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Effects of climate variation on timing of nesting, reproductive success, and offspring sex ratios of red-winged blackbirds

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Abstract Predicting ecological consequences of climate change will be improved by understanding how species are affected by contemporary climate variation, particularly if analyses involve more than single ecological variables and focus on large-scale climate phenomena. I used 18 years of data from red-winged blackbirds (*Agelaius phoeniceus*) studied over a 25-year period in eastern Ontario to explore chronological and climate-related patterns of reproduction. Although blackbirds started nesting earlier in years with warmer springs, associated with low winter values of the North Atlantic Oscillation Index (NAOI), there was no advance in laying dates over the study. Nesting ended progressively later and the breeding season lasted longer over the study, however, associated with higher spring values of NAOI. As the length of the nesting season increased, offspring sex ratios became more female biased, apparently as a result of females adjusting the sex of the eggs they laid, rather than from sex-biased nestling mortality. Clutch size did not vary systematically over the study or with climate. Opposing trends of declining nest success and increasing productivity of successful nests over the study resulted in no chronological change in productivity per female. Higher productivity of successful nests was associated with higher winter NAOI values, possibly because synchrony between nesting and food availability was higher in years with high NAOI values. Other than the association between the start of nesting and spring temperatures, local weather (e.g., temperature, rainfall) patterns that linked NAOI with reproduction were not identified, suggesting that weather patterns may be complex. Because climate affected most aspects of red-winged blackbird reproduction examined, focusing on associations between climate and single variables (e.g., first-egg dates) will have limited value in predicting how future climates will affect populations.

Keywords Breeding season · Clutch size · Nest success · North Atlantic Oscillation · *Agelaius phoeniceus*

Introduction

A better understanding of how different species are affected by current climates and why they sometimes respond differently to climate change is necessary for predicting future effects of climate change. For example, analyses of trends in laying dates of British birds showed that approximately one third of 65 species initiated laying significantly earlier, apparently in response to trends in spring temperatures and in the North Atlantic Oscillation (Crick et al. 1997; Forchhammer et al. 1998; McCleery and Perrins 1998; Crick and Sparks 1999). Because species that nested earlier were ecologically and taxonomically diverse, however, it was not apparent why these species responded to climate change while others did not. Of course, it is possible that some of the other species were responding to climate change, but in ways other than altering their first-egg date. Understanding how birds respond to climate change requires ecological studies that consider more than just how single factors (e.g., first-egg dates) are affected by climate. Here, I use data on red-winged blackbirds (*Agelaius phoeniceus*) collected over a 25-year period to assess whether there has been any systematic change in breeding biology through time, and how various aspects of breeding biology vary with climate.

Documenting that the timing of egg laying is affected by climate is valuable, but ultimately we need to determine whether climate affects reproductive success. For example, reproductive success could decline if a shift in the timing of breeding disrupts synchrony between food

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demand of nestlings and timing of food abundance. Such a mismatch of supply and demand of food negatively affects nestling growth and adult breeding site fidelity in blue tits (*Parus caeruleus*) (Thomas et al. 2001a, b). Climate can also affect avian productivity by changing the duration or quality of the breeding season, and thus the frequency of second clutches (Visser et al. 2003). Although Møller (2002) found that climate affected the relative size of first and second clutches of barn swallows (*Hirundo rustica*), overall breeding success did not vary with climate nor did it vary significantly through time. In the Mexican jay (*Aphelocoma ultramarina*), however, greater winter and spring precipitation enhanced reproductive success by allowing more females to breed (Li and Brown 1999). Sillett et al. (2000) found that annual variation in the El Niño Southern Oscillation affected both adult survival and fecundity of black-throated blue warblers (*Dendroica caerulescens*).

Red-winged blackbirds should be affected by climatic variation because North American birds show the same climate-mediated trend toward earlier nesting documented for European birds (Dunn and Winkler 1999), and red-winged blackbirds respond to having food available earlier by nesting earlier (Ewald and Rohwer 1982; Wimberger 1988). Also, the most important climate variable affecting European birds should also affect North American birds. The North Atlantic Oscillation (NAO) is a large-scale climatic phenomenon that affects temperature and rainfall in northern latitudes. Among European birds, variation in index values of the NAO (NAOI) has been associated with the timing of spring migration (Huppop and Huppop 2003), laying date (Przybylo et al. 2000; Sanz 2002), and clutch size (Przybylo et al. 2000; Møller 2002; Sanz 2003). In North America, variation in NAOI explained from 50% to 90% of the annual variation in productivity (assessed from age ratios of birds captured at a banding station) of ten landbird species that breed in the Pacific northwest (Nott et al. 2002). Finally, variation in the El Niño Southern Oscillation (ENSO) also appears to have widespread effects on north-temperate North American species (Sillett et al. 2000; Nott et al. 2002). Large-scale systems such as NAO and ENSO may be the mechanisms through which climatechange is occurring (e.g., Hurrell 1996; Visbeck et al. 2001). Here, I assess whether the nesting biology of red-winged blackbirds varies with the NAO and ENSO at a site in eastern Canada. When nesting biology is associated with either NAO or ENSO, I attempt to identify the local weather variable responsible for the pattern.

Materials and methods

Field methods

Data presented here come from studies of red-winged blackbirds conducted at the Queen's University Biological Station in eastern Ontario (45°37′N, 76°13′W) between 1974 and 2000. The individual studies had a number of field methods in common and were conducted using the same group of cattail marshes. Although every site was not used in every study, every study used multiple sites and each study had multiple sites in common with other studies. Data were collected for 18 years between 1974 and 2000. In most years, every nest at a site was found and its fate determined. In 1981–1983, however, eggs were collected late in incubation, precluding determination of nest success, and in 1999–2000, reduced nest searching later in the season precluded determination of last nest dates. Detailed methods for specific years are available from the following: 1974–1975 (Weatherhead and Robertson 1977), 1981 (Weatherhead 1983), 1982–1983 (Weatherhead 1985), and 1985–1995 (Weatherhead and Sommerer 2001). Methods for 1999–2000 are unpublished, but with the exception noted above, were similar to those in Weatherhead and Robertson (1977) for aspects relevant here. Unless otherwise indicated, in each analysis I include all years for which data were available.

Nesting variables

Previous studies have not adopted a standard approach for quantifying the onset of nesting, and most have explicitly excluded second nests and re-nests to ensure that measures used reflected when females, individually or collectively, started laying. Because my goal was to assess both when nesting started and ended, I used mean first-egg dates for the first 20% of all nests initiated and mean first-egg dates for the last 20% of all nests initiated each year. I used the difference between these start and end dates as a measure of the length of the breeding season. Hereafter, when I refer to the birds starting to nest earlier or later I mean that the mean date of the first 20% of nests was either earlier or later in the spring. The same also applies to how late the birds nested each year (i.e., the mean date of the last 20% of nests). The mean initiation date of the first 20% of nests was strongly correlated with the first-egg date for the population each year ($r=0.82$, $F=33.6$, df = 17, $P<0.0001$), so various metrics used by different studies to quantify nesting chronology are probably comparable. Julian dates (1 January = 1) are used throughout.

I estimated mean clutch size from all nests that reached incubation. I considered a nest to have been preyed on if the complete contents disappeared prior to the expected fledging date. The productivity of successful nests was quantified as the number of fledglings produced. All nestlings were measured daily or on alternate days in 1985–1993 and in 1995. I used these measurements to determine fledgling sex ratios based on sexual size dimorphism (Holcomb and Twiest 1970; Fiala 1981; Westneat et al. 1995) for approximately 90% of fledglings (details provided in Weatherhead and Dufour 2000, 2005). I computed the fledging sex ratio for a given year as the mean of the sex ratios of all nests that fledged young.

I could not estimate the productivity of the population each year simply by summing the number of fledglings produced because the suite of study areas used differed among years. Instead, I estimated productivity per female each year by dividing the total number of fledglings produced by the total number of females in the study areas that were used. I estimated the number of females on each male's territory as the maximum number of simultaneously active nests at any time in the breeding season. I then summed these values across all territories studied that year to estimate the total female population.

Weather variables

Indices of spring weather that have been associated with the onset of nesting by birds include "warmth sum" (the sum of daily temperature maxima from 1 March to 25 April; McCleery and Perrins 1998), minimum temperatures during the months in which females began laying (Brown et al. 1999), mean monthly temperatures in April–June (Dunn and Winkler 1999), winter values of NAOI (Przybylo et al. 2000; Sanz 2003), and average daily maximum temperatures in the first four, five-day periods in May (Hussell 2003). I arbitrarily selected "warmth sum" for the spring temperature variable, calculated as the sum of daily maxima from 1 April to 15 May, because red-winged blackbirds in my study population return in late March and begin nesting in early May.

Local weather variables used to identify links between climate (below) and reproduction included mean daily maximum, minimum, and mean temperatures for each of May, June, and July, and the total precipitation and number of days with precipitation in each of those months. Temperature and precipitation data were obtained from Environment Canada from weather stations located within 40 km of the study area.

Climate variables shown to affect nesting productivity include annual mean monthly values of the standardized Southern Oscillation Index (SOI) representing annual ENSO conditions (Sillett et al. 2000), winter values of NAOI (Sanz 2003), and spring values of NAOI and an ENSO precipitation index (ESPI) (Nott et al. 2002). NAO is the dominant factor influencing winter weather over the North Atlantic (Wettstein and Mearns 2002). Although NAO is broadly associated with colder, drier winters in Canada, local weather conditions are not affected uniformly everywhere (e.g., Stone et al. 2000; Wettstein and Mearns 2002). Because I was unable to find definitive evidence of predictable weather patterns in eastern Ontario associated with either ENSO or NAO, a first step in analyzing climate and weather data was to identify local weather patterns associated with variation in climate patterns.

I obtained monthly mean NAOI and SOI values from the National Oceanic and Atmospheric Administration's Climate Prediction Center (http://www.cpc.ncep.noaa.gov/data/). Consistent with previous studies, I treated winter (December–February) and spring (March–May) NAOI values separately. For the years of my study, they were not significantly related ($r=0.28$, $F=1.33$, df = 17, $P=0.27$). Monthly ESPI values were obtained from NASA (http://www.trmm.gsfc.nasa.gov/). Preliminary analysis indicated that March–May values of ESPI strongly covaried with annual SOI values ($r=0.67$, $P=0.005$). Because ESPI values were only available back to 1979, I used SOI rather than ESPI. In relating aspects of red-winged blackbird breeding biology in a given year to SOI, I used the mean of the monthly values of SOI for the 12 months preceding that nesting season (i.e., April of the previous year to March of the current year).

The general analytical approach I followed was to look for linear relationships between climatic and reproductive variables. Given the large number of potential combinations of dependent and independent variables, the issue arises as to how one should adjust probabilities. Following the example of other studies that have examined the effects of multiple climatic variables on multiple reproductive variables, I simply report unadjusted P values and focus more on the explanatory power of the independent variables.

Results

Climate and weather

I looked for associations between climate variables (SOI, winter NAOI, spring NAOI) and weather variables for years for which I had red-winged blackbird breeding data. SOI was not associated with any of the weather variables (all $|r| < 0.42$, all $P > 0.09$). High winter NAOI values were associated with low warmth sum values ($r=-0.54$, $F=6.55$, df = 17, $P=0.02$) but not with any other weather variable (all $|r| < 0.41$, all $P > 0.10$). High spring NAOI values were weakly associated with cooler temperatures in May and July (May maximum: $r=-0.42$, $F=3.43$, df = 17, $P=0.08$; July maximum: $r=-0.39$, $F=2.81$, df = 17, $P=0.11$) and more days with rain in May ($r=0.41$, $F=3.25$, df = 17, $P=0.09$), but not with any other weather variables (all $|r| < 0.34$, all $P > 0.17$). Overall, therefore, the only association between climate patterns and weather was a trend toward high NAO years having cooler, wetter springs and cooler weather later in the summer.

Neither SOI nor NAOI values exhibited an overall increase or decline over the course of the study, either when analyses include all years from 1974 to 2000 (SOI: $r=-0.20$, $F=1.10$, df = 26, $P=0.30$; winter NAOI: $r=0.10$, $F=0.27$, df = 26, $P=0.61$; spring NAOI: $r=0.29$, $F=2.35$, df = 26, $P=0.14$) or just years for which blackbird data were available (SOI: $r=-0.14$, $F=0.31$, df = 17, $P=0.58$; winter NAOI: $r=0.17$, $F=0.45$, df = 17, $P=0.51$; spring NAOI: $r=0.31$, $F=1.72$, df = 17, $P=0.26$).

Chronological patterns of reproduction

Over the 18 years for which nesting data were obtained, I monitored 1,855 nests that reached incubation. The birds did not start nesting earlier over the course of the study ($r=-0.20$, $F=0.67$, df = 17, $P=0.43$, Fig. 1). However, nesting ended later as the study progressed ($r=0.64$, $F=9.58$, df = 15, $P=0.008$, Fig. 1), with the consequence that the nesting season became longer ($r=0.50$, $F=4.65$, df = 15, $P=0.05$, Fig. 1). Functionally, longer breeding seasons could result from females re-nesting more following nest failure, or attempting second nests more following success. I have too few years with data for individually marked females to assess the relative importance of these possibilities.

Mean clutch size did not vary systematically with the year of the study ($r=-0.12$, $F=0.22$, df = 17, $P=0.64$, Fig. 2). Nest success declined over the study ($r=-0.51$, $F=4.55$, df = 14, $P=0.05$, Fig. 2). The mean number of fledglings per successful nest did not vary significantly

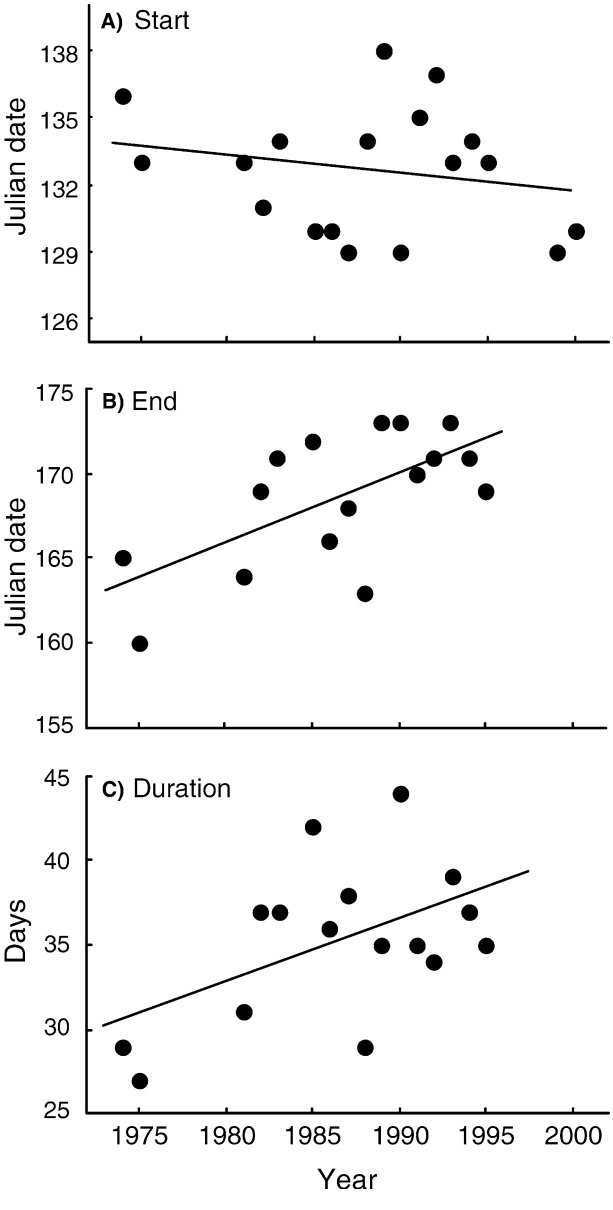

Fig. 1 Change in the **a** start ($r=-0.20$, $P=0.43$), **b** end ($r=0.64$, $P=0.008$), and **c** duration ($r=0.50$, $P=0.05$) of the nesting season of red-winged blackbirds (*Agelaius phoeniceus*) from 1975 to 2000 in eastern Ontario, Canada. The start and end of nesting were respectively the mean first-egg dates for the first 20% of nests initiated and the mean first-egg dates for the last 20% of nests initiated each year, with the duration of the season the difference between them

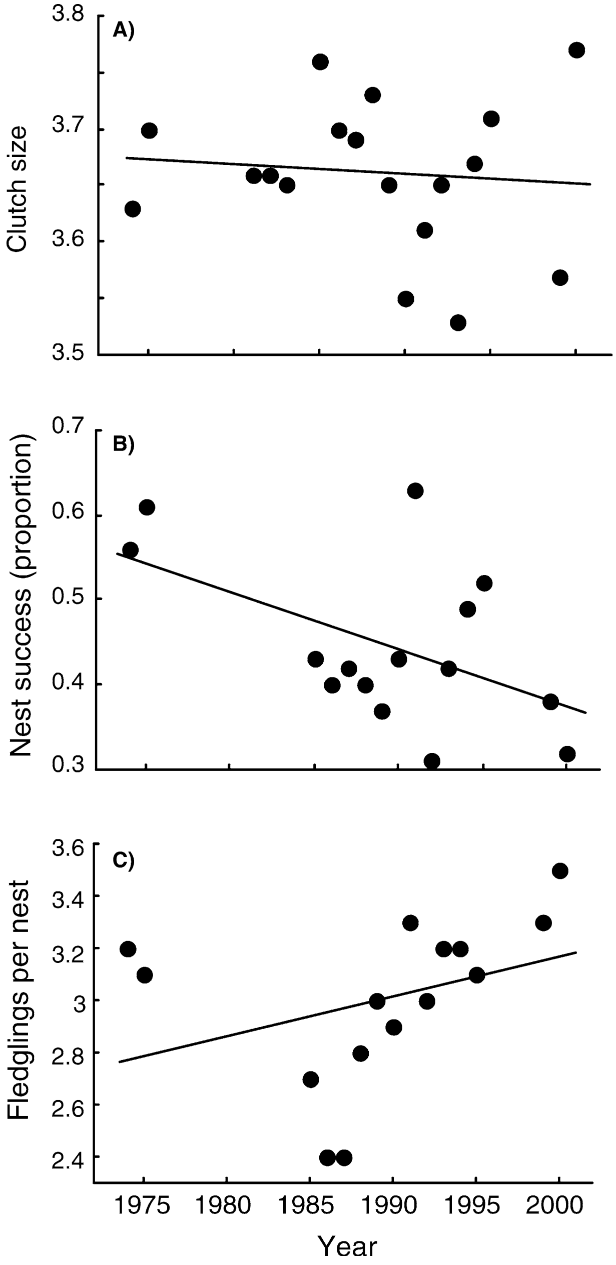

Fig. 2 Annual variation in **a** mean clutch size ($r=-0.12$, $P=0.64$), **b** proportion of nests that were successful (fledged at least one young; $r=-0.51$, $P=0.05$), and **c** the mean number of young fledged per successful nest for red-winged blackbirds during the 25-year study ($r=0.35$, $P=0.21$)

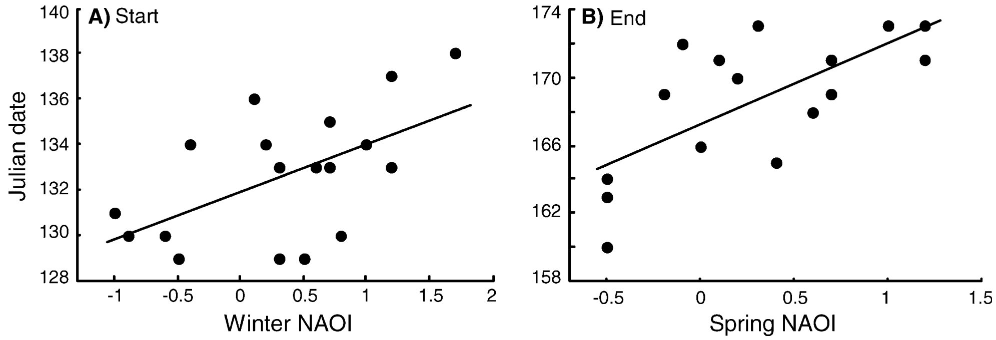

Fig. 3 Annual variation in the **a** start of the nesting season of red-winged blackbirds relative to winter North Atlantic Oscillation Index (NAOI) values ($r = 0.53$, $P = 0.02$) and in the **b** end of nesting relative to spring NAOI values ($r = 0.68$, $P = 0.004$). The start and end of nesting were respectively the mean first-egg dates for the first 20% of nests initiated and the mean first-egg dates for the last 20% of nests initiated each year

with the study year overall ($r = 0.35$, $F = 1.76$, df = 14, $P = 0.21$), but from Fig. 2 it appears there was a rise in productivity of successful nests from 1985 onwards. The opposing trends of increasing young per successful nest and decreasing nest success over the study resulted in there being no change in productivity (fledglings per nesting female) over the study ($r = 0.10$, $F = 0.12$, df = 12, $P = 0.13$).

Climate, weather, and reproduction

I found no association between any aspect of reproduction and SOI (all $|r| < 0.28$, all $P > 0.31$). Also, the mean clutch size and percentage of nests successful each year did not vary significantly with either winter or spring NAOI (all $|r| < 0.40$, all $P > 0.11$). However, nesting started later in years with higher winter values of NAOI ($r = 0.53$, $F = 6.41$, df = 17, $P = 0.02$, Fig. 3) and lower warmth totals ($r = -0.61$, $F = 9.61$, df = 17, $P = 0.007$), reflecting the association between higher winter values of NAOI and cool spring temperatures reported above. Nesting ended later in years with higher spring NAOI values ($r = 0.68$, $F = 12.22$, df = 15, $P = 0.004$, Fig. 3), producing a weak association between spring NAOI and the length of nesting seasons (NAO: $r = 0.46$, $F = 3.67$, df = 15, $P = 0.08$). Higher spring values of NAOI were weakly associated with cooler July temperatures (above), which might affect how long the birds nested. However, I found no evidence that either the end or the duration of the nesting season was associated with July temperatures (all $|r| < 0.31$, all $P > 0.25$).

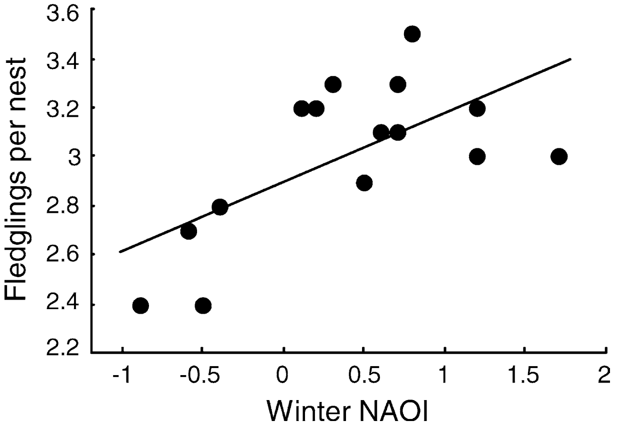

Fig. 4 Mean number of young fledged per successful red-winged blackbird nest each year relative to winter North Atlantic Oscillation Index (NAOI) values ($r = 0.64$, $P = 0.01$)

It is possible that the decline in nest success over the course of the study was related to the breeding season becoming longer, and thus to NAO. Predation on nests in this population of red-winged blackbirds is higher later in the breeding season (Weatherhead and Sommerer 2001), so the increase in predation could be a consequence of more nests being active later as the breeding season ended later. However, the percentage of nests that was successful varied independently of both the length of the nesting season ($r = -0.35$, $F = 1.53$, df = 12, $P = 0.24$) and spring NAOI ($r = -0.33$, $F = 1.57$, df = 14, $P = 0.23$), and the trends were in the opposite direction from those predicted.

Successful nests fledged more young in years with higher winter NAOI values ($r = 0.64$, $F = 9.04$, df = 14, $P = 0.01$, Fig. 4). However, I found no relationships that even approached significance between fledging success and either precipitation or temperature in May, June, or July, the months in which most nesting occurred (all $|r| < 0.26$, all $P > 0.33$).

Data on egg sex ratios at hatching collected from this study population in 1981 showed that females disproportionately produced sons in the middle of the nesting season and daughters early and late in the season (Weatherhead 1983). Given the variation in the length of the nesting season with NAOI reported above, I assessed whether offspring sex ratios (proportion male) varied with the length of the nesting season. The longer the nesting season, proportionately fewer male fledglings were produced ($r = -0.64$, $F = 5.62$, df = 9, $P = 0.04$, Fig. 5). This relationship was not a function of changes in just the start or end of the breeding season because neither alone was associated with sex ratio as strongly as was the length of the nesting season (start: $r = 0.47$, $F = 2.24$, df = 9, $P = 0.17$; end: $r = -0.40$, $F = 1.54$, df = 9,

$P = 0.25$). Variation in sex ratios was not a function of starvation (i.e., greater male starvation producing female-biased sex ratios) because the (weak) tendency was actually for the sex ratio to be more male biased in years with fewer fledglings per nest ($r = 0.25$, $F = 0.52$, df = 9, $P = 0.49$). Finally, sex ratios did not vary significantly with either winter or spring NAOI (both $|r| < 0.42$, all $P > 0.24$), but that was also true for the length of the nesting season (above).

Discussion

Most evidence of the ecological effects of climate variation is in the form of either systematic biological change through time (e.g., Hughes 2000), or variation in association with large-scale climate phenomena such as El Niño or the North Atlantic Oscillation, where the chronological patterns tend to be cyclic rather than monotonic declines or increases (e.g. Sillett et al. 2000; Hallet et al. 2004). Over the 25-year period in which data were collected in this study, there were few systematic chronological changes in red-winged blackbird reproduction, but there were clear associations of several aspects of reproduction with the North Atlantic Oscillation. As I review each of these patterns in turn, I consider the extent to which these patterns can be linked to variation in local weather. Among the reproductive variables, I do not consider clutch size any further because I found no association between clutch size and climate, and I do not consider El Niño further, because none of the reproductive variables was associated with the variation in SOI.

The clearest chronological pattern involved the timing of nesting. Over the course of the study, red-winged blackbirds did not begin nesting earlier (although the trend was in that direction), but they did stop nesting later, resulting in the nesting season becoming longer. The start and end of nesting were also associated with NAOI, with both occurring later in years with high winter and spring NAOI values, respectively. Thus, aspects of the timing of nesting varied both chronologically and in association with a cyclic climatic phenomenon. Not surprisingly, therefore, a simple link between all of these patterns and local weather was not identified.

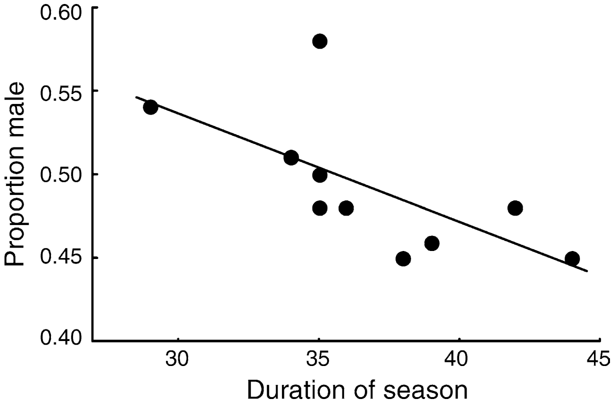

Fig. 5 Mean annual sex ratio (proportion male) of red-winged blackbird fledglings relative to the duration of the nesting season (days) ($r = -0.64$, $P = 0.04$). Duration of the nesting season was the difference between the start and end of nesting, which were respectively the mean first-egg dates for the first 20% of nests initiated and the mean first-egg dates for the last 20% of nests initiated each year

Interpreting the start of nesting was most straightforward. Based on evidence that red-winged blackbirds nest earlier in response to food provisioning (Ewald and Rohwer 1982; Wimberger 1988), I predicted earlier nesting in years with milder spring weather, assuming the insects on which blackbirds feed during the breeding season (McNicol et al. 1982) would be available earlier. I did find earlier breeding in years with milder springs, and low winter NAOI values were also associated with warmer spring weather. The lack of a significant advance in laying dates over the study is consistent with both winter NAOI and spring temperatures not changing systematically over the study. Dunn and Winkler (1999) found that across North America, tree swallows (*Tachycineta bicolor*) advanced their laying date by up to 9 days over three decades. In a study of tree swallows in southern Ontario, however, Hussell (2003) found no advance in laying dates. This difference appears to result from spring temperatures in southern Ontario not having increased over the past three decades (Hussell 2003), despite a general increase in temperatures across North America (Dunn and Winkler 1999). The lack of a significant increase in spring temperatures over the course of my study appears to explain the absence of an advance in laying dates in red-winged blackbirds. Across North America, however, I predict that red-winged blackbirds are nesting earlier now than they did historically.

I did not find a local weather variable that explained the systematic change in how late the birds nested and the length of the breeding season, nor one that explained the link between spring NAOI values and when nesting ended. Whether both these patterns are explained by the same weather variable(s) also remains unknown. Associations between local weather and ecological processes can be complex, making it easier to predict those processes from large-scale climate pheonomena such as NAO than from local weather (Hallett et al. 2004). Presumably variation in NAO captures the complexity of the relationship between local weather and ecology. To identify the weather variables that are affected by NAO and that in turn affect the length of the red-winged blackbird breeding season may require first determining the proximate factors (e.g., food availability) that trigger the onset or termination of nesting.

The percentage of nests that produced at least one fledgling (i.e., nest success) declined over the study. However, the lack of association between nest success and any of the climate variables analyzed, or with the length of the nesting season (which is associated with predation), suggests that the overall chronological trend may best be interpreted as a spurious effect of having 2 years with high success early in the study (Fig. 2). The productivity of successful nests did not change chronologically overall, but did show a steady rise in the latter half of the study. Whether that increase in productivity is part of a long-term cycle or a systematic change that began midway through the study and is still ongoing will require an assessment of current productivity. However, because the clutch size did not change over the study and mean productivity was approaching the mean clutch size, there was little room for productivity to improve further. Fledging success was strongly associated with winter NAOI values, but as with the timing of nesting, no weather variables were identified that explained the chronological pattern.

Nest productivity reflects food availability, so years with high winter values of NAOI might correspond to years with high insect abundance (Nott et al. 2002). In Nott et al.'s (2002) study in the Pacific northwest, however, high positive values of NAOI were associated with warmer and drier spring conditions, exactly the opposite pattern from Ontario. Because I found no association between fledging success and local weather variables, the link between nest productivity and NAO may have been caused not by variation in absolute food abundance, but by variation in synchrony between the birds' nesting season and availability of the insects on which the birds feed (e.g., Thomas et al. 2001a, b). Thus, higher productivity of red-winged blackbirds in years with higher NAOI values could be associated with the later start of nesting in those years. This explanation requires that the birds and insects respond differently to variation in NAO.

Offspring sex ratios were more female biased as the length of the nesting season increased. A number of avian studies have identified seasonal patterns of offspring sex allocation (e.g., Howe 1977; Cordero et al. 2001; Andersson et al. 2003). Weatherhead (1983) interpreted the relatively higher number of females in red-winged blackbird eggs early and late in the nesting season as a response to varying food abundance. Females produce more of the cheaper sex to rear (females) when resources are scarcer. Lengthening the nesting season could have had no effect on sex ratios if females perceived that all parts of the season (early, middle, and late) had increased proportionately. Because more females are produced in years with longer breeding seasons, however, females may perceive the tails of the season to have increased disproportionately. For the 10 years with sex ratio data, the mean sex ratio did not deviate from unity (Weatherhead and Dufour 2005). However, the length of the nesting season did not change systematically over those years. If the length of the nesting season continues to increase as suggested by the full data set, then offspring sex ratios should be getting progressively more female biased.

A goal of most current studies that examine the ecological effects of climate is to use their results to predict the effects of future climate change. To predict how demographic processes and population size will be affected by climate will usually require knowing much more than just how one aspect of an animal's ecology (e.g., first-egg dates) is affected by climate. In this study I examined how several aspects of red-winged blackbird ecology vary with climate. Predicting the net effect of all of these factors will be challenging. When the birds nest, their productivity and the sex ratio of their offspring all appear to be affected directly or indirectly by the climate. Long-term declines in population size that are independent of any of the patterns identified here and are probably attributable to factors away from the breeding grounds (Weatherhead, in preparation) will further complicate efforts to predict the future for this population of red-winged blackbirds.

Two research needs are apparent. First, links between climate(NAO), ecological effects, and local weather need to be identified (e.g., Hallett et al 2004). Red-winged blackbirds may be a good model species for these efforts because they are widely distributed and extensively studied. Combining data from different studies may facilitate the search for links between climate, weather, and ecology. Second, NAO emerged as the climate variable that was associated with many of the ecological patterns observed in this study, adding to previous studies that have documented NAO effects on migration and/or reproduction of birds in the Pacific northwest (Nott et al. 2002) and through much of western Europe (e.g., Crick et al. 1997; Forchhammer et al. 1998; Jonzen et al. 2002; Sanz 2002, 2003; Huppop and Huppop 2003). Variation in the NAO has also been implicated as affecting insect outbreaks (Nott et al. 2002), timing of breeding of amphibians (Beebee 1995), and sexual dimorphism in deer (Post et al. 1999). Given the geographic and biological breadth of NAO effects, accurate projections of the ecological consequences of climate change in North America and Europe will rely on improved understanding of the NAO. This view is consistent with the general proposition that research in global climate change ecology should focus on effects of large-scale climate phenomena (Forchhammer and Post 2004).

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