PROCEEDINGS OF THE ROYAL SOCIETY B

Proc. R. Soc. B (2005) **272**, 2313–2317
doi:10.1098/rspb.2005.3211
Published online 31 August 2005

Long-term decline in a red-winged blackbird population: ecological causes and sexual selection consequences

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Habitat loss and large-scale climate phenomena are widely implicated as causing decline in animal populations. I examined how both factors contributed to a precipitous decline in an Ontario red-winged blackbird (*Agelaius phoeniceus*) population using 16 years of data collected between 1974 and 1995. The decline was manifested as an almost 50% reduction in mean harem size, which reduced the opportunity for sexual selection threefold. Regional hay production, which should affect recruitment into the study population, also declined substantially. Correlation between blackbirds and hay may be coincidental, however, because annual changes in harem size were not associated with annual changes in hay production. This study coincided with an unprecedented positive phase of the North Atlantic Oscillation (NAO). Changes in harem size were correlated with winter NAO index values, suggesting that winter mortality contributed to the population decline. Positive correlation between harem size change and male return rates also supported the winter mortality hypothesis. Continued declines will cause this blackbird population to change from socially polygynous to socially monogamous. Study of red-winged blackbird winter ecology is needed to identify the proximate causes of mortality, whereas breeding studies can explore the consequences of relaxed sexual selection.

Keywords: climate change; North Atlantic Oscillation; demography; agriculture; land use; birds

1. INTRODUCTION

Ecologists increasingly explore how anthropogenic factors influence organisms, with population decline being the usual pattern of interest. Loss of habitat is viewed as the most general cause of population decline (Meffe & Carroll 1997), but more recently, climate change has also been implicated (Parmesan & Yohe 2003; Root *et al.* 2003; Thomas *et al.* 2004). I use 16 years of data collected over a period of 22 years to document a steep decline in the breeding population of red-winged blackbirds (*Agelaius phoeniceus*) in eastern Ontario. I assess the relative importance of habitat change and climate change for the decline and assess the consequences of the decline for sexual selection.

Clearing forests for agriculture in eastern North America expanded grassland habitat. Resulting increases in populations of grassland birds were subsequently reversed by more recent changes in agricultural practices (O'Connor & Boone 1992; Askins 1999). Although red-winged blackbirds nest in marshes, they readily adapted to nesting in hayfields (Searcy & Yasukawa 1995; Beletsky 1996), where most of the population often nests (e.g. Clark & Weatherhead 1986). Continental red-winged blackbird populations are in decline, and changes in abundance and suitability of grasslands have been implicated (Blackwell & Dolbeer 2001; Murphy 2003). A 60% decline of blackbirds in Ohio over 30 years appeared to be largely explained just by loss of land planted to hay (Blackwell & Dolbeer 2001). My first goal was to use long-term data to determine if a local population of red-winged blackbirds had declined, and if so, whether trends in hay production accounted for the change. Because the study population nested exclusively in marshes in non-agricultural habitat, changes in hay production could only affect my population indirectly through regional productivity of blackbirds. Low natal philopatry (Weatherhead & Dufour 2000) meant that most birds breeding in my population were produced elsewhere in the region (Dolbeer 1982). Thus, this aspect of the study tests the hypothesis that recruitment drives changes in population size.

The El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) are global climate phenomena that affect numerous aspects of avian reproduction and demography (e.g. Sillet *et al.* 2000; Nott *et al.* 2002; Forchhammer & Post 2004). These influences presumably arise through geographically widespread changes in temperature and precipitation produced by both ENSO and NAO. For the blackbirds studied here, variation in NAO is associated with timing of reproduction, nest productivity and offspring sex ratios (Weatherhead 2005). Given the importance of climate phenomena to avian ecology, and specific relevance of NAO to red-winged blackbirds, it is plausible that climatic factors contribute to decline in blackbird populations by affecting winter mortality. Blackwell & Dolbeer (2001) found no effect of nine weather variables on blackbird declines in Ohio, but did not assess effects of ENSO or NAO. My second goal was to determine if trends in my study population are affected by either ENSO or NAO. This aspect of the study tests the hypothesis that survival of birds outside the breeding season drives changes in population size.

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Received 10 March 2005
Accepted 12 June 2005

My final goal was to determine how a change in population size affected the opportunity for sexual selection. Red-winged blackbirds are socially polygynous (Searcy & Yasukawa 1995). Despite substantial extra-pair mating, variation in the number of social mates accounts for most of the variance in male reproductive success (Weatherhead & Boag 1997). Because surplus reproductive males in the population should occupy vacancies created by males that do not return (Shutler & Weatherhead 1992), whereas there are no replacements for females, a population decline should first be detected as a decline in the breeding sex ratio (i.e. the number of social mates per breeding male). Thus, as populations decline, breeding sex ratios should become more even, reducing the opportunity for sexual selection.

2. MATERIAL AND METHODS

I used data from a series of studies conducted in 16 breeding seasons spanning the period from 1974 to 1995 at the Queen's University Biological Station in eastern Ontario (45°37′ N, 76°13′ W). All studies were conducted using the same group of marshes. Every marsh was not used in every year, but multiple marshes were used each year and every marsh was used in multiple years. Each year territories were mapped and beginning in 1985, territorial males were individually banded. Because returning males are highly site faithful, annual return rates of banded males were used to estimate male survival (Weatherhead & Clark 1994). Detailed methods are available from the following: 1974–1975 (Weatherhead & Robertson 1977), 1981 (Weatherhead 1983), 1982–83 (Weatherhead 1985), 1985–1995 (Weatherhead & Sommerer 2001).

I estimated harem size as the maximum number of simultaneously active nests on a territory. I estimated the opportunity for sexual selection (Wade & Arnold 1980) as the standardized variance (I=variance/mean^2) in harem size for all territories sampled each year. I did not have measures of reproductive success in all years, but harem size explains a substantial proportion of the variance in male fledging success (Weatherhead & Boag 1997) and was the best measure of sexual selection available for most years.

I could not estimate the number of breeding males by summing territories across all marshes because the same suite of marshes was not used each year. Therefore, for each marsh I calculated the number of males present each year as the percentage of the mean number of males on that marsh over all the years it was sampled. I combined those percentages for all marshes sampled each year as 'mean percentage of territorial males'. I excluded one marsh from these estimates because water levels fluctuated in response to the state of a beaver dam, altering availability of nesting habitat.

I obtained estimated land planted to hay in Ontario from Statistics Canada. The hypothesis I considered with regard to hay was that land area in year $x-1$ should affect the size of my blackbird population in year x. Note that I consider this hypothesis only for female blackbirds. Females start to breed at one year of age, whereas males usually delay breeding (Searcy & Yasukawa 1995). Thus, changes in regional production of females in year $x-1$ should be reflected by changes in harem size in my study population in year x.

I obtained climate and weather data from the National Oceanic and Atmospheric Administration. I used monthly mean NAO index (NAOI) and ENSO index (southern oscillation index (SOI)) values for 6 months (October–March) and 12 months (April–March) preceding the breeding season. To associate climate effects with weather on the birds' wintering grounds in southeastern US (Dolbeer 1978), I used mean temperature and precipitation records for December through February for the Southeast Region for each winter preceding a year for which I had breeding data.

In addition to regressing blackbird numbers against independent variables to identify associations, I examined how differences in blackbird numbers from year to year varied with annual changes in independent variables. The latter approach helped differentiate between coincidental and causal associations between variables, where both exhibited chronological trends.

3. RESULTS

Harem size declined from approximately three females per male in the mid-1970s to 1.6 in the mid-1990s ($r=-0.76$, $F=19.60$, $p=0.0006$, $n=16$; figure 1*a*). Standardized variance in harem size decreased by a factor of 3 over the study ($r=-0.74$, $F=16.60$, $p=0.001$, $n=16$; figure 1*b*). The population of breeding males on the study area did not change systematically through time ($r=-0.28$, $F=1.22$, $p=0.29$, $n=16$).

Hay production declined over the study ($r=-0.69$, $F=18.68$, $p=0.0003$, $n=22$; figure 2*a*). Harem size in year x was positively associated with hay production in year $x-1$ ($r=0.59$, $F=7.52$, $p=0.02$, $n=16$). The percentage change in harem size from year to year, however, was unrelated to the annual percentage change in hay production in the preceding year ($r=-0.30$, $F=1.12$, $p=0.31$, $n=13$; figure 2*b*).

Annual changes in harem size were not significantly associated with variation in NAOI for the full year preceding a given breeding season ($r=-0.41$, $F=2.24$, $p=0.16$, $n=13$), but changes in harem size were negatively correlated with NAOI the previous 6 months ($r=-0.63$, $F=7.07$, $p=0.02$, $n=13$; figure 3). Annual changes in harem size were unrelated to SOI for either the preceding 12 months ($r=0.34$, $F=1.42$, $p=0.26$, $n=13$) or six months ($r=0.42$, $F=2.38$, $p=0.15$, $n=13$). The NOA results suggest that mortality on the wintering grounds contributed to demographic changes. Change in harem size, however, was not associated with winter (December–February) mean temperature, precipitation or both combined (sum of annual ranks, where high precipitation and low temperature were ranked low) for the southeastern US (temperature: $r=-0.07$, $F=0.06$, $p=0.81$; precipitation: $r=-0.23$, $F=0.64$, $p=0.44$; combined: $r=0.17$, $F=0.32$, $p=0.58$, all $n=13$).

If winter mortality contributes to the decline in harem size, then annual changes in harem size should be correlated with annual variation in return rates for banded territorial males. For the 10 years for which data were available, harem size changes and male return rates were positively correlated ($r=0.72$, $F=8.57$, $p=0.02$; figure 4). The relationship between male return rates and winter NAO values ($r=-0.50$, $F=2.69$, $p=0.14$, $n=10$) was similar to that between changes in harem size and NAO, albeit not as strong.

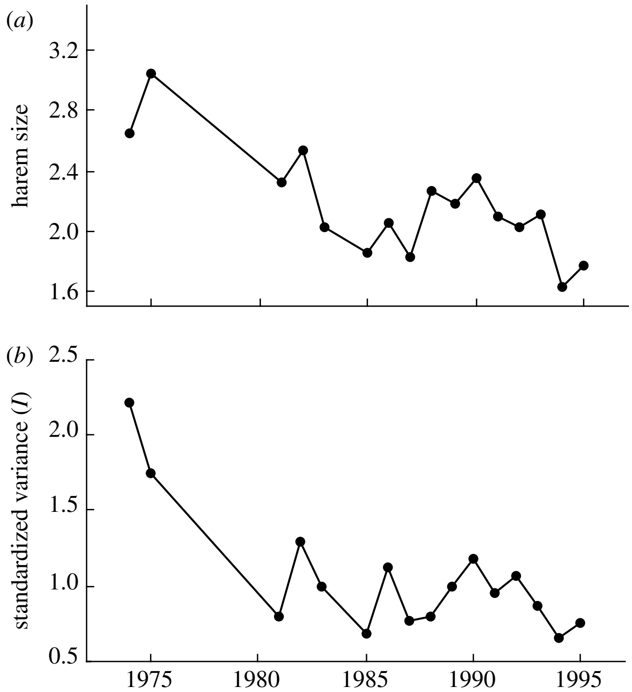

Figure 1. Annual variation in (*a*) mean harem size and (*b*) opportunity for sexual selection (I=variance/mean harem size^2) for red-winged blackbirds in eastern Ontario between 1974 and 1995.

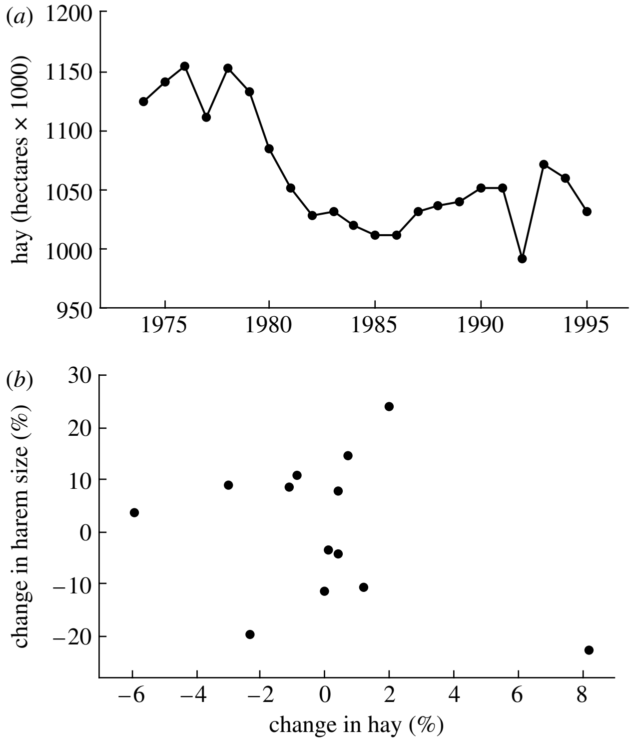

Figure 2. (*a*) Area (hectares×1000) of land in Ontario planted to hay from 1974 to 1995 and (*b*) percentage change in mean harem size of red-winged blackbirds on the study area from year x to year $x+1$ relative to the change in land area in Ontario planted to hay from year $x-1$ to year x.

4. DISCUSSION

Between 1974 and 1995, the number of females breeding on the study area declined precipitously, but breeding males did not. Surplus, non-territorial males (Shutler & Weatherhead 1992) can account for this difference.

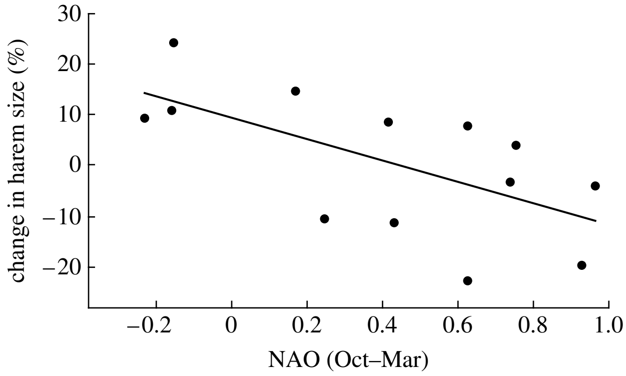

Figure 3. Percentage change in mean harem size from the previous year relative to the mean North Atlantic Oscillation (NAO) index value for the six months preceding the breeding season.

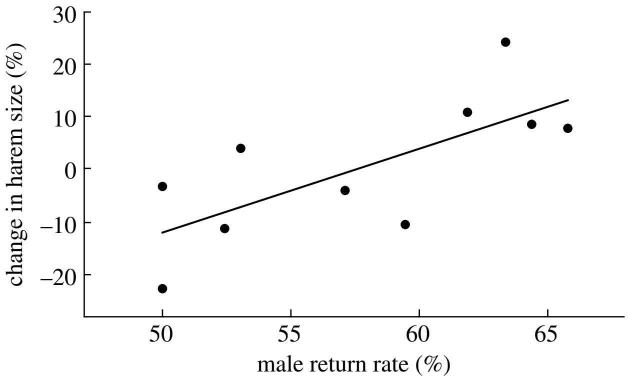

Figure 4. Percentage change in mean harem size from the previous year relative to the percentage of territorial males that returned from the previous year.

Presumably males could decline in concert with females without a detectable decline in territorial males until harem size equals one, at which point all available males would hold territories. Thereafter, further decline in females should be paralleled by decline in males. It is noteworthy that regional censuses (e.g. breeding bird survey (BBS)) that count birds observed from roadsides may be insensitive to demographic changes in socially polygynous species. Greater detectability will cause territorial males to be over-represented in counts, masking changes in abundance of females and non-territorial males, and thus of the total population.

Land planted to hay regionally declined over the study. Thus, less nesting habitat could have reduced regional blackbird productivity, causing a decline in recruitment to the study population. Although mean harem size was significantly correlated with hay production the previous year, annual changes in harem size were not correlated with changes in hay production. Therefore, concurrent declines in blackbirds and hay may have no causal link. Blackwell & Dolbeer (2001) produced a multiple regression model that explained 88% of the variation in their BBS index of blackbird abundance in Ohio. Hay accounted for most of the variance explained by their model. Because their analysis examined the relationship between absolute annual values rather than changes in annual values, the strong association between blackbirds and hay through time could have arisen because both variables were changing chronologically for unrelated reasons (i.e. the correlation between hay and birds could have been coincidental rather than causal). To assess whether the relationship held when annual changes were considered, I estimated values from their fig. 2 (page 664) which plotted observed (i.e. BBS) blackbird population indices against values predicted from their multiple regression model (i.e. hay). Using values for the same year (their data were surveys of birds in agricultural landscapes where changes in hay should affect blackbirds directly), the relationship between annual changes in observed and predicted populations was significant ($r=0.50$, $F=9.38$, $p=0.005$, $n=30$). Compared to Blackwell & Dolbeer's (2001) analysis, however, explained variance dropped from 88 to 25%. Therefore, in addition to effects of declining hay production, other factors (e.g. climate) might be contributing to the decline in blackbirds in Ohio.

Changes in harem size in my study were associated with both male return rate and winter NAO, implicating winter survival as contributing to decline in red-winged blackbirds in Ontario. Although females winter further south than males (Dolbeer 1982), regional weather patterns should affect both males and females. Mean winter temperature and precipitation data for southeastern states did not explain variation in harem size. Because associations between demography and weather are likely to be complex, however, large-scale climate phenomena that represent 'packages of weather' are better predictors of demography (Stenseth *et al.* 2003; Hallet *et al* 2004). My study coincided with an unprecedented positive phase of NAO (Hurrell 1995; Visbeck *et al.* 2001), bringing warmer, wetter, stormier winters to southeastern US (Visbeck *et al.* 2001; Stenseth *et al.* 2003). Extreme weather can cause pronounced avian mortality (e.g. Bumbus 1899; Brown & Brown 1998), suggesting that more frequent or severe winter storms could be causing red-winged blackbird declines.

Future trends in NAO are uncertain, but greenhouse effects could maintain the positive phase (Visbeck *et al.* 2001). If further declines in red-winged blackbirds result, my study population could become socially monogamous, with the opportunity for sexual selection further reduced. Whereas these changes are of concern environmentally, they create a unique research opportunity. Potential consequences of relaxed sexual selection in red-winged blackbirds are manifold, including effects on sexual dimorphism, reproductive strategies of males and females, and the behaviour and delayed plumage maturation of one-year old males. Investigation of these effects would benefit greatly from our extensive knowledge about sexual selection in this species (e.g. Searcy & Yasukawa 1995). Simultaneously, investigation of the poorly studied winter ecology of red-winged blackbirds would help identify circumstances associated with winter mortality that may have ecological effects much broader than just those experienced by blackbirds.

I thank everyone who helped collect the data I report here, particularly Kevin Dufour, Drew Hoysak and Kit Muma. I am grateful to Dylan Maddox for commenting on the manuscript, Queen's University for use of the Biological Station, and the Natural Sciences and Engineering Research Council of Canada, Carleton University and the University of Illinois for financial support.

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