

PARENTS OR PREDATORS: EXAMINING INTRASEASONAL VARIATION IN NEST SURVIVAL FOR A MIGRATORY PASSERINE

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Abstract. For birds, risk of nest predation can vary within a breeding season, but few data exist that explain why such variation occurs. We investigated intraseasonal variation of nest survival of the Acadian Flycatcher (*Empidonax vireescens*) in Midwestern forests and tested whether four of the adults' reproductive strategies (clutch size, nest concealment, nest visitation rates, nest height) explained trends in survival across the breeding season. We also used video cameras to identify predators at 40 nests, which allowed us to determine whether variation in predation rates by category of predator (e.g., birds, mammals, snakes) explained overall seasonal variation in predation rates. The flycatchers' nest survival had a quadratic relationship with Julian date but generally increased through the breeding season. Nest height increased as the breeding season progressed but did not explain any variation in nest survival. No other reproductive trait exhibited significant intraseasonal variation. Overall, predator-specific predation rates did not vary seasonally, but there was a marginal decline in the risk of failure from avian predators as the season progressed. Of the explanations we considered, changes in predator abundance or activity were likely the primary contributor to intraseasonal variation in survival of Acadian Flycatcher nests.

Key words: *Acadian Flycatcher*, *Empidonax vireescens*, nest survival, nest-visitation rates, reproductive strategies, seasonality.

Padres o Depredadores: Examen de la Variabilidad Intraestacional de la Supervivencia en Nido de un Ave Paserina Migratoria

Resumen. En las aves, el riesgo de depredación del nido puede variar durante una estación reproductiva, pero existen pocos datos que expliquen a qué se debe dicha variabilidad. Investigamos la variabilidad intraestacional de la supervivencia del nido para *Empidonax vireescens* en bosques del medio oeste de los Estados Unidos y contrastamos si cuatro estrategias reproductivas de los adultos (tamaño de camada, ocultación del nido, tasas de visita del nido, altura del nido) explicaban las tendencias de supervivencia a lo largo de la estación reproductiva. También identificamos a los depredadores con cámaras de video en 40 nidos para determinar si la variación en las tasas de depredación por grupo de depredadores (por ejemplo, aves, mamíferos, serpientes) explicaba la variabilidad estacional en conjunto de las tasas de depredación. La supervivencia del nido de *Empidonax vireescens* mostró una relación cuadrática con la fecha juliana pero aumentó en general a lo largo de la estación reproductiva. La altura del nido aumentó a medida que transcurría la estación reproductiva pero no explicó variabilidad alguna en la supervivencia del nido. Ninguna otra característica exhibió variabilidad intraestacional significativa. En conjunto, las tasas de depredación específicas de cada depredador no variaron estacionalmente, pero se produjo un descenso marginal en el riesgo de fracaso debido a los depredadores de aves a medida que transcurría la estación. Es probable que la variabilidad intraestacional de la supervivencia del nido de *Empidonax vireescens* se deba principalmente a cambios en la abundancia o en la actividad de los depredadores.

INTRODUCTION

In birds, nest predation is the primary cause of reproductive failure (Ricklefs 1969, Martin 1993) and is an important component of songbird demography (Donovan and Thompson 2001). Traditionally, researchers studying nest predation used analytical methods that assumed nest survival to be constant across the period being sampled (Mayfield 1961). This restrictive assumption is false for ducks (Klett and Johnson

1982), but the lack of viable analytical alternatives resulted in relatively few subsequent studies examining intraseasonal temporal variation in nest survival. Recent advances in nest-survival analysis (e.g., logistic exposure [Shaffer 2004]) have eliminated the assumption of constant survival, and one frequently sees significant temporal variation in nest survival. For example, Small et al. (2007) found that survival of Spotted Towhee (*Pipilo maculatus*) nests declined by >50% from the

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beginning to the end of the breeding season, whereas Fisher and Wiebe (2006) found that survival of Northern Flicker (*Colaptes auratus*) nests was lowest in the middle of the season and highest at the end. By contrast, Shustack and Rodewald (2010) found that period survival of Acadian Flycatcher (*Empidonax vireescens*) nests increased from ~30% in early summer to ~55% in late summer. Such variation may not always be constant from year to year (Smith and Wilson 2010), which can make the demographic implications of seasonal patterns less clear.

In most cases, the cause of such temporal variation in nest survival remains unclear. Predator activity can correlate strongly with temporal variation in songbirds' risk of predation (Sperry et al. 2008), and there is evidence that risk of predation from some species of predators varies seasonally (Weidinger 2009, Benson et al. 2010). Spatial (Patten and Bolger 2003) and annual (Schmidt and Ostfeld 2003) variation in predator abundance can influence risk of nest predation, but this may not always explain intraseasonal variation in nest predation. The contribution of generalist predators to overall predation rates also depends upon the availability of other food resources (Smith and Wilson 2010), and predators' diets may shift as their young become larger or independent (Sieving and Willson 1999).

Though few data exist, other factors may also explain intraseasonal variation in nest survival. Adult birds can evaluate the risk of nest predation and adjust their behavior accordingly (Fontaine and Martin 2006, Lima 2009); such behavioral shifts across a breeding season might reduce the risk of nest predation. For example, shorebirds tend to defend older, more valuable nests more aggressively (Smith and Wilson 2010), which could reduce nest-failure rates later in a breeding season even if predator abundance and/or activity remained unchanged.

To better understand seasonal trends in nest survival, we identified nest predators by video to determine whether rates of predation by particular predators (grouped by taxonomic relationships) varied seasonally. We also evaluated four reproductive traits (clutch size, nest-visitation rates, nest height, nest concealment) that may influence passerines' risk of nest predation to determine whether they varied seasonally. Species laying smaller clutches tend to have a reduced risk of predation (Slagsvold 1982, Martin et al. 2000), and, within a species, females sometimes lay fewer eggs when perceived predation risks are high, to increase the chance of successfully raising young (Doligez and Clobert 2003, Eggers et al. 2006, Fontaine and Martin 2006). Adults can reduce the number of trips they make to the nest to avoid drawing attention to its location (Skutch 1949, Martin et al. 2000, Fontaine and Martin 2006). Nest-site selection may also change in response to predation. For example, higher nests can have a reduced risk of predation (Burhans et al. 2002), and, though the evidence is equivocal, some birds may build more concealed nests to reduce the risk of predation (reviewed in Martin 1992, Lima 2009). We tested whether seasonal shifts in predator-specific predation rates or reproductive strategies of adult birds explained seasonal trends in survival of nests of the Acadian Flycatcher, a neotropical migrant.

METHODS

FIELD METHODS

We conducted this study at ten field sites in Missouri and southern Illinois (Table 1). Most sites were oak–hickory forests; three sites in Illinois also featured mature sugar maples (*Acer saccharum*) and American beech (*Fagus grandifolia*). The Acadian Flycatcher nests in understory trees of the forest

TABLE 1. Location and years in which data were collected for each variable to assess Acadian Flycatcher nest survival in Missouri and Illinois, 2006–2009.

Region, site, and coordinates	Clutch size and nest height	Nest concealment	Nest predator and visitation rates
Central Missouri			
Baskett Wildlife Area (38° 44' N, 92° 12' W)	2007–2009	2007, 2009	2007, 2009
Bennett Conservation Area (39° 15' N, 92° 28' W)	2007–2009	2007, 2009	2007, 2009
Whetstone Creek Conservation Area (38° 57' N, 91° 43' W)	2007–2009	×	×
Hungry Mother Conservation Area (39° 14' N, 92° 33' W)	2007–2009	×	×
Southern Missouri			
Current River Conservation Area (37° 11' N, 91° 02' W)	2006–2007, 2009	2006–2007, 2009	2006–2007, 2009
Mark Twain National Forest: Doniphan (36° 37' N, 90° 55' W)	2007, 2009	2007, 2009	2007, 2009
Illinois			
Ferne Clyffe State Park (37° 32' N, 89° 01' W)	2008	2008	2008
Saline Conservation Area (37° 42' N, 88° 24' W)	2008	2008	2008
Thompsonville (private land) (37° 56' N, 88° 40' W)	2008	2008	2008
Trail of Tears State Forest (37° 30' N, 89° 21' W)	2008	2008	2008

interior. At our field sites, it often attempts to raise multiple broods and tends to breed late into the summer, making it an ideal focal species.

We found and monitored nests from May to August, 2006–2009. Nest searching continued through the first week of August, and we are confident that the number of nests we located accurately describes temporal patterns of breeding activity. We located nests by using behavioral cues and monitored them every 2–4 days, following Martin and Geupel (1993). We considered nests to have fledged young successfully if we found fledglings or extremely agitated adults within 2 days of the expected date of fledging. We measured nest height with an electronic clinometer and nest concealment by calculating the average percent of the nest hidden by vegetation 1 m above, below, and from the side of each nest in the four cardinal directions. We typically measured concealment at a distance of 1 m, but many nests were relative high, so we also estimated concealment from farther away if it provided a better angle of view. We did not record measurements for nests too high for us to record concealment accurately. We used constant-surveillance video systems to identify nest predators on a subset of the nests we monitored. The video systems and our field protocols for their use are described in Cox et al. (2012b). We used video footage from nest cameras to determine nest-visitation rates. We recorded the average number of visits to the nest by both adults from 06:30 to 10:30 CST on the second, third, or fourth day of the nestling period to control for variation in daily activity patterns related to nestling age. We did not record visitation rates on days when a field technician visited the nest between 06:00 and 11:00 CST. Because of logistical constraints, we did not measure any of our variables at all sites in all years (Table 1).

STATISTICAL ANALYSIS

We tested for covariance between Julian date and our response variables (clutch size, nest concealment, nest height, and nest-visitation rates), then used the response variables that covaried with date as parameters within candidate models that we evaluated with an information-theoretic approach (Burnham and Anderson 2002). We used the date of nest initiation as the independent variable in each test. We estimated this date for nests found after the laying stage by subtracting 17 days (the mean duration of laying and incubation for the Acadian Flycatcher) from the estimated date of hatching or by subtracting 31 days (the mean nest period) from the estimated date of hatching for nests found after hatching. We excluded nests found after the laying stage that were depredated before the eggs hatched. We did not include nests with cowbird eggs or young in analyses of either visitation rate or clutch size.

We used SAS (SAS Institute 2004) for all statistical tests. Normality tests for clutch size and nest height indicated that our data were not suitable for parametric tests, so we used Spearman's rank-correlation coefficient to test for covariance between

each variable and Julian date. We used linear regression to test for a relationship between Julian date and concealment and a mixed linear model with year as a random effect to test for a relationship between nest-visitation rates and Julian date.

We employed the logistic-exposure method (Shaffer 2004) for our nest-survival analyses, which allowed us to model survival as a function of our covariates of interest. Nest-predation rates at the incubation and nestling stages differ (Cox 2012a), so we included nest stage as a covariate in all survival models to avoid confounding seasonal effects with nest-stage effects (i.e., most observations early in the breeding season are during the incubation period, whereas those late in the season are primarily during the nestling period). We did not include exposure days during the laying stage in our analyses because our sample at that stage was small in comparison to that at the incubation and nestling stages.

Our initial set of candidate models described potential relationships among nest survival, Julian date, and nest stage (a categorical variable: incubation or nestling). We considered linear and quadratic effects of date as well as an interaction between date and nest stage. We included additional candidate models after completing our initial analysis of reproductive traits. We used the second-order Akaike's information criterion (AIC_c ; Burnham and Anderson 2002) for model selection and calculated differences in AIC_c values (ΔAIC_c) and Akaike weights (w_i) to evaluate relative support for each candidate model. We considered models within two AIC_c units of the top-ranked model to be well supported and averaged parameter estimates across these models.

Our predator-specific analysis did not require the link function specific to the logistic-exposure method because all nests were monitored continuously, so we used multinomial logistic regression. This allowed us to have more than two response variables (more than just active or failed). Because we knew a priori that our sample sizes would be too small for estimation of rates of nest predation for particular predator species, we categorized predators by broad taxonomic relationships and foraging behavior and had five response variables: active, depredated by bird, snake, or mammal, or other. The "other" category included nests that failed from other causes (such as weather), nest abandonment, nestling mortality, and nests with unknown fates (such as camera failure or technician error). We limited the complexity of our analysis because of our expected small sample size and evaluated support for a linear model that included only nest stage and Julian date.

RESULTS

We found 514 Acadian Flycatcher nests. We excluded 43 nests from all analyses because they were abandoned before an egg was laid or because their fate could not be accurately determined. Clutch size ($n = 243$, $r_s = -0.07$, $P = 0.28$), nest-visitation rates ($n = 42$, $P = 0.69$), and nest concealment ($n = 233$,

TABLE 2. Model-selection results from a logistic-exposure analysis of survival of Acadian Flycatcher nests through the breeding season in Missouri and Illinois, 2006–2009.

Candidate model	K^a	ΔAIC_c^b	w_i^c
Date ² + stage	4	0.00	0.42
Date × stage	4	1.81	0.17
Date + stage	3	2.48	0.12
Date × stage + height	5	3.21	0.09
Date ² × stage	6	3.26	0.08
Date + stage + height	4	3.87	0.06
Date + stage × height	5	5.36	0.03
Stage	2	5.41	0.03
Null	1	29.54	0.00

^aNumber of parameters in the model.

^bThe value of the second-order Akaike's information criterion (AIC_c) for the top model was 1458.82.

^cAkaike weight, relative support for the model with respect to other candidate models, given the data.

$P = 0.50$) did not vary seasonally. Nest height increased as the breeding season progressed ($n = 328$, $r_s = 0.20$, $P < 0.001$), so we included it in three candidate models.

The 471 nests we included in our nest-survival analysis included 7454 observation days. The top model included a quadratic date term and stage, and the second-ranked model ($\Delta AIC_c = 1.81$) included an interaction between date and stage (Table 2). The two models had a combined Akaike weight (w_i) of 0.59, and no other model was within two AIC_c units of the top-ranked model; therefore, we used model-averaged parameter estimates to model nest survival. Period survival was 49% (95% CI: 37–60%) in early June and decreased slightly before increasing to 67% (95% CI: 47–81%) at the end of the breeding season (Fig. 1). This increase was driven by an intra-seasonal increase in survival during the nestling period; nest survival during the incubation period was invariant throughout the season (Fig. 2).

We identified predators at 40 nests. Birds were the primary predators ($n = 25$), with raptors ($n = 14$), corvids ($n = 8$), Yellow-billed Cuckoos ($n = 2$; *Coccyzus americanus*), and an unknown species ($n = 1$) depredating nests. Mammals ($n = 8$) and snakes ($n = 7$) depredated nests less frequently. We coded the cause of failure of 22 nests as “other”; we did not record a predator at 14 nests because of camera failure or technician error, and eight nests failed from nestling mortality, weather, or structural failure. Modeled predator-specific predation rates did not vary seasonally (overall $P = 0.41$), but there was a marginal trend for a reduced risk of predation from avian predators as the breeding season progressed ($P = 0.11$; Fig. 3).

DISCUSSION

Modern analytical approaches have helped researchers document intraseasonal variation in nest survival for numerous species. At our study sites, in nest survival of the Acadian Flycatcher

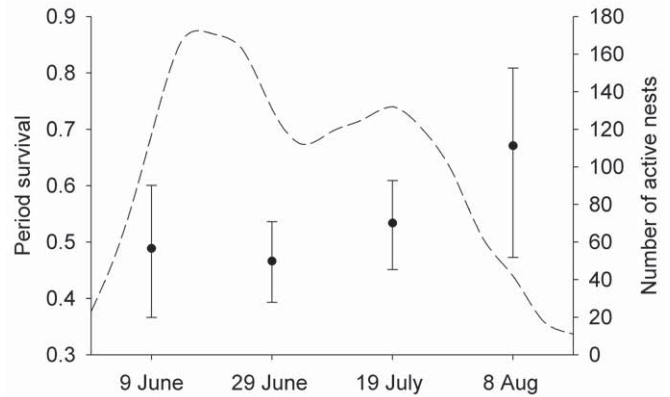


FIGURE 1. Period survival and the number through the breeding season of active Acadian Flycatcher studied in Missouri and Illinois, 2006–2009. Survival is modeled with nest stage held constant as a function of date calculated from model-averaged parameter estimates from the two most supported models. Survival increased from 49% early in the summer to 67% at the end of the summer. Error bars represent 95% confidence intervals. The dashed line indicates the number of active nests.

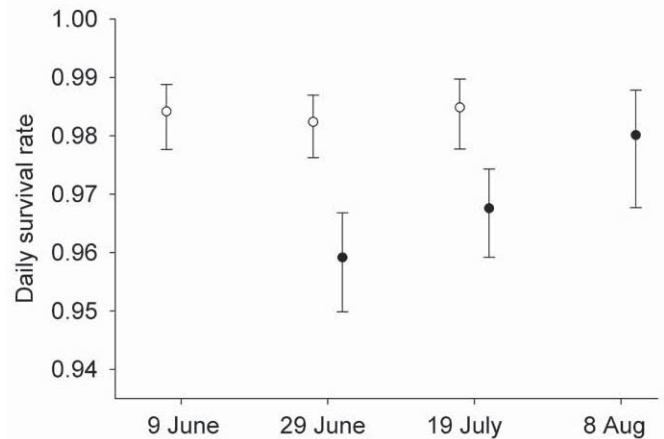


FIGURE 2. Modeled daily survival of Acadian Flycatcher nests in Missouri and Illinois, 2006–2009, as a function of date during the incubation (white circles) and nestling (black circles) stages, calculated from model-averaged parameter estimates from the two most supported models. The number of nests with nestlings ($n = 7$) on 9 June and with eggs ($n = 3$) on 8 August was small, so we do not provide survival estimates. Error bars represent 95% confidence intervals.

increased significantly through the breeding season. The direction and magnitude of the increase was similar to that for Acadian Flycatchers in Ohio (Shustack and Rodewald 2010), suggesting that in this species the pattern may be prevalent across the Midwest. At our study sites, daily nest survival during the incubation period did not change appreciably through the breeding season. Rather, the overall pattern was driven by an increase in nest survival during the nestling period.

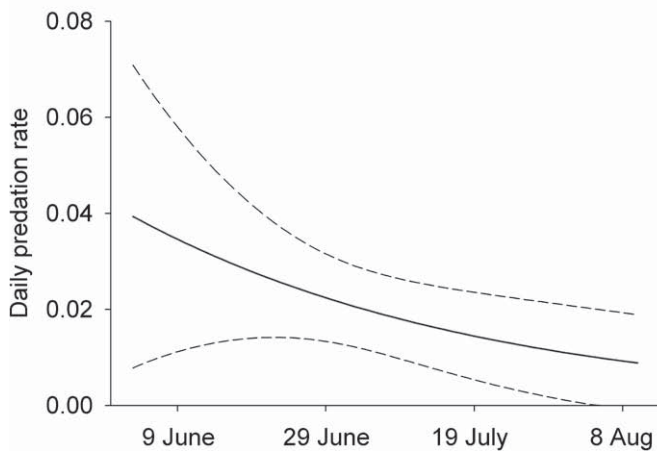


FIGURE 3. Modeled daily rates of predation of Acadian Flycatcher nests in Missouri and Illinois, 2006–2009, from avian predators through the season during the nestling stage, during which 92% of instances of avian predation occurred ($n = 25$). Dashed lines represent 95% confidence intervals for the nestling stage.

We found no evidence that a shift in reproductive strategies of adult birds was responsible for the observed seasonal pattern of nest survival. In the temperate zones, passerines' clutch sizes often decrease later in the breeding season (Crick et al. 1993), and smaller clutch sizes may reduce the risk of nest predation (Slagsvold 1982, Martin et al. 2000). The Acadian Flycatcher's clutch size at our field sites did not vary seasonally; therefore, clutch size did not explain the observed variation in nest survival. Similarly, both nest concealment and nest-visitation rates may influence the risk of nest predation (reviewed in Lima 2009), but Acadian Flycatchers did not build more concealed nests or visit nests less frequently as the season progressed.

Adults did build higher nests later in the breeding season. Other studies have associated higher nests with greater nest survival (Wilson and Cooper 1998, Burhans et al. 2002, Peluc et al. 2008), and there is experimental evidence that adult birds can actively assess the risk of predation, recognize specific predators, and adjust the height at which they build nests accordingly (Peluc et al. 2008). Adults of some species defend more vigorously at low nests when terrestrial predators are present than at high nests when avian predators are present (Kleindorfer et al. 2005), which further suggests birds can respond dynamically to their perceived risk of nest predation. At our study sites, Acadian Flycatchers built higher nests following nest failure, but they made no such adjustment after fledging young successfully (Hirsch-Jacobson 2011). This suggests that birds are responding to predation rather than to other factors such as seasonal shifts in microclimate (Balda and Bateman 1970, Finch 1983). Nevertheless, in our nest-survival analysis, candidate models that included nest height were not well supported. Avian nest predators are not expected to be affected by nest height as much as terrestrial predators (Schmidt 1999), so an increase

in nest height may not result in increased nest success where the primary nest predators are avian. It is unclear why this behavioral plasticity persists for the Acadian Flycatcher, whose primary predators are generally avian, at least throughout the Midwest (Cox 2012a).

To reduce the risk of predation from their avian counterparts, Acadian Flycatchers might modify other behaviors that we did not measure (e.g., adults become less vocal as the breeding season progresses; R. Hirsch-Jacobson, unpubl. data). But, as found in other studies (Post van der Burg et al. 2010), the seasonal trend in the flycatcher's nest survival was not linear, and attributing nonlinear patterns to shifts in adults' behavior seems problematic. In such cases, patterns of predation are likely driven by changes in the abundance or activity of predators. In our study, birds were the major predators and were the only category of predator from which predation rates declined through the season even marginally. Small sample sizes precluded us from distinguishing between statistical and biological significance regarding these patterns for all three predator groups, and our results should be considered qualitative. Nevertheless, the decline in the risk of nest failure from avian predators, combined with the lack of any behavioral change by the parents that corresponded with a reduction in predation, suggests that a reduction in either the activity or abundance of avian predators contributes to the Acadian Flycatcher's seasonal increase in nest survival.

The birds that contribute most to failure of Acadian Flycatcher nests are generalists; contents of stomachs of the Barred Owl (*Strix varia*; Mazur and James 2000), Blue Jay (*Cyanocitta cristata*; Tarvin and Woolfenden 1999), and Broad-winged Hawk (*Buteo platypterus*; Goodrich et al. 1996) all indicate that eggs and nestlings are not these species' primary prey during the breeding season. Prey switching by generalist predators has been shown to affect rates of predation on both adults (Angelstam et al. 1984) and nests (Schmidt and Ostfeld 2003). The reduced predation rates we observed at the beginning and end of the breeding season when relatively few nests were active probably represents a response by avian generalist predators to the pulse in an available resource. Schmidt (1999) demonstrated that the activity of generalist predators can decline when a food source such as songbird nests diminishes. Furthermore, at our field sites, breeding of all species peaks in late June (W. A. Cox, pers. obs.) when nest survival is lowest, with few species breeding into August, as the Acadian Flycatchers does. Predators may also switch prey in response to the needs of their own young. Steller's Jays (*Cyanocitta stelleri*) depredate nests predominately when raising their own nestlings but shift their diet when their young are no longer dependent upon them (Sieving and Willson 1999).

Alternatively, other food items may become more abundant irrespective of nest densities, and predators may switch to them (Murdoch 1969). Although this often accounts for variation in

nest survival from year to year (Schmidt and Ostfeld 2008), we are not aware of any evidence of strong intraseasonal variation in the abundance of rodents (the primary prey of raptors), nor are we aware of pulses in late July of other of the Blue Jay's food sources. Finally, it is possible that changes in predator abundance drove the patterns we observed, but we do not have data sufficient to assess this hypothesis. We did not estimate abundances of avian predators at our field sites, and the lack of published data on their vital rates make it difficult to assess whether their abundances decline through the breeding season. During the summer, survival of adult forest birds is high (e.g., Sillett and Holmes 2002), suggesting that abundances should remain fairly constant, but survival rates for raptors of post-fledging raptors tend to be low (e.g., McFadzen et al. 1996, Sunde 2005, Davies and Restani 2006), and such mortality may reduce predatory pressures on breeding birds.

Although the increase in nest survival at the end of the Acadian Flycatcher's breeding season was substantial, the demographic implications may be rather modest. Relatively few nests were still active in late July and August when nest-survival rates were highest, suggesting that overall recruitment was not significantly affected. However, nests that were still active usually belonged to breeding pairs that had yet to successfully fledge young within the breeding season (Hirsch-Jacobson 2011). Thus high nest survival in August might have little influence at the population level but still have fitness consequences for individuals who extend their breeding season in a final effort to produce young. Whether the demographic implications of the patterns we observed remain modest into the future is not clear. Many avian species have advanced dates of laying in response to climate change (Parmesan and Yoh 2003, Dunn and Winkler 2010). Such a change could create a mismatch between the activity of flycatchers and their nest predators and affect breeding performance, as has been seen elsewhere (Both et al. 2009). However, flycatchers face a diverse suite of predators (Cox 2012a), and it is unclear whether a mismatch of timing between nesting birds and nest predators (some of which are also nesting birds) would occur or persist through time. Future studies that document seasonal variation in predator abundance and activity will enhance our understanding of why nest survival is not constant through the breeding season and will help us better predict how changes in the breeding phenology of birds in response to climate change will influence productivity.

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