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Impacts of nest predators and weather on reproductive success and population limitation in a long-distance migratory songbird

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Although avian nesting success is much studied, little is known about the relative importance of the factors that contribute to annual reproductive success and population limitation, especially for long-distance migratory songbird species. We combined a field experiment limiting access to nests by mammalian predators with modeling of long-term field data of American redstarts (Parulidae: *Setophaga ruticilla*) to assess the effects of multiple environmental variables on breeding success and population limitation. Experimental treatment (baffles placed around tree boles beneath active nests; n = 71) increased nesting success of this single-brooded species significantly (77 vs 50% in controls; n = 343), demonstrating that scansorial mammals, primarily red squirrels *Tamiasciurus hudsonicus* and eastern chipmunks *Tamias striatus*, reduced reproductive success. Based on unbaffled nests (n = 466), daily nest survival varied annually, and was positively influenced by May temperature and negatively by sciurid nest predator abundance. Daily nest survival was also influenced positively by June rainfall, and declined with nest age but not with calendar date. Since nest failure was overwhelmingly caused by nest predation, these significant climate and nest-age effects in our models are indirect, likely influencing nest predator and/or nesting bird behaviors that in turn influenced nest predation. Redstart population density had no effect on nesting success, after accounting for other factors. Annual reproductive success accounted for 34% of the variability in annual population change in redstarts in our study area. Our findings document 1) breeding season population limitation in this species, 2) a link between tree masting and bird population dynamics via mammal population fluctuations, 3) the independent contributions of summer versus winter population processes in a migratory species, and 4) the potential complexity of climate-biotic interactions.

Population growth in many vertebrate taxa is most sensitive to adult survival rate, but annual variation in reproductive success can also drive population dynamics (Sæther and Bakke 2000, Stahl and Oli 2006). Reproductive success is relatively well studied in birds in relation to their nesting behavior, and has been linked to extrinsic factors like nest predators (Ricklefs 1969, Martin 1993, Robinson et al. 1995, Thompson 2007), food (Sillett et al. 2000, Etterson et al. 2007, Norris et al. 2013) and weather (Morrison and Bolger 2002, Collister and Wilson 2007, Townsend et al. 2013). Such extrinsic factors may themselves be influenced by larger scale ecological phenomena (Ostfeld and Keesing 2000, Sillett et al. 2000, Norris et al. 2013) such as masting tree seed crops that elevate the abundance of mammalian nest predators and indirectly reduce reproductive success (Rimmer et al. 2001, Schmidt and Ostfeld 2003, Clotfelter et al. 2007).

Reproductive success in birds also depends on intrinsic factors such as population density. A variety of studies have documented negative density-dependence of reproductive variables (Arcese et al. 1992, Schmidt and Whelan 1999, Gunnarsson et al. 2005, Gunnarsson and Elmberg 2008, McKellar et al. 2014; but see Ringelman et al. 2012) capable of regulating populations (Sillett and Holmes 2005), and multiple regulatory mechanisms have been documented for a long-distance migrant, the black-throated blue warbler *Setophaga caerulescens* in New Hampshire (Rodenhouse et al. 2003). Few studies, however, have analyzed both extrinsic and intrinsic factors contributing simultaneously to reproductive success, let alone considered mechanisms and interactions among multiple factors over long enough time periods to gauge their relative importance.

Annual fecundity may contribute to population fluctuations, as evidenced by the correlation between the reproductive success in one year and the recruitment of new adults into the population in the following year (Johnson and Geupel 1996; reviewed by Holmes 2011). Indeed, whether migratory birds are controlled more by winter or breeding circumstances is controversial (Sherry and Holmes

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1995, Greenberg and Marra 2005). Population dynamics also depend on circumstances throughout the annual cycle, necessitating the integration of ecological factors that affect reproduction, survival, and interactions thereof (Sillett et al. 2000, Runge and Marra 2005, Passinelli et al. 2011). Populations of migratory species can also be impacted by geographically isolated circumstances (Newton 2008). For example, winter conditions can affect annual adult survival of long-distance migratory songbirds (Sillett et al. 2000, Johnson et al. 2006, Szep et al. 2006) and abundance in the following breeding season (Wilson et al. 2011). Conditions on the wintering grounds may carry-over to influence subsequent reproductive success (Marra et al. 1998, Norris et al. 2004, Calvert et al. 2009, Reudink et al. 2009, Sorensen et al. 2009, Rockwell et al. 2013), suggesting the possibility that conditions in winter may be stronger than those in summer by impacting both annual survival and fecundity. Although much has been learned about the seasonal cycle in migratory birds (Faaborg et al. 2010), few studies have compared ecological controls on reproductive success with non-breeding ecology in the same species.

Here, we examine and evaluate multiple extrinsic and intrinsic ecological factors that potentially limit reproductive success and population size in a long-distance migratory songbird, the American redstart (hereafter redstart). This species is advantageous for such studies because its demography has been addressed in winter (Johnson et al. 2006, Studds and Marra 2007, Wilson et al. 2011), migration (Smith and Moore 2004, Smith et al. 2007), summer (Sherry and Holmes 1992, Norris et al. 2004, McKellar et al. 2014), and via carry-over effects between seasons (Marra et al. 1998, Norris et al. 2004, Reudink et al. 2009). First, we hypothesized that scansorial mammals significantly affect nesting success of redstarts. We expected this effect because nest predation is the most prevalent cause of nesting failure in most birds (Ricklefs 1969) including redstarts (Sherry and Holmes 1997) and because populations of scansorial mammals – important nest predators at temperate latitudes (Thompson 2007) – fluctuate in response to mast fruiting of seed-bearing trees (Bergeron et al. 2011, Holmes 2011). The influence of these scansorial nest predators was examined experimentally, by limiting their ability to access nests, and by comparing sciurid predator abundance to annual nest success. Second, we hypothesized that seasonal climatic conditions affect nesting success. Our most parsimonious expectation was that nesting success would decline in years with colder May temperatures, thus delaying plant and insect phenology. Also, during wet weather, cooler temperatures might directly impact birds' ability to incubate eggs or provision young, as well as affect food (insect) availability. Third, we hypothesized that nesting success would be density-dependent, as documented in other birds (reviewed above). Fourth, we tested the hypothesis that reproductive success helps drive population dynamics. Because redstarts are single-brooded (i.e. fledge at most one brood per nesting season), nesting success directly estimates annual fecundity (Sherry and Holmes 1992). We thus expected that nesting success one year would be related to population size the next. Finally, fifth, we compared the effects of reproductive success with potential drivers of population change operating during other periods of the annual cycle.

Methods

Study site and species

Fieldwork was conducted from 1983–1995 in the Hubbard Brook Experimental Forest (HBEF), Woodstock, NH, USA. The forest consisted of uneven-aged, unmanaged second-growth northern hardwoods, following clear-cutting in the early 1900s, and was dominated by three deciduous tree species: American beech *Fagus grandifolia*, sugar maple *Acer saccharum*, and yellow birch *Betula alleghaniensis*, interspersed with isolated or small patches of conifers such as red spruce *Picea rubens* and balsam fir *Abies balsamea* especially at higher elevations and eastern hemlock *Tsuga canadensis* in cool stream drainages (Holmes 2011). Redstarts were studied primarily within the 180-ha area described by Sherry and Holmes (1985) and in nearby plots with similar elevations and vegetation.

Redstarts are small (~6–9 g), open-cup nesting, long-distance migrant songbirds that breed across North America from Louisiana north to southeastern Alaska and Newfoundland (Sherry and Holmes 1997). It is sexually dichromatic in plumage, allowing sex identification readily by sight and song behavior. Redstarts at Hubbard Brook nest adjacent to the main tree trunk or another vertical stem, and the majority of females in our study site nested low enough (median height 4–6 m) for their nests to be monitored directly from the ground or with the use of an extensible pole with a mirror (which allowed viewing of nest contents up to ~10 m). Nests built higher than 10 m (~34%) were monitored visually from the ground (e.g. incubation and nestling-feeding behavior) and with the aid of ladders and the extensible pole with mirror (clutch or brood sizes; see below and Supplemental material Appendix 1). Female redstarts are single-brooded (Sherry and Holmes 1997), but if nests failed due to predation or other causes, females re-nested, sometimes up to four times per season.

Field methods

Nest searching and monitoring

We concentrated efforts and tried to find nests of all redstarts occurring in a 34-ha core area (37.1% of 553 nests), located within the larger 180-ha study plot. We also located and monitored nests in other parts of the 180-ha area during our density surveys (see below), although not every nest was found in this larger area each year. Once found, nests were checked at least every 3–4 d but daily when we expected a nesting stage transition, e.g. start of incubation, hatching, or fledging.

We considered nest survival for just the incubation and nestling periods. We excluded daily egg survival during the laying period because a substantial proportion of nests were too high to monitor nest contents accurately from the ground on a day-by-day basis (Supplementary material Appendix 1). Unlike the start of laying, the start of incubation could be defined precisely as the day the female started sitting on the nest, which was readily observable from the ground, even at nests high in the canopy. We assumed the female began incubation the day the penultimate egg was laid, which was verified visually at low nests that could be monitored daily. The incubation period for this species is 11 d and the nestling period nine days, giving a 20-d nesting cycle not including the laying period (Sherry and Holmes 1997). We used these modal stage durations to back-calculate the start date of incubation and hatching at those nests located after one or the other of these transition dates but that survived to the next stage, hatching or fledging, respectively.

Experimental nest site protection

To test the hypothesis that ground-based, scansorial predators affected nesting success of redstarts, we applied metal baffles to a subset of nest trees in the years 1985–1989 and 1991–1995. These baffles were either cone-shaped sheet metal with the cone facing downwards, or an aluminum metal sleeve wrapped tightly around the tree bole, below and around the same stem as nests ($n = 71$; Fig. 1); we were unable to compare effects of the two types of baffles. The baffles were intended to prevent access to the nest from scansorial predators, particularly the two common sciurids, American red squirrel (henceforth red squirrel) and eastern chipmunk. These are the two nest predator species at Hubbard Brook most likely to be prevented from approaching tree-trunk nests characteristic of the redstart from below. Across all years, nest trees used in the experiment (i.e. containing baffles) tended to be smaller trees (mean diameter at breast height [DBH] ± SE = 11.82 cm ± 1.39 cm, mean tree height = 6.31 m ± 0.60 m) than the control nests (mean DBH = 17.01 cm ± 0.86 cm, mean height = 8.67 m ± 0.37 m); and nest height is correlated with tree height (TWS unpubl.). Nest tree height and DBH were included in models to control for any influence of tree size on daily nest survival while testing treatment effects.

Annual covariates of nest survival

Nest predator abundance

A variety of animals prey facultatively on the eggs and nestlings of small open-cup nesting birds at Hubbard Brook, including mice, sciurid and mustelid mammals, blue jay *Cyanocitta cristata*, sharp-shinned hawk *Accipiter striatus*, and probably at least two species of owl (Reitsma et al. 1990, Sherry and Holmes 1997, Sloan et al. 1998; RTH unpubl.). No arboreal snakes occur at Hubbard Brook. The two common sciurid predators (red squirrel, eastern chipmunk) were considered to be particularly important due to their relatively high abundances in some years and to several personal and video observations of these two species depredating actual nest contents of redstarts and other songbird species (Reitsma et al. 1990, Sloan et al. 1998, TWS and RTH unpubl.). Thus, as a covariate for our nest survival models, we used an estimate of sciurid abundance, based on the summed detections per observer hour of chipmunk plus red squirrel individuals, data which were collected by field workers in the study area at Hubbard Brook during the years of this study, 1983–1995 (Holmes 2011, and Supplementary material Appendix 1). A validation of this index independently of our study comes from the significant relationship between black-throated blue warbler nesting success at Hubbard Brook and this index (Supplementary material Appendix 1).

Weather data

To examine how annual breeding season weather affected nest survival, we obtained temperature and precipitation data for May and June, 1983–1995, representing the pre-nesting and nesting periods, respectively, for redstarts at Hubbard Brook. Daily weather data were available from multiple stations across the Hubbard Brook Experimental Forest (Campbell 2013a, b), and we used data from the two stations (1 and 6) located near our study areas to calculate monthly values: mean daily temperatures averaged by month and daily rainfall summed by month. The selection of monthly rather than daily values as covariates in our models was intended to represent the longer term (monthly) climatic conditions that breeding redstarts experience each breeding season, not how they might respond to daily fluctuations in weather.

Density

We estimated density of our study population using a proxy, the number of territories (i.e. singing males) occurring simultaneously on the 180-ha portion of our study area (males ha^{-1}, Supplementary material Appendix 1, Table A2; see also McKellar et al. 2014). Redstart territory density was determined each year by one or two observers systematically walking through this area during an approximately two-week

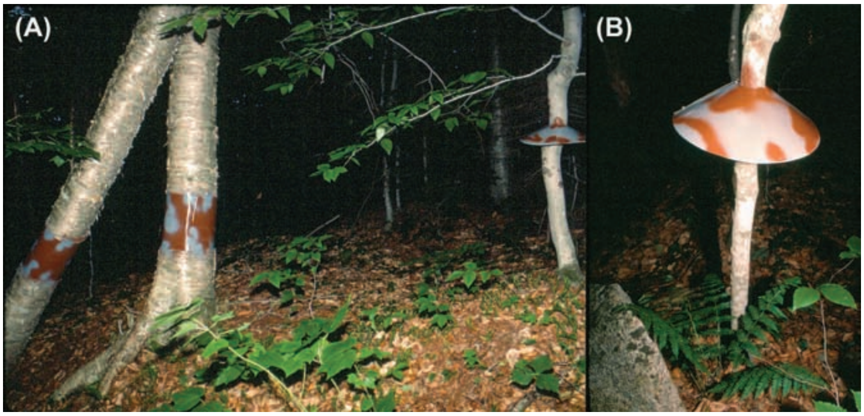

Figure 1. Sheet metal baffles used to prevent scansorial predators from climbing trees containing active American redstart nests. (A) Conical baffles were placed on smaller trees and sleeve baffles on trunks of larger trees. In a few cases, as in this photo, multiple baffles were used to keep scansorial predators from accessing a single nest. (B) Close-up of conical baffle below a nest in am American beech sapling.

period in mid-June, the peak of redstart nesting activity. We took advantage of the most intense singing behavior in the morning hours (details in Sherry and Holmes 1991; see also Staicer et al. 2006) to obtain multiple observations of all singing male individuals. We then compiled onto a composite map of the entire study area the locations of all singing males. To facilitate the field mapping, the 180 ha area was flagged every 25 m along the four transect lines (see 'Bird Transect Area', Fig. 1 in Holmes 2011), and in addition many areas between these lines were also flagged in a grid at 25-m intervals, particularly the relatively deciduous forest areas where redstarts were most abundant.

We used male territories in the 180-ha study area as the single best proxy for annual redstart population size in calculations of population growth rate. Numbers of territories, doubled to account for females, has been used to estimate population size for many species including redstarts at Hubbard Brook, based on many different bird population and community studies using the 10-ha long-term site (reviewed by Holmes 2011) embedded within the much larger 180-ha study area used in the present study. Moreover, trends in numbers of redstart territories on the 10-ha area paralleled the negative population trend throughout NH (1969–1998) and the same trend as three other 10-ha study areas spread out in the White Mountains of NH (1986–1998; Holmes and Sherry 2001). In both cases, patterns indicate that population trends using territories at Hubbard Brook mirrored much larger scale, regional trends. However, we could not simply double the number of territories in the 180-ha area to estimate the total population (males plus females) because some of these redstart territories were occupied by unmated males, most of which were yearlings (SY or Second Year) (Sherry and Holmes 1997). The numbers of such SY males (Sherry and Holmes 1991, 1992) and their spatial distribution within our study area varied annually (Sherry and Holmes 1985). For example, Sherry and Holmes (1991) estimated that an area needed to be at least 64 ha to give reliable estimates of the age ratio (SY to After Second Year = ASY) of males, which is important because the SY males are the new recruits into the population in a particular year, potentially reflecting good reproductive success the previous year (Holmes 2011). Numbers of territories have been used to test hypotheses about population dynamics in other studies of redstarts (McKellar et al. 2014) and other birds (Murphy 2001).

Analytical methods

Daily nest survival rate was analyzed using the nest survival module in Program MARK 6.0 (White and Burnham 1999, Dinsmore et al. 2002). To test the first hypothesis that scansorial predators were a key determinant of nest success, we compared nest survival from the experimentally baffled nests against controls, for which we included all other nests from the same years as the baffled nests (see Results). The model with only an intercept represented a null effect, while a model with treatment tested for a difference in daily nest survival due to the effect of the baffles. Year was included as a variable in this analysis to account for annual variation while estimating daily nest survival of control and baffled nests. To account for differences in nesting tree characteristics between treatments, we also included in the analyses the DBH and nest height of the tree in which the nest was located. These two variables are strongly correlated ($r = 0.87$), and before including treatment effects we compared support for models with each variable. The reduction in Akaike's information criterion for small samples (AIC_c, Burnham and Anderson 2002) was greater for DBH, and it was retained for subsequent analyses. The influence of the baffle treatment was examined by comparing the direction and strength of the beta coefficient for the treatment effect and the difference in model support between the two models.

To complement the experimental test of our first hypothesis, we also analyzed daily nest survival using data from all non-experimental nests to examine how nest success was related to annual variation in scansorial mammal abundance, climate, and population density. Because daily nest survival may also vary within years, either in relation to nest age (Dinsmore et al. 2002, Grant et al. 2005, Collister and Wilson 2007) or time of season (Smith and Wilson 2010), we analyzed temporal covariates within a year using 1) nest age, defined on a continuous scale with day 1 equal to the first day of incubation for an individual nest, and 2) time of season, with day 1 scaled to equal the first day of incubation in the study population. Nest age effects were tested in a linear fashion assuming daily nest survival might increase or decrease through the nest cycle, while time of season was tested with a linear model and a quadratic model, the latter testing whether daily nest survival was highest or lowest during the middle of the breeding season. As with the baffle experiment, DBH of the nest tree was included for every nest to control for differences in nest tree size among years and over the course of the nesting season.

Analysis of factors contributing to natural annual variation in nest success used 30 candidate models including a global and a null model. Model development first considered seasonal effects (nest age, time of season), then used the best model from this comparison to test annual effects. Models were ranked using Akaike's information criterion for small samples (AIC_c), and the ΔAIC_c values and Akaike weights (w_i) were used to infer support for each of the candidate models. Models within two units of the top model were considered to have support, except those cases where the secondary model was the same as the top model with one extra parameter. Parameter estimates were obtained by model averaging across all models containing the respective variables, except time, which was only averaged across models with the linear term.

To test the hypothesis that reproductive success influences population dynamics, we used a linear regression of population growth rate (lambda) from year t to year $t + 1$ as a function of average annual nesting success in year t. Population growth rate was defined as the natural logarithm of the ratio of abundance of territorial male redstarts in year $t + 1$ to that in year t, using redstart abundances in the 180-ha study area; thus, we assume only that the annual changes in the number of male territories is a reasonable surrogate for the number of total individual redstarts. Average yearly estimates of daily nest survival were obtained from program MARK using a model with year and DBH. Daily nest survival estimates were converted to nesting success over a 20-d period as described above.

Variance in the 20-d nest survival estimates was obtained using the delta method (Powell 2007).

Data available from the Dryad Digital Repository: < http://dx.doi.org/10.5061/dryad.73870 > (Sherry et al. 2015).

Results

Experimental nest protection

Our experiment included 71 nests that received the baffle treatment and 343 control (non-baffled) nests for a total of 4977 exposure days. Baffling was not done in 1983, 1984, or 1990, and we excluded nests from these three years in the control sample. For the other 10 yr, the proportion of baffled nests that was baffled ranged from 9 to 29% of all redstart nests found in the study area in those seasons (Supplementary material Appendix 1, Table A2). Comparison of models with and without nest baffles indicated a strong and positive effect of nest protection on nest success ($\hat{\beta}_{\text{baffled}} = 0.98 \pm 0.25$, Table 1a). Average daily nest survival across all years was 0.987 (95% CI: 0.979–0.992) for baffled nests and 0.966 (0.960–0.972) for control nests. These estimates extrapolated over the 20-d nesting cycle yielded average annual nest success rates of 0.77 (95% CI: 0.68–0.87) for baffled nests and 0.50 (0.44–0.57) for control nests. This difference suggests that at a minimum, scansorial nest predators were directly responsible for just over half of all nest failures in this population. Including nest tree DBH in the model was important since daily nest survival was higher in larger trees ($\hat{\beta}_{\text{DBH}} = 0.022 \pm 0.006$), so we would have underestimated the difference in nest success between treatments by 3% without controlling for this influence.

Annual and seasonal effects of predation, weather, and density on reproductive success

We obtained a sample size of 466 non-experimental redstart nests over 13 yr (all except the baffled nests) to analyze annual and seasonal variation in daily nest survival (effective sample size = 5374 exposure days). These 466 unbaffled nests experienced a variety of fates: 54.3% fledged, 39.6% had all contents depredated, 2.8% experienced starvation of the entire brood, 1.5% terminated with adult (female) mortality (and thus brood failure due to the absence of the female), 0.6% represented a clutch in which some chicks fledged and some starved, and 0.4% involved simultaneous nest depredation plus adult female predated. For analytical purposes nests were considered successful if at least one chick fledged per nest, and unsuccessful otherwise. A very small percent of nests (0.2%) were excluded from further analysis due to human interference, caused, e.g. by inadvertent disturbance to the nest or to the nesting adult.

Although many clutches were initiated at about the same time of the season each year, typically in the first week of June, redstarts continued to re-nest through the season following nest failures, initiating clutches as late as 4 July. However, we found no influence of time of season (calendar effects) on nest success, either as a linear ($\hat{\beta}_{\text{time}} = -0.002 \pm 0.008$ (SE)) or a quadratic effect (linear term: $\hat{\beta}_{\text{time}} = 0.009 \pm 0.030$, quadratic term: $\hat{\beta}_{\text{time}^2} = -0.0002 \pm 0.0005$). In contrast, there was support for a linear decline in daily nest survival with the age of the nest ($\hat{\beta}_{\text{nest age}} = -0.024 \pm 0.011$), ranging from 0.972 on day 1 to 0.961 on day 20 (Table 1b), indicating that depredation tended to be higher on nests later in the nesting cycle. Therefore, we retained nest age in models that considered annual covariates.

In terms of annual factors, nest predator abundance ($\hat{\beta}_{\text{predators}} = -0.104 \pm 0.034$) and May temperature ($\hat{\beta}_{\text{May temp}} = 0.256 \pm 0.078$, Table 1b, Fig. 2, 3) had the strongest influence, and models without either of these variables had no support. Sciurid nest predator abundance varied annually from 0 to 7.6 animals per observer-hour. Nesting success was negatively related to this estimate of abundance as predicted, ranging from nearly 60% in years when predators were least abundant to about 33% when they were most abundant (Fig. 3).

Average May temperature at Hubbard Brook over the study years ranged from 8.9 to 12.4 degrees Celsius, and

Table 1. Model selection results for daily nest survival of American redstarts at Hubbard Brook Experimental Forest, New Hampshire, USA (1983–1995) in relation to a) experimental nest protection and b) variation in sciurid nest predator abundance, redstart breeding population density, climatic conditions and intra-seasonal effects of time and nest age. For b), 30 candidate models were run, of which those shown here account for ~98% of the total model weights (w_i). Values in brackets after 'temp' and 'rain' refer to May (M) and June (J). All models had nest tree diameter (DBH) to account for differences in nest tree size among years or treatments. The model with only DBH for b) was 24.05 AIC units higher than the top model.

Model	ΔAIC_c	w_i	K	Deviance
a) Experimental nest protection				
nest protection + year	0.00	1.000	12	1153.6
year	16.48	0.000	11	1172.1
null	41.44	0.000	2	1227.1
b) Annual effects				
predators + temp(M) + rain(J) + nest age	0.00	0.327	6	1410.6
predators + temp(M) + rain(M, J) + nest age	1.07	0.191	7	1409.7
predators + temp(M, J) + rain(J) + nest age	1.37	0.165	7	1410.0
predators + density + temp(M) + rain(J) + nest age	1.99	0.120	7	1410.6
predators + temp(M) + rain(J)	2.20	0.109	5	1414.8
predators + temp(M) + rain(M) + nest age	5.21	0.024	6	1415.8
predators + temp(M) + nest age	5.31	0.022	6	1417.9
predators + density + temp(M) + rain(M) + nest age	5.73	0.019	7	1414.3

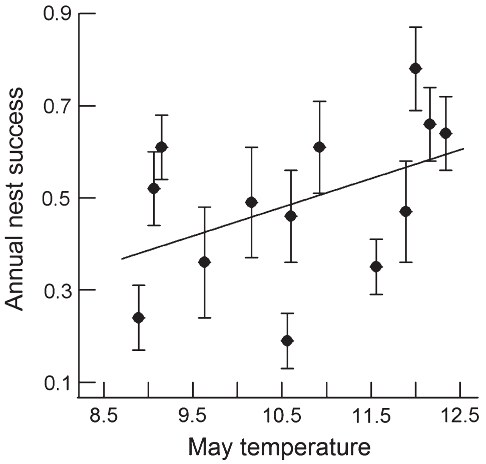

Figure 2. Nesting success of American redstarts in relation to annual May temperature. Nest success was estimated annually using program MARK and daily nest survival raised to the power of the length of the nesting cycle (20 d = incubation + nestling stage). Error bars represent the standard error in each year estimated using the delta method.

model predictions showed a positive response with nest success increasing from 31 to 62% over this range assuming average values for the other covariates. In contrast to the effect of May temperature, we found little influence of temperature during the main nesting period in June ($\hat{\beta}_{\text{June temp}} = -0.080 \pm 0.101$; model 3 in Table 1b). Rainfall showed the opposite pattern, with little effect of precipitation in May ($\hat{\beta}_{\text{May rain}} = 0.014 \pm 0.015$, model 2 in Table 1b), but a positive effect in June ($\hat{\beta}_{\text{June rain}} = 0.039 \pm 0.014$). We found no discernible impact of redstart population density on daily nest survival ($\hat{\beta}_{\text{density}} = 0.054 \pm 0.501$, model 4 in Table 1b).

Redstart male territory density in the study area fluctuated in abundance between 1983 and 1995, from a high of 0.87 to a low of 0.22 birds ha^{-1}, with a declining overall trend. Because of this decline in abundance we first examined trends in breeding success (i.e. nest success) before relating it to population change. However, while breeding success has fluctuated among years, there was no consistent trend over time ($\hat{\beta}_{\text{year}} = -0.008$, $R^2 = 0.03$, $p = 0.54$). Breeding success ranged from 0.19–0.79 (Supplementary material Appendix 1, Table A2), and had a significant positive effect on population growth rate λ (adjusted $R^2 = 0.34$; $F = 6.58$, on 10 DF, $p = 0.028$; Fig. 4). Thus, the number of territories in our population tended to increase in the breeding seasons following summers when breeding success was relatively high (~0.6 or greater), and decrease when it was lower, with a range of annual population growth rates between –0.6 and + 0.3.

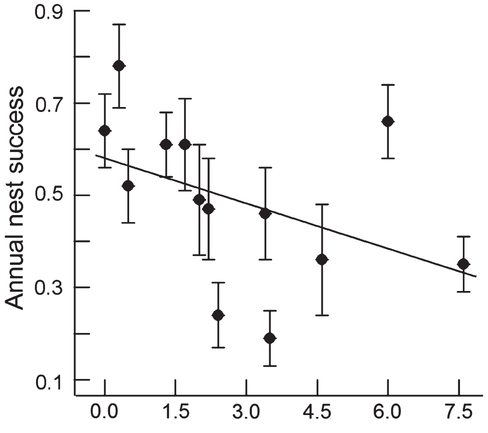

Figure 3. Nesting success of American redstarts in relation to annual predator (sciurid) abundance (summed red squirrel plus eastern chipmunk individuals sighted per hour per observer). Nest success and error calculated as in Fig. 2.

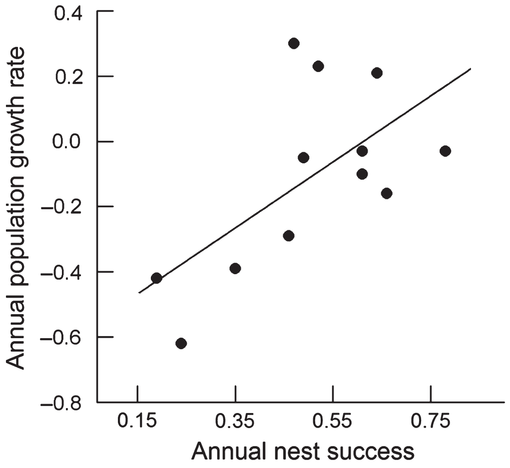

Figure 4. Population growth of American redstarts at Hubbard Brook in relation to their annual nesting success in the preceding year (1983–1995; $Y = 1.01 \times X - 0.62$; adjusted $R^2 = 0.34$). Population growth was calculated as the natural logarithm of the ratio of abundance of territorial male redstarts (on a 180-ha area) in year t + 1 over the abundance in year t. Average annual daily nest survival rates were estimated in program MARK and then converted to the 20-d nest success rates (equal to the length of the incubation and nestling stages) shown on the x-axis. Population abundance and annual nesting success data are given in Supplementary material Appendix 1, Table A2.

Discussion

Based on the best supported models of nest survival, multiple ecological factors including nest predators, May temperature, June rainfall, and nesting stage influenced the annual reproductive success of redstarts at Hubbard Brook. The first hypothesis was strongly supported in that experimentally limiting access to nests by scansorial predators increased nest success from 50 to 77%, on average. These predators were therefore responsible at a minimum for just over half of all nest failures (27 of the 50%) in this population. Average annual redstart nest success at unbaffled nests varied from about 19 to 78% during the 13 yr of this study. The second hypothesis on the effects of weather was also supported, but the patterns were more complex than predicted. Nesting success was higher in years when spring temperature in May was warmer, while precipitation had a positive influence on nesting success only in June, the opposite of our prediction. We found no support for our third hypothesis on the effects of population density on nest success. The fourth hypothesis on nesting success predicting growth rate of the population was supported. These results prompt questions about the ecological mechanisms that account for the variability in redstart nesting success in this northern hardwoods ecosystem, and how these patterns help understand year-round population processes in this species.

Mechanisms behind the patterns

The results of the nest tree baffle experiment and the importance of the nest predator covariate in our top models involving non-baffled nests support predation on eggs and chicks as a principal cause of nesting failure in birds (Ricklefs 1969, Martin 1993, Faaborg et al. 2010, but see Etterson et al. 2007), and implicate sciurid mammals (primarily red squirrel and eastern chipmunk) as the likely main cause of that failure. Although both of these species likely contributed to nesting failure, red squirrels probably had a greater influence because they are more arboreal than chipmunks, an assertion supported by the finding that red squirrels were photographed more often than chipmunks at artificial nests placed in trees and baited with quail eggs during an earlier study at Hubbard Brook (Sloan et al. 1998). Mustelids, especially fisher *Martes pennanti*, may have contributed to the effects of the baffle experiment since they are scansorial, and capable of learning to locate nests (Sloan et al. 1998). As top predators, however, they are less abundant than the sciurids and therefore less likely to be frequent predators. In other temperate forests, rodents also affect fledgling survival (Schmidt et al. 2008, Haché et al. 2014), which potentially contributes to population limitation, but we are unable to evaluate this possibility in our system. Although we did not identify predators using nest cameras (Ribic et al. 2012), the nest tree baffles allowed us to test the importance of a specific ecological category of nest predators (scansorial mammals) on the breeding success of redstarts over many years and at low expense.

Identifying sciurids as the most important nest predators on redstarts indicates an important link between a large-scale ecosystem process, masting by forest trees, and breeding success and population change for a migratory songbird. Annual variability in abundance of sciurids in the northern hardwoods ecosystem is related to seed masting, particularly by two of the dominant tree species, American beech and sugar maple (Holmes 2011). Sciurid abundance at Hubbard Brook typically peaks during the spring and summer following a large masting event in the previous autumn, with lower numbers in the intervening years (Holmes 2011). Studies in temperate oak forests in eastern North America have similarly linked acorn mast production with higher abundance of small mammals (eastern chipmunks and *Peromyscus* mice) and subsequent declines in nest success of songbird abundance (Schmidt and Ostfeld 2003, Clotfelter et al. 2007, Schmidt et al. 2008). Similarly, Bicknell's thrush *Catharus bicknelli* populations fluctuate in mountaintop habitats in New England on a two-year cycle, driven by balsam fir fruiting effects on red squirrels (Rimmer et al. 2001; see also Mahon and Martin 2006).

Multiple weather effects on breeding success were also documented in the present study, but only partially as predicted. Both May temperature and June rainfall remained in all the top models, and both were positively associated with nesting success, although the predicted May temperature effect was by far the greater of the two based on model support. Weather can impact nesting success directly, as evidenced by nestling starvation accounting for ~45% of nest failures in 1984 due to unusually cool and rainy weather in June of that year (Sherry and Holmes 1992), but on average over a long time period, nest predators accounted for the greatest proportion (90%) of redstart nest failures.

The fact that weather was so influential in models of nest survival, yet rarely a direct cause of nest failure in our study system, suggests that predators and weather interact to influence nesting success in this ecosystem, but the mechanisms are not well understood. Warmer May temperatures could accelerate vegetation phenology, providing greater nest concealment from predators earlier in the season (Martin 1992, Weidinger 2002), and both warmer temperature and rainfall might lead to a greater availability of insects during the nesting period (Sherry and Holmes 1997, Sillett et al. 2000). Higher food abundance could lead to shorter and less frequent incubation recesses for females (Rastogi et al. 2006), reducing adult activity at nests that might attract predators (Martin et al. 2000, Hannon et al. 2009). Increased temperature and precipitation might also result in a greater abundance of alternative foods (other than birds' eggs and chicks) for nest predators (Schmidt and Whelan 1999), such as more larval insects in leaf litter, corms of vernal herbs, or mushrooms.

Our results did not support an effect of redstart population (male territory) density on nesting success, consistent with earlier Hubbard Brook results showing nest depredation per se was not density-dependent either for black-throated blue warblers (which nest in shrubs, not trees) or for artificial nests placed in shrubs (0.25–1.5 m; Reitsma 1992). By contrast, McKellar et al. (2014) found that redstart nesting success in Ontario, Canada – inferred to be largely predator-controlled, as in our study – was strongly density-dependent. Their study found density dependence both among years, using the same measure of density as in our study, and spatially within-years (number of neighboring territories within 200 m). Different nest predator communities might explain this discrepancy: in the McKellar et al. study, although quantitative predator abundance data were not presented, nest predators were two corvid species (American crow *Corvus brachyrhynchos* and blue jay), two raptors (broad-winged hawk *Buteo platypterus* and sharp-shinned hawk), and the black rat snake *Elaphe obsolete*. Unlike red squirrels and chipmunks at Hubbard Brook, several of these predators have large home ranges, which may have facilitated more encounters and learning to find redstart nests at relatively higher densities (Schmidt and Whelan 1999, McKellar et al. 2014). These contrasting impacts of nesting density in the same bird species reinforce the importance of identifying the nest predator species (Cox et al. 2012a, Ribic et al. 2012).

Population implications

Our results support the hypothesis that reproductive success affects redstart population size. Annual nest success in our study population explained over 34% of the variance in population growth rate using territories as a proxy for population size. Redstart populations also fluctuate in synchrony across locations in the White Mountains of New Hampshire and the state of New Hampshire (Holmes and Sherry 2001, Jones et al. 2003), suggesting regional impacts of seed masting on the abundance of mammalian nest predators, although regional effects of climate on food abundance (Jones et al. 2003) may also have contributed. Support for the validity of using male territories as a proxy for population size and population growth rate estimates in the present study comes from the parallel trends identified using local territory counts in comparison with population changes at larger spatial scales (see references in Methods), the correlationss in Hubbard Brook redstarts between reproductive success one year and recruitment of yearling males the following year (Sherry and Holmes 1992), and success using territories to study population processes elsewhere (McKellar et al. 2014).

Other evidence supports the importance of reproductive success to population dynamics of redstarts. Populations have declined in response to forest fragmentation in eastern North America (Sherry and Holmes 1997, Sauer et al. 2011), as have many other species. These declines are due at least in part to increased nest predators and brood parasites associated with fragmented forest edges (Robinson et al. 1995). The brood parasitic brown-headed cowbird *Molothrus ater*, although not occurring at Hubbard Brook, not only limits redstart populations in some regions of the Canadian boreal forest but also interacts there with the effects of predators on nesting success via multiple mechanisms (Hannon et al. 2009; see also Cox et al. 2012b). Longer-term trends in the abundance of redstarts are also related to forest succession and maturation on the breeding grounds (Hunt 1996). At Hubbard Brook, redstarts were one of the most common breeding species in the late 1980s and 1990s when the site was pre-dominantly forest of mid-successional age, but have declined dramatically over the past 10–15 yr following a progression to older-aged forests (Holmes and Sherry 2001, Holmes 2011). Taken together, these results indicate that populations in this species are limited at least in part by breeding season processes that vary geographically, represent multiple temporal and spatial scales, and include annual fluctuations in climate, seed masting, predator abundance, redstart territory density, habitat quality (e.g. fragmentation), and forest succession.

Other studies reinforce breeding season limitation in migratory species, involving climate, seed masting, and nest predators (Rimmer et al. 2001, Schmidt and Ostfeld 2003, Clotfelter et al. 2007). Breeding season limitation also occurs in spruce woods warbler species responding numerically following outbreaks of spruce budworm caterpillars *Choristoneura fumiferana* across the North American boreal forest (Crawford and Jennings 1989, Venier and Holmes 2010), in cavity nesting birds in western North America responding similarly to outbreaks of spruce budworm and mountain pine beetle (Norris et al. 2013), and in the endangered Kirtland's warbler *Setophaga kirtlandii* rebounding from near extinction following fires that created optimal breeding habitat combined with a reduction in the abundance of brown-headed cowbirds that cause nest failure (reviewed by Bocetti et al. 2012). Even red knots *Calidris canutus*, often cited as a species that is limited by events during the migration period, may in fact be limited by nest predators on the breeding grounds as well (Fraser et al. 2013).

While our study and the above examples highlight the importance of breeding season limitation, the non-breeding season also influences the population dynamics of migratory birds (Greenberg and Marra 2005, Faaborg et al. 2010). Rainfall and its effect on vegetation during the dry season in the Caribbean region is linked to redstart abundance in eastern North American breeding habitats (Wilson et al. 2011, 2013), probably via mechanisms that influence physiological condition in winter (Marra and Holmes 2001, Studds and Marra 2007, Angelier et al. 2009) and ultimately annual adult survival (Johnson et al. 2006). Although winter habitat use influences individual fecundity (Marra et al. 1998, Norris et al. 2004, Reudink et al. 2009), the magnitude of this carry-over fecundity impact compared to the effects of nest predation documented in the present study is not yet clear. In the related black-throated blue warbler, fecundity and recruitment are strongly influenced by food availability during the breeding season, which is influenced by weather, but annual adult survival is affected by winter climate (Sillett et al. 2000) and density-independent mortality during migration (Sillett and Holmes 2002). Some Palearctic migrants also appear to be regulated in summer and winter including the red-backed shrike *Lanius collurio* (Saino et al. 2004, Passinelli et al. 2011) and leaf warblers (Phylloscopidae, Goldberg et al. 2012). However, in all these cases the relative magnitudes of winter vs summer (and migration) impacts, and their carry-over effects, on population dynamics remain to be determined, a task that will help focus conservation efforts.

Rainfall in the Caribbean region influences redstart adult survival (Johnson et al. 2006) and population dynamics (Wilson et al. 2011) via food abundance (Johnson et al. 2006, Cooper et al. 2015). We infer that these winter processes are independent of ecological conditions affecting redstart populations via nest predator population fluctuations in New England forests, the latter of which occur via mast fruiting of deciduous hardwood species. If so, then limiting factors in winter are independent of those operating in summer, and factors influencing survival to the extent they are determined in winter are independent of those influencing reproduction. Complicating this picture, seasonal carry-over effects from winter in redstarts and other species (Marra et al. 1998, Calvert et al. 2009, Reudink et al. 2009, Rockwell et al. 2013, Cooper et al. 2015) also impact reproduction; and a future task is to partition the effects of summer conditions on reproductive success vs winter carry-over effects. We also recognize that summer ecosystem processes such as mast fruiting of trees, forest fragmentation, and drought likely vary in their effects on migratory bird populations geographically (Hannon et al. 2009, Wilson et al. 2011, McKellar et al. 2014), necessitating comprehensive studies of limiting factors both geographically and throughout the annual cycle.

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Supplementary material (Appendix JAV-00536 at <www.avianbiology.org/readers/appendix>). Appendix 1.