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*Research Papers*

# Contributions of Weather and Predation to Reduced Breeding Success in a Threatened Northern Loggerhead Shrike Population

# Influence du climat et de la prédation sur le faible succès de reproduction d'une population de Pie-grièche migratrice nordique et menacée

*Douglas M. Collister*[1] *and Scott Wilson*[2]

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ABSTRACT. Populations on the periphery of a species' range may experience more severe environmental conditions relative to populations closer to the core of the range. As a consequence, peripheral populations may have lower reproductive success or survival, which may affect their persistence. In this study, we examined the influence of environmental conditions on breeding biology and nest survival in a threatened population of Loggerhead Shrikes (*Lanius ludovicianus*) at the northern limit of the range in southeastern Alberta, Canada, and compared our estimates with those from shrike populations elsewhere in the range. Over the 2-year study in 1992–1993, clutch sizes averaged 6.4 eggs, and most nests were initiated between mid-May and mid-June. Rate of renesting following initial nest failure was 19%, and there were no known cases of double-brooding. Compared with southern populations, rate of renesting was lower and clutch sizes tended to be larger, whereas the length of the nestling and hatchling periods appeared to be similar. Most nest failures were directly associated with nest predators, but weather had a greater direct effect in 1993. Nest survival models indicated higher daily nest survival during warmer temperatures and lower precipitation, which may include direct effects of weather on nestlings as well as indirect effects on predator behavior or food abundance. Daily nest survival varied over the nesting cycle in a curvilinear pattern, with a slight increase through laying, approximately constant survival through incubation, and a decline through the nestling period. Partial brood loss during the nestling stage was high, particularly in 1993, when conditions were cool and wet. Overall, the lower likelihood of renesting, lower nest survival, and higher partial brood loss appeared to depress reproductive output in this population relative to those elsewhere in the range, and may have increased susceptibility to population declines.

RÉSUMÉ. Les populations situées dans le pourtour de l'aire de répartition d'une espèce peuvent subir des conditions environnementales plus rigoureuses que celles situées plus près du centre de l'aire. En conséquence, les populations excentriques peuvent avoir un succès de reproduction ou une survie moins élevé, ce qui peut avoir un effet sur leur pérennité. Dans la présente étude, nous avons examiné l'influence des conditions environnementales sur la biologie reproductive et la survie des nichées d'une population menacée de Pie-grièche migratrice (*Lanius ludovicianus*) située à la limite nord de l'aire de répartition de l'espèce, dans le Sud-Est de l'Alberta, au Canada. Nous avons comparé nos résultats avec ceux provenant de populations réparties ailleurs dans l'aire. Au cours des deux années qu'a duré l'étude (1992 et 1993), la taille moyenne de la ponte était de 6,4 œufs et la plupart des nids étaient initiés entre la mi-mai et la mi-juin. Le taux de ponte de remplacement suivant l'échec d'une première nichée était de 19 %, et nous n'avons documenté aucun cas de seconde nichée. Comparativement aux populations méridionales, le taux de ponte de remplacement était plus faible et la taille de la ponte était plus élevée, tandis que les durées d'incubation et de séjour au nid semblaient similaires. La plupart des échecs de nidification étaient directement associés aux prédateurs de nichées, mais les conditions climatiques ont eu un effet direct plus important sur ces

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[1] Faculty of Environmental Design, University of Calgary, [2] Centre for Applied Conservation Research, University of British Columbia

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échecs en 1993. Les modèles sur la survie des nichées ont prédit une survie journalière plus grande lorsque les températures étaient plus chaudes et les précipitations plus faibles, ce qui peut être le résultat d'effets directs du climat sur les oisillons aussi bien que d'effets indirects sur le comportement des prédateurs ou la quantité de nourriture. La survie journalière des nichées a varié de façon curvilinéaire au cours du cycle de nidification, montrant une légère hausse au cours de la ponte, une relative constance au cours de l'incubation, puis un déclin au cours de la période d'élevage des jeunes au nid. La perte partielle des nichées durant la période d'élevage des jeunes au nid était élevée, particulièrement en 1993, où les conditions ont été fraîches et humides. Dans l'ensemble, la probabilité de nidification de remplacement plus faible, la survie des nichées plus faible et la fréquence plus élevée de perte partielle des nichées semblent concourir à diminuer le succès de reproduction de cette population, en comparaison à celui de populations d'autres sites dans l'aire de reproduction; ces facteurs pourraient donc contribuer à augmenter le risque que cette population nordique décline.

Key Words: *Age effects; Lanius ludovicianus*; Loggerhead Shrike; nest survival; partial brood loss; southern Alberta; weather

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## INTRODUCTION

Predation is often the dominant factor affecting avian reproductive success (Ricklefs 1969), but weather can play an important role through impacts on timing of breeding (Wilson and Arcese 2003, Preston and Rotenberry 2006) and nest survival (Dinsmore et al. 2002, Mahony et al. 2006). Weather might directly affect nest survival if extreme conditions lower hatchability of eggs or increase nestling mortality (Diehl and Myrcha 1973, Webb 1987, Dawson and Bortolotti 2000), whereas indirect impacts might arise through effects on food abundance (Takagi 2001) and the behavior of predators (Morrison and Bolger 2002). Such indirect effects of weather, particularly on the activity of and prey selection by predators, may often go unrecognized (Rodriguez and Bustamente 2003). Weather may have a greater impact on reproductive success for populations at the edge of the range, because they are breeding under the limits of environmental tolerance for that species (Maurer and Brown 1989). Such variability has been observed in peripheral populations of some passerines, including Brewer's Sparrows (*Spizella breweri*, Mahony et al. 2006) and Pied Flycatchers (*Ficedula hypoleuca*, Thingstad et al. 2006). Predicting the sensitivity of peripheral populations to environmental stochasticity may be particularly important because altered environmental conditions driven by climate change may be especially pronounced along the edge of a species' range (Parmesan et al. 2005).

In this study, we examined the breeding biology and nest survival of a Loggerhead Shrike (*Lanius ludovicianus*) population in southeastern Alberta at the northern edge of the species' range. Loggerhead Shrikes in this region are threatened and have been declining over the past few decades (Committee on the Status of Endangered Wildlife in Canada (COSEWIC) 2004, Sauer et al. 2004). We previously showed that shrikes in this area tend to hold larger territories than many other parts of the range, perhaps because the arid habitats support low food abundance relative to core areas (Collister and Wilson 2007). Additional information on the factors influencing demography of this population would aid in management plans and predictions on the potential impacts of climate change. Here, we first compare the basic breeding biology for this population relative to other areas of the species' range. We then consider the impacts of predators, weather, nest age, and nest placement on daily nest survival rates. Until recently, it was difficult to simultaneously consider how multiple factors interact to influence nest survival, but recently developed analytical tools have greatly facilitated our ability to test such questions (Dinsmore et al. 2002, Shaffer 2004, Grant et al. 2005). The population was studied over a 2-year period (1992–1993) where weather conditions were average in the first year and, colder and slightly wetter than normal in the second. This provided an opportunity to examine breeding sensitivity of this population to annual fluctuations in weather.

## METHODS

### Study Area

The study site was a 36 km by 1 km strip in the Dry Mixed Grass ecoregion of southeastern Alberta, between Atlee (50º50' N, 111º00' W) and Cavendish (50º48' N, 110º28' W). At the time of this study, approximately half of this ecoregion had been disrupted by agriculture (Strong 1992). The study area itself consists of two major subdivisions. The core is made up of an approximately 100 m wide ungrazed right-of-way consisting of disturbed prairie now dominated by crested wheat grass (*Agropyron cristatum*) and brome (*Bromus* spp.). The 450 m on either side of the right-of-way are mixed grass prairie, including blue grama (*Bouteloua gracilis*), needle-and-thread (*Stipa comata*), and northern and western wheatgrass (*Agropyron dasystachyum, A. smithii*). Thorny buffaloberry (*Shepherdia argentea*) is a common shrub within these habitats, and is the primary species used for nesting by shrikes (Collister 1994). The climate of the study area falls within the Prairie climatic regime (Strong 1992). From mid-May through mid-July 1992, average mean daily temperature (°C) was 13.98 (1 SD = 4.60) and ranged from 1.3 to 23.5°C. In 1993, average mean daily temperature over the same period was 13.22° C (1 SD = 2.76) and ranged from 6.5 to 23.5°C. Total precipitation (mm) was 134.7 (SD = 4.76) and 152.5 (SD = 6.42) in 1992 and 1993, respectively. Precipitation patterns are erratic, and frequently occur as summer storms. Temperature and precipitation data were obtained from the Atlee Weather Station (50º49' N, 110º57' W) located approximately 4 km SE of the study site and provided by Environment Canada (http://climate.weatheroffice.ec.gc.ca/climateData).

### Field Methods

The study was conducted from 21 May–15 July 1992 and 25 May–16 July 1993. Shrikes typically arrive in the study area during the first week of May. Nests were located by observing the behavior of shrikes and systematically searching all suitable nesting habitat throughout the season. We considered the first nest found in each territory to be the first attempt by that pair. In a few cases, a nest was not located until late June, and it is likely that the first attempt failed before it was found. Nests found during egg laying were monitored every other day until clutch size was established. We estimated the date of first egg by observing nests during the laying stage or back-dating from the date of hatch or fledge, and then calculated the mean onset of initiation for each year. This estimate may be biased if not adjusted for nests that failed before they were found. To correct for this, we used the Horvitz-Thompson estimator described by Dinsmore et al. (2002). This method uses the top nest survival model (see next section) to calculate the probability that each found nest survived until it was found. By dividing the observed frequency of each nest (i.e., 1) by this probability, we can estimate how many other nests might have been initiated on the same day but failed before they were found. We applied this approach to each nest in the sample and used the expected number of nest initiations as our corrected estimate of mean initiation date for each year.

Incubation was assumed to begin with the laying of the next to last egg. After the onset of incubation, nests were visited every 3–5 d except near the expected hatch and fledging times, when they were checked on alternate days to determine hatch and fledge date respectively. At approximately day 7, nestlings were banded with an aluminum United States Fish and Wildlife Service band on one tarsus and a light green plastic band on the other. For estimates of the length of the incubation and nestling periods, we only used nests if we were certain when incubation started and the exact hatch and fledge dates. If a nest was found empty around the expected time of fledging, we confirmed a successful nest by locating the fledglings, and observing parents carrying food and engaged in defensive behavior. Despite these efforts, there was uncertainty on nest fate for five of the nests. For all failed nests, we followed the approach of Etterson et al. (2007) and assigned the cause of failure as either predation (nest cup disturbed, all eggs or young gone from nest or present with physical injuries) or other, which includes weather, abandonment, and starvation (parents absent on two consecutive visits, cold eggs or dead chicks still in nest). There were no cases of complete infertility or brood parasitism in this population. Etterson et al. (2007) note that assigning failure in this manner is subject to classification error. In particular, we may underestimate the influence of weather or starvation on nest failure because scavengers may remove nest contents after failure due to these causes, thus giving the appearance of nest predation. Therefore, we consider our estimates of failure due to "other" causes as a minimum estimate. Results for breeding parameters are presented as mean with the 95% upper and lower confidence interval (CI) in brackets.

## Nest Survival

We examined potential causes of variation in nest survival using program MARK (White and Burnham 1999, Dinsmore et al. 2002). This approach requires the following assumptions: 1) nest ages are correctly determined, 2) nest fates are known with certainty, 3) investigator disturbance does not influence nest survival, and 4) nest fates are independent. For the five uncertain fates noted earlier, we only used nest information up to the last date the nest was confirmed active and then denoted the nest as successful over that period. If there was uncertainty in nest age or if survival was influenced by human disturbance, that nest was not used in the analysis. Because Loggerhead Shrikes are a territorial species and nests were well dispersed throughout the study site, we assumed that nest fates were independent.

We constructed a set of 17 candidate models to examine how nest survival might be affected by year, nest age, temperature, precipitation, and nest height. We began with a constant survival model and then added year as a categorical factor because annual variation in weather, predator abundance, and food availability might lead to yearly differences in nest survival. Nest survival might vary with the age of the nest because of the susceptibility of eggs or nestlings to weather or predators, or changes in parental behavior across the nest cycle (Martin et al. 2000, Grant et al. 2005). Therefore, we included a linear and quadratic effect of nest age in the model. A linear effect would indicate increasing or decreasing survival as the nest ages, whereas a quadratic effect would indicate a curvilinear relationship with higher or lower daily nest survival during the middle of the nest cycle. To test for effects of weather, we also included mean daily temperature and daily precipitation in the model. Finally, to the model with the most support, we added nest height, because higher nests may be less susceptible to certain predators such as mammals and snakes. Nest survival may also vary across the breeding season (Dinsmore et al. 2002, Nur et al. 2004, Wilson et al. 2007). However, we chose not to include seasonal trends because it can be difficult to separate effects of nest age and time of season when the onset of nest initiation is relatively synchronous and there is little re-nesting, as was the case in our study. It is possible that seasonal variation in ecological factors, such as the abundance of alternative prey or predator activity, might cause temporal changes in nest survival, and we consider these possibilities in our interpretation.

We used a sine link function for the constant survival model and a logit link for models with covariates. There is currently no suitable goodness of fit test for nest survival models in MARK (Dinsmore et al. 2002), and therefore, we have not used one here. We used Akaike’s information criterion for small samples (AICc, Akaike 1973, Burnham and Anderson 2002) to rank candidate models, and the ΔAICc and Akaike weights ($w_i$) to to evaluate the support for each model. We constructed a confidence set on the models and considered models with ΔAICc ≤2 to be well supported by the data (Burnham and Anderson 2002). Although model averaging is a useful means to represent variable uncertainty, we chose not to use it here because it would have meant averaging across models with linear and quadratic terms. This can be problematic because the estimates do not necessarily reflect the initial hypotheses that were tested (Burnham and Anderson 2002, Blums et al. 2005). Instead, we use the model weights to qualitatively compare parameter estimates from the top models.

# RESULTS

## Breeding Biology

In 1992, we observed 69 nests in total, of which 60 were first attempts. Two of these first attempts had uncertain fates, and one was believed to have failed because of researcher activity and was excluded. Of the remaining nests, 25 failed and 31 were successful. There were nine re-nest attempts after failure, and of these, six failed and one fate was unknown. In 1993, we observed 73 nests of which 67 were first attempts. Forty-two of these first attempts failed and there were two with unknown fates. Six pairs re-nested and two of these attempts failed. There were no known cases of double-brooding in either year. Mean Julian date of first egg (DFE) based on found nests in 1992 and 1993, respectively, was 144.7 (May 24) and 141.6 (May 22), and the adjusted mean DFEs based on the Horvitz-Thompson estimator were 143.4 and 141.1, respectively. Across both years, nest initiation dates ranged from 4 May to 15 June, although 96% were initiated between 11 May and 5 June. Mean size of the first clutch was 6.2 eggs (95% CI: 6.0, 6.5) in 1992 and 6.5 eggs (CI: 6.3, 6.7) in 1993. Length of the incubation period was similar between the 2 years and averaged 16.46 d (CI: 16.03, 16.89) in the first, and 16.75 d (CI: 16.20, 17.30) in the second. Hatching occurred from 2 June through 10 July, and the nestling period averaged 17.23 d (CI: 16.79, 17.67) in 1992, and 16.82 d (CI: 16.32, 17.32) in 1993. Fledgling production was higher in 1992, with 176 fledglings produced (2.7 fledged young/female), whereas only 92 were produced in 1993 (1.3 fledged young/female). Lower fledgling production in the second year was partly attributed to lower nest survival because of colder and wetter weather (see below), but was also related to a higher rate of partial brood loss. Although clutch sizes were similar between years, an average of 5.0 nestlings fledged per successful attempt in the first year (95% CI: 4.5, 4.6) compared with only 3.6 in the second (CI: 2.9, 4.3). This difference was primarily due to losses during the nestling stage, as the 2 years were similar in the number of eggs that were inviable or lost before hatch (1992: 0.6 eggs (CI: 0.3, 0.9); 1993: 0.6 eggs (CI: 0.3, 0.8)). By contrast, only 0.8 nestlings were lost per successful brood in 1992 (CI: 0.2, 1.3) compared with 2.3 in 1993 (CI: 1.7, 3.0).

## Nest Survival

Predators were the main apparent cause of nest loss, but their direct impacts on nest survival differed between years. In 1992, we assigned cause of failure to 31 nests, all of which were believed to have directly failed because of predators. In 1993, we assigned cause of failure to 44 nests, of which 33 failed because of predators whereas 11 failed because of weather, abandonment, or starvation. There were no suspected cases of complete nest loss because of infertility. For nest survival analyses, 67 of the 69 nests in 1992 had sufficient information whereas all 73 did in 1993. Nests were monitored over 2792 exposure days across the 2 years. Estimates of daily nest survival from the constant model without year or covariates was 0.973 (95% CI: 0.967, 0.978). The top three models, with a combined weight ($w_i$) of 0.95, contained a quadratic nest age effect, mean daily temperature, and daily precipitation, providing strong evidence that these three variables were influential in determining nest survival in this population (Table 1). Parameter values for nest age were positive for the linear term (from the top model, $\beta_{age}$ = 0.150, 95% CI: 0.056, 0.244) and negative for the quadratic term ($\beta_{age}{}^2$ = -0.005, 95% CI: -0.007, -0.003). Using the top model, we predict a pattern of increasing daily nest survival during egg laying and approximately constant survival through the incubation period (Fig. 1). Daily nest survival then declined through the nestling stage and ranged from approximately 0.99 just after hatch to <0.93 at fledging. Daily nest survival also covaried with weather and was positively correlated with temperature ($\beta_{temp}$ = 0.175, 95% CI: 0.049, 0.301) and negatively correlated with precipitation ($\beta_{precip}$ = -0.049, 95% CI: -0.073, -0.025, Fig. 1). There appeared to be little influence of nest height on daily nest survival ($\beta_{height}$ from the second model in Table 1: 0.199, 95% CI: -0.344, 0.741). We considered uncertainty in model parameter estimates by qualitatively comparing results from the top models (range of the β estimate across the top three models: $\beta_{precip}$ = 0.0019, $\beta_{temp}$ = 0.0073, $\beta_{age}$ = 0.0060, $\beta_{age}{}^2$ = 0.0001).

There was some support for the addition of year to a constant survival model, however, when temperature and/or precipitation were in the model, the effects of year dropped out. This suggests that variance between years may be largely caused by annual differences in effects of weather. Using the top nest survival model, we estimated the survival probability for a nest with a 37-d cycle (assuming 4 d laying, 16 d incubation and 17 d nestling stage) that was initiated on 24 May (average DFE across both years) and including values of temperature and precipitation experienced in each year. The resulting nest survival estimates were 0.42 for 1992 and 0.29 for 1993. For comparison, the apparent nest survival estimates were 0.51 and 0.38 for 1992 and 1993, respectively, although these estimates were based on all nests throughout the season.

# DISCUSSION

## Breeding Biology on the Periphery

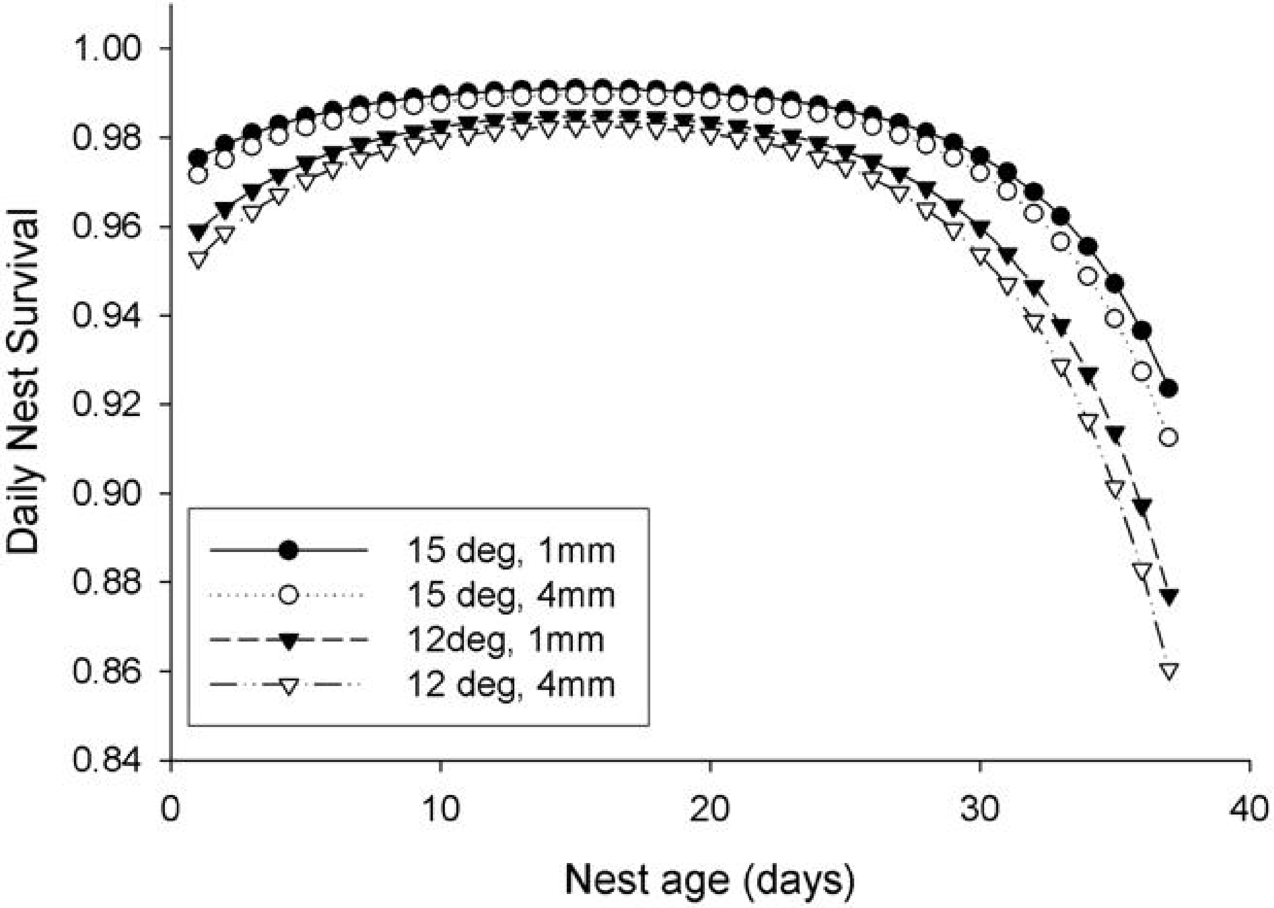
Rates of re-nesting and double-brooding in Alberta were low compared with values reported in more southern populations. Only 19% of pairs re-nested after their first attempt failed, and there were no known cases of double-brooding. However, we cannot rule out that some pairs initiated a second attempt in late July and August after observations ended, and therefore, these are minimum estimates. Re-nesting after failure and double-brooding was

**Table 1.** Summary of model selection results for nest survival of Loggerhead Shrikes in southeastern Alberta in 1992 and 1993. Analyses were performed using program MARK and models are ranked by ascending Akaike's Information Criterion for small samples (AICc). ΔAICc is the change in AICc between that model and the best fitting model, $w_i$ is model weight (a measure of the relative likelihood of each model) and k is the number of model parameters. Deviance is the difference in the -2*log-likelihood between that model and the saturated model. Nest age refers to the linear age model, whereas nest age2 refers to the quadratic model. Models without nest age assume constant survival across the nest cycle.

| Model | AICc | ΔAICc | $w_i$ | k | Deviance |
|---|---|---|---|---|---|
| $S_{\text{Nest age2 + Precip + Temp}}$ | 451.99 | 0.00 | 0.499 | 5 | 441.97 |
| $S_{\text{Nest age2 + Precip + Temp + Nest height}}$ | 453.47 | 1.48 | 0.238 | 6 | 441.44 |
| $S_{\text{Nest age2 + Precip + Temp + Year}}$ | 453.67 | 1.68 | 0.215 | 6 | 441.64 |
| $S_{\text{Nest age2 + Precip}}$ | 457.27 | 5.29 | 0.036 | 4 | 449.26 |
| $S_{\text{Nest age2 + Temp}}$ | 459.61 | 7.62 | 0.011 | 4 | 451.59 |
| $S_{\text{Nest age + Precip + Temp}}$ | 465.66 | 13.67 | 0.001 | 4 | 457.65 |
| $S_{\text{Nest age2}}$ | 465.71 | 13.72 | 0.001 | 3 | 459.70 |
| $S_{\text{Nest age + Precip + Temp + Year}}$ | 467.66 | 15.67 | 0.000 | 5 | 457.64 |
| $S_{\text{Precip + Temp}}$ | 473.43 | 21.44 | 0.000 | 3 | 467.42 |
| $S_{\text{Precip}}$ | 473.66 | 21.67 | 0.000 | 2 | 469.66 |
| $S_{\text{Precip + Year}}$ | 474.75 | 22.76 | 0.000 | 3 | 468.74 |
| $S_{\text{Precip + Temp + Year}}$ | 475.15 | 23.16 | 0.000 | 4 | 467.13 |
| $S_{\text{Nest age}}$ | 475.65 | 23.66 | 0.000 | 2 | 471.65 |
| $S_{\text{Temp}}$ | 477.86 | 25.88 | 0.000 | 2 | 473.86 |
| $S_{\text{Year}}$ | 477.87 | 25.89 | 0.000 | 2 | 473.87 |
| $S_{\text{Constant}}$ | 477.90 | 25.91 | 0.000 | 1 | 475.90 |
| $S_{\text{Temp + Year}}$ | 478.68 | 26.69 | 0.000 | 3 | 472.67 |

more common for breeding shrikes in Florida (Yosef 2001), Virginia (Luukkonen 1987), and Missouri (Kridelbaugh 1983). Such variation among sites is likely related to differences in phenology across latitudes, which would influence breeding season length and the frequency of multiple attempts. For resident shrikes in Florida, breeding takes place from January through June, whereas for migrant shrikes in Alberta, the season is restricted to May through July. Other southern populations also have an earlier onset of breeding than observed in our study (Esely and Bollinger 2001, Boal et al. 2003). Although latitudinal effects on phenology are almost certainly important, other factors such as habitat quality may also influence the number of attempts (Nagy and Holmes 2005). Studies in Oregon, where latitude is more similar to our site, found re-nesting rates of 34% and double-

**Fig. 1.** Change in daily nest survival across the 37-d nest cycle for Loggerhead Shrikes in southeastern Alberta. Values were generated using estimates from the top model (Table 1) and include predicted daily nest survival rates when daily temperature averages 12 and 15°C, and, when precipitation averages 1 and 4 mm per day. Stages of a typical nest cycle include laying (days 1–5), incubation (days 5–20) and nestling (days 21–37).



brooding on 27% of territories (Humple and Holmes 2006).

Annual reproductive output is often positively related to the number of nesting attempts (Wilson and Arcese 2003) and thus for populations on the northern periphery, a short breeding season with reduced re-nesting will likely lower annual reproductive output (e.g., Nagy and Holmes 2004). Across 2 years, mean fledglings per female and fledglings per clutch at our site was 2.0 and 1.8, respectively. Productivity was also low in Manitoba at 0.9 young fledged per clutch (De Smet 1993), whereas further south, rates (fledged young/clutch) averaged 4.1 in southern Ontario (Chabot et al. 2001), 3.3 in Missouri (Esely and Bollinger 2001), 2.3 in Arizona (Boal et al. 2003), and 3.6 in Colorado (Porter et al. 1975). Tyler (1992) observed low rates in Oklahoma, with only 1.33 fledglings/clutch. In Oregon, pairs averaged 3.11 fledglings per territory

(Humple and Holmes 2006), and some of the highest rates were observed in Florida, where shrikes averaged 5.1 fledglings per pair over a 3-year study (Yosef 2001, see Yosef 1996 for other studies).

Clutch sizes for Loggerhead Shrikes increase with latitude, and tend to be larger in western populations (Yosef 1996). In our study, clutch sizes averaged 6.2 and 6.5 over the 2 years. Estimates from other populations include 3.8 in Florida (Yosef 1994), 5.6 in Missouri (Esely and Bollinger 2001), 5.8 in Oklahoma (Tyler 1992), 6.1 in Manitoba (De Smet 1993), and 4.9 and 5.6 across 2 years in southern Ontario (Chabot et al. 2001; see appendix in Yosef 1996 for other studies). There was less variation across latitudes in the average incubation and nestling periods, although our estimates for the latter are slightly shorter than values reported from more southern locations (Yosef 1996).

### Influence of Weather on Daily Nest Survival and Partial Brood Loss

Nest survival estimates based on program MARK were 0.42 and 0.29 for each of the 2 years, whereas apparent survival estimates were 0.51 and 0.38. These values tend to be low compared with other populations (although within the range of observed estimates), where rates of 0.5 to 0.7 are more common (Yosef 1996). Examination of cause-specific failure rates indicated that predators appeared to be the primary factor behind nest loss in both years, but losses to weather, abandonment, and starvation were more frequent in 1993. Other studies have also indicated that predation is typically the dominant cause of nest failure in this species (Porter et al. 1975, Yosef 1994, Chabot et al. 2001), although other factors such as weather are often influential (Etterson et al. 2007). Assigning failure due to apparent causes may underestimate nest failure due to weather, abandonment, or starvation because scavengers may remove the contents of nests that fail due to these causes, thus giving the appearance of nest predation (Etterson et al. 2007). Therefore, we consider our estimates of apparent failure due to causes other than nest predation to be a minimum rate. For many songbird species, temporal and spatial variation in predator abundance can have marked effects on songbird reproductive success (Arcese and Smith 1999, Wilson and Arcese 2006). Likely predators in the study area include American Crows (*Corvus brachyrhynchos*), Black-billed Magpies (*Pica hudsonia*), bullsnakes (*Pituophis catenifer*), and long-tailed weasels (*Mustela frenata*), and several species of raptors may take nesting females or foraging adults. Sargeant et al. (1993) examined abundance of waterfowl nest predators across the prairie region and found that avian species were relatively abundant in southern Alberta, whereas mammalian species were less so. This region appears to have lower predator diversity compared with the southern United States (Yosef 1994), but estimates of abundance for all species would be needed for direct comparison across sites.

Although predators were the ultimate cause of failure for most nests, daily nest survival rates were lower during cool, wet weather. These effects may have included some cases where weather was directly responsible for abandonment or nestling mortality. However, weather can also have an indirect impact by affecting the behavior or efficiency of predators (Post et al. 1999). For example, Rufous-crowned Sparrows (*Aimophila ruficeps*) in California have higher nest success during cool, wet weather, which may be due to thermoregulatory constraints on foraging by snakes (Morrison and Bolger 2002). Methods that assign failure to specific causes will not detect cases where weather influenced nest survival through effects on predator behavior. Approaches that examine survival of all nests with weather as a covariate may better capture the overall effects of weather (Dinsmore et al. 2002). In our study area, insect or small mammal prey may be less abundant during rain or cold temperatures, which may force predators to seek out alternative prey such as nesting birds. Lower prey availability for shrikes during these periods may also require parents to spend more time foraging and less time defending the nest. Further studies could examine how temperature and precipitation affect predator activity or the abundance of alternative prey.

Our top model also suggested strong effects of nest age on daily nest survival, which tended to increase from laying to incubation, remained approximately constant through incubation, and then declined through the nestling stage. A similar pattern was found for a Loggerhead Shrike population in Oregon (Nur et al. 2004). Other grassland birds including Lark Buntings (*Calamospiza melanocorys*, Jehle et al. 2004) and Chestnut-collared Longspurs (*Calcarius ornatus*, Lloyd and Martin 2005) have showed declining daily nest survival with nest age. During the nestling period, nests may attract greater attention because of begging chicks and frequent movements to and from the nest by foraging adults (Martin et al. 2000, Jehle et al. 2004). Nestlings may also be more susceptible than eggs to inclement weather (Diehl and Myrcha 1973). Some studies also show that daily nest survival might increase within the nestling period because older chicks are less susceptible to weather or predators (Grant et al. 2005), however, this was not the case in our study. Because of synchrony in the onset of breeding and low re-nest rates, we were unable to separately identify effects of nest age and time of season. Most nests would be in the incubation stages in late May–early June, and the nestling stage in mid- to late June. Therefore it is also possible that declining survival for older nests is actually influenced by a seasonal change in the environment, perhaps changes in predator behavior or the abundance of alternative prey throughout the season.

Partial brood loss was notable during the study, particularly in 1993 when for each successful nest, more than two young on average were lost between hatch and fledging. We suspect this loss was largely due to the effects of weather, either directly or indirectly, on nestling survival because there was little partial egg loss earlier in the season. Changes in food abundance unrelated to fluctuations in weather may also have led to increased partial brood loss. In Japan, mortality of nestling Bull-headed Shrikes (*Lanius bucephalus*) was positively correlated with daily precipitation during a severe weather year (Takagi 2001). This led to a lower overall reproductive output in that year relative to the previous one, similar to our observations. Partial brood loss was also observed for Red-backed Shrikes (*Lanius collurio*) in Poland, but appeared to be driven primarily by variation in food abundance rather than direct effects of weather on chick survival (Golawski 2006, see also Dawson and Bortolotti 2000, Rodriguez and Bustamente 2003).

## CONCLUSION

Our results suggest three mechanisms behind lower reproductive success of Loggerhead Shrikes relative to other sites in the range. First, the shorter breeding season restricts the ability to re-nest following failure or to initiate second-broods after a successful first attempt. Second, nest survival is lower, which may be due to the additional direct effects of weather on nest success and a possible interaction between weather and predators. The mechanism by which weather affects predator behavior in this region would be a useful area for further study. Third, inclement weather appears to lead to greater partial brood loss during the nestling stage. Our results are consistent with the idea that peripheral populations experience more extreme environmental conditions and have lower demographic rates as a result (Maurer and Brown 1989, Mahony et al. 2006). Over the past few decades, there has been an increase in the average amount and frequency of rainfall events during the summer months in the study region (Akinremi et al. 2001). Given our findings, a continuation of this trend may further depress reproductive output and increase the susceptibility of this population to declines, especially if juvenile and/or adult survival are similarly affected. Additional data on survival would be useful to examine these possibilities. Individuals in this population also appear to require larger territories than those in core parts of the range (Collister and Wilson 2007), which, combined with the lower reproductive output, may limit the growth potential for this population and contribute to its recent declines.

*Responses to this article can be read online at:*
*http://www.ace-eco.org/vol2/iss2/art11/responses/*

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