained by the size of the territory.

Daily nest survival was not different following a successful nest attempt compared with a failed nest attempt (Figure 3). This does not support the hypothesis that, of the paired females, some individuals are better at successfully fledging a nest than others. Some individuals may be better at getting a mate, may lay larger clutches, or may produce young with higher fitness than others, and therefore have a higher fitness themselves. However, increased female quality does not seem to equate with a higher probability of fledging a nest. It appears predation risks following failed nest attempts are reduced by the “lose-switch” strategy. It is also possible that the “win-stay” strategy has a cost if predators had started to pick up on behavioral cues from the previous nest attempt. Therefore, the fact that daily nest survival is similar regardless of previous nest fate could be both from an increase in daily survival from the birds that change habitat characteristics and a decrease in daily nest survival for the birds that nest in a similar nest site.

CONCLUSION

It does appear that behavioral plasticity in nest location and placement provide a reproductive benefit to the Acadian Flycatcher, and that the “win-stay, lose-switch” strategy is effective. Overall the period survival of a nest attempt for Acadian Flycatchers was ~44% (Hirsch-Jacobson in prep), which is high compared to other migrant forest birds from the same region (Donovan et al. 1995). Period survival was low early in the season (~23%) and increased as the

season progressed (up to 71%) (Hirsch-Jacobson in prep). Throughout the year, 89% of pairs fledged at least one brood, even though there were high rates of nest failure early in the season (Hirsch-Jacobson in prep). Being able to renest successfully after failed nest attempts is critical to enable such a high rate of individual success. It is unclear if changes in nest site characteristics, or changes in predator abundance and/or activity (Hirsch-Jacobson et al. *in review*), is a stronger factor in seasonal fecundity. However, both are important factors that influence the success of renesting attempts, and allow 89% of females to fledge at least one nest.

REFERENCES

- Burhans, D. E., D. Dearborn, F. R. Thompson III, and J. Faaborg. 2002. Factors affecting predation at songbird nests in old fields. *Journal of Wildlife Management* **66**:240-249.
- Catlin, D. H., and D. K. Rosenberg. 2008. Breeding dispersal and nesting behavior of burrowing owls following experimental nest predation. *American Midland Naturalist* **159**:1-7.
- Chalfoun, A. D., and T. E. Martin. 2009. Habitat structure mediates predation risk for sedentary prey: experimental tests of alternative hypotheses. *Journal of Animal Ecology* **78**:497-503.
- Chalfoun, A. D., and T. Martin. 2010a. Facultative nest patch shifts in response to nest predation risk in the Brewer's sparrow: a "win-stay, lose-switch" strategy? *Oecologia* **163**:885-892.
- Chalfoun, A. D., and T. E. Martin. 2010b. Parental investment decisions in response to ambient nest-predation risk versus actual predation on the prior nest. *The Condor* **112**:701-710.
- Donovan, T. M., F. R. Thompson III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. *Conservation Biology* **9**:1380-1395.
- Donovan, T. M., and F. R. Thompson III. 2001. Modeling the ecological trap hypothesis: A habitat and demographic analysis for migrant songbirds. *Ecological Applications* **11**:871-882.

- Dow, H., and S. Fredga. 1983. Breeding and natal dispersal of the goldeneye, *Bucephala clangula*. *Journal of Animal Ecology* **52**:681-695.
- Eggers, S., M. Griesser, M. Nystrand, and J. Ekman. 2006. Predation risk induces changes in nest-site selection and clutch size in the Siberian Jay. *Proceedings of the Royal Society B: Biological Sciences* **273**:701-706.
- Forstmeier, W., and I. Weiss. 2004. Adaptive plasticity in nest-site selection in response to changing predation risk. *Oikos* **104**:487-499.
- Ghalambor, C. K., and T. E. Martin. 2000. Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. *Animal Behaviour* **60**:263-267.
- Ghalambor, C. K., and T. E. Martin. 2002. Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. *Behavioral Ecology* **13**:101-108.
- Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics*. Volume 13:1-21.
- Greig-Smith, P. W. 1982. Dispersal between nest-sites by Stonechats *Saxicola torquata* in relation to previous breeding success. *Ornis Scandinavica* **13**:232-238.
- Hildén, O. 1965. Habitat selection in birds. *Annales Zoologici Fennici* **2**:53–75.
- Hirsch-Jacobson, R., W. A. Cox, E., Tewes, F. R. Thompson III, J. Faaborg. *In review*. Parents or Predators: Examining intraseasonal variation in nest survival for a migratory passerine.

- Howlett, J. S., and B. J. M. Stutchbury. 1997. Within-season dispersal, nest-site modification, and predation in renesting Hooded Warblers. *The Wilson Bulletin* **109**:643-649.
- Jackson, W. M., S. Rohwer, and V. Nolan, Jr. 1989. Within-season breeding dispersal in prairie warblers and other passerines. *The Condor* **91**:233-241.
- Lang, J. D., L. A. Powell, D. G. Krementz, M. J. Conroy, and T. Grubb. 2002. Wood Thrush movements and habitat use: effects of forest management for Red-Cockaded Woodpeckers. *The Auk* **119**:109-124.
- Martin, T. E. 1993. Nest predation and nest sites. *BioScience* **43**:523-532.
- Martin, P. R., and T. E. Martin. 2001. Ecological and fitness consequences of species coexistence: A removal experiment with wood warblers. *Ecology* **82**:189-206.
- Martin, T. E., and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* **64**:507-519.
- Martin, T. E., and J. J. Roper. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. *The Condor* **90**:51-57.
- Marzluff, J. M. 1988. Do pinyon jays alter nest placement based on prior experience? *Animal Behaviour* **36**:1-10.
- Mumford, R. E. 1964. The breeding biology of the Acadian Flycatcher. Museum of Zoology, University of Michigan, No. **125**.

- Nowak, M., and K. Sigmund. 1993. A strategy of win-stay, lose-shift that outperforms tit-for-tat in the Prisoner's Dilemma game. *Nature* **364**:56-58.
- Peluc, S. I., T. S. Sillett, J. T. Rotenberry, and C. K. Ghalambor. 2008. Adaptive phenotypic plasticity in an island songbird exposed to a novel predation risk. *Behavioral Ecology* **19**:830-835.
- Powell, L. A., and L. L. Frasch. 2000. Can nest predation and predator type explain variation in dispersal of adult birds during the breeding season? *Behavioral Ecology* **11**:437-443.
- Ricklefs, R. E. 1969. An analysis of nestling mortality in birds. *Smithsonian Contributions to Zoology* **9**:1-48.
- SAS Institute. 2004. SAS/STAT user's guide. Version 9.1. SAS Institute, Inc., Cary, NC.
- Schmidt, K. A. 1999. Foraging theory as a conceptual framework for studying nest predation. *Oikos* **85**:151-160.
- Schroeder, M. A., and L. A. Robb. 2003. Fidelity of Greater Sage-Grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape. *Wildlife Biology* **9**:291-299.
- Shaffer, T. L. 2004. A unified approach to analyzing nest success. *Auk* **121**:526-540.
- Switzer, P. V. 1993. Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology* **7**:533-555.
- Walkinshaw, L. H. 1966. Studies of the Acadian Flycatcher in Michigan. *Bird-Banding* **37**:227-257.

Whitehead, D. R., and T. Taylor. 2002. Acadian Flycatcher (*Empidonax virescens*). Cornell Lab of Ornithology, Ithaca.

Wilson, R. R., and R. J. Cooper. 1998. Acadian flycatcher nest placement: Does placement influence reproductive success? *Condor* **100**:673-679.

FIGURE LEGENDS

FIGURE 1. The change in nest height following a failed nest and following a fledged nest. The error bars represent standard error.

FIGURE 2. The distance between nest attempts following a fledged and successful nest attempt. The error bars represent standard error.

FIGURE 3. The period survival of a nest attempt after the previous nest fledged or failed. The error bars are 95% confidence intervals.

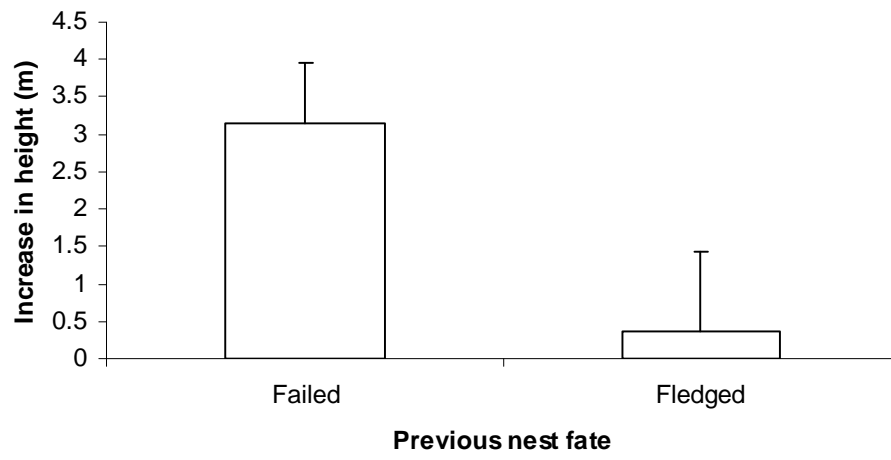


FIGURE 1

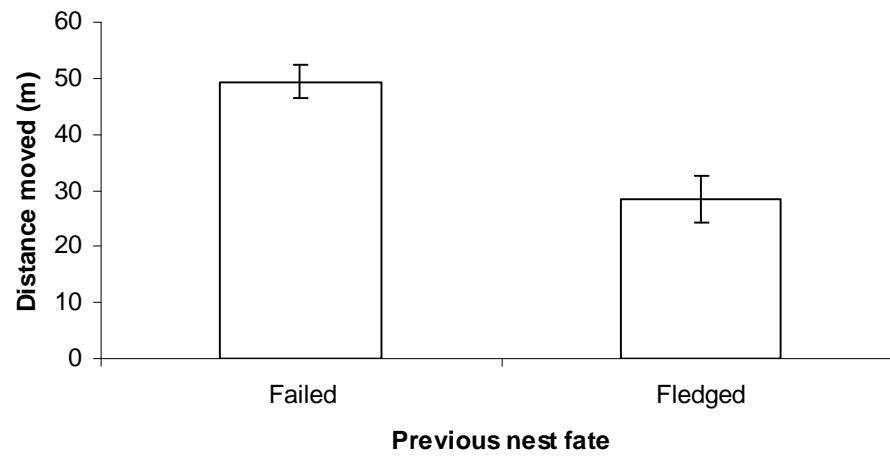


FIGURE 2

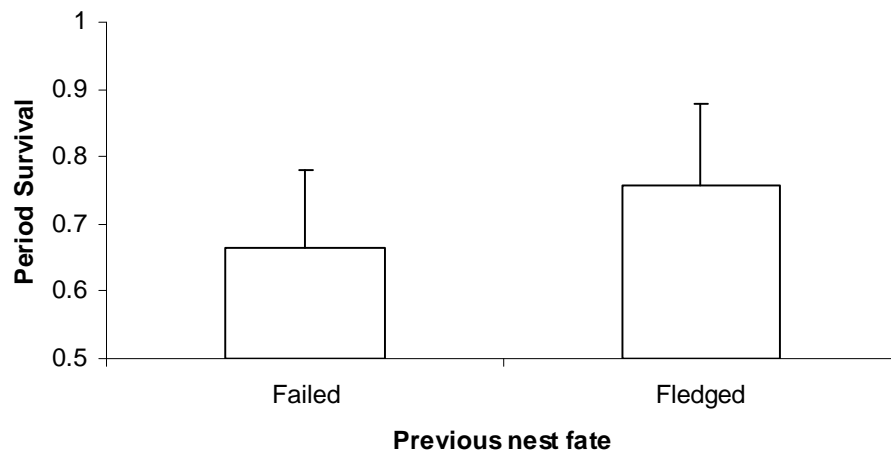


FIGURE 3

Table 1. Study sites with GPS locations, overall site size, and amount of area that is forested.

Site name and Coordinates	Size (ha)	Forest area (ha)
Baskett Wildlife Area (38° 44'N, 92° 12'W)	917	Most
Rudolph Bennitt Conservation Area (39° 15'N, 92° 28'W)	1446	1146
Whetstone Creek Conservation Area (38°57'N, 91°43'W)	2082	1123
Hungry Mother Conservation Area (39°14'N, 92°33'W)	110	92

Table 2. The number of nests, the number of breeding pairs that we included in the analyses, and the previous fate of the nests included in the analyses from each year. In 2008, 17 nests were excluded from the change in nest height analysis from user error (13 failed, 4 fledged).

Year	# of nests	# of pairs included in the analyses	Previous nest fate of nests included in the analyses	
			Failed	Fledged
2007	70	15	11	5
2008	113	45	47	13
2009	114	43	33	19
Total	297	103	91	37

VITA

Robin Hirsch-Jacobson was born and raised in Northern California. He received his B.A. in Environmental Sciences and his B.S. in Marine Biology in 2001 at the University of California, Santa Cruz. He bounced around the state of California, from field job to field job, primarily working with the Point Reyes Bird Observatory. He joined the University of Missouri in 2005. He currently works as a tenure-tracked biology faculty at William Woods University.