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SPECIAL SECTION: RANGEWIDE ECOLOGY OF THE DECLINING RUSTY BLACKBIRD

RUSTY BLACKBIRD: MYSTERIES OF A SPECIES IN DECLINE

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Abstract. The Rusty Blackbird (*Euphagus carolinus*) breeds across the boreal forest zone of North America and winters throughout the eastern United States. Over the past four decades, the North American Breeding Bird Survey and the Christmas Bird Count have shown high rates of population decline ranging from approximately 5 to 12% per year. Regional surveys suggest declines and range retractions in the southern boreal zone. Analyses of historical accounts suggest that the Rusty Blackbird's abundance has been dropping steadily for over a century. A number of hypotheses have been proposed to explain the decline. The species relies on wooded wetlands throughout the year, so loss and degradation of these habitats—particularly in the winter range—is a prime suspect. Blackbird-control programs may have contributed. In recent decades, habitat disturbance, global warming, and environmental contamination in the boreal zone may have taken their toll on breeding populations. In 2005, the International Rusty Blackbird Working Group was formed to develop research efforts toward understanding the mysterious decline. This special section presents the group's research findings—the first on the species' use of breeding and winter habitat, reproductive success, parasite prevalence, patterns of molt, and migratory connectivity. Data on the levels of methylmercury in tissues and the role of timber management on reproductive success are intriguing. We outline research needed for assessment of the roles of various factors in causing the decline of the Rusty Blackbird.

Key words: *boreal wetlands*, *breeding ecology*, Euphagus carolinus, *range-wide conservation*, *Rusty Blackbird*, *winter ecology*, *wooded wetlands*.

Euphagus carolinus: Misterios de una Especie en Disminución

Resumen. *Euphagus carolinus* es una especie distribuida a lo largo de la zona de los bosques boreales de América del Norte durante la época reproductiva y que pasa el invierno a lo largo del este de los Estados Unidos. Durante las últimas cuatro décadas, el Censo Norteamericano de Aves Reproductivas y el Conteo de Aves de Navidad muestran altas tasas de disminución de poblaciones en un rango aproximado que va del 5 al 12% anual. Los censos regionales sugieren disminuciones de población y retracciones de distribución en la zona boreal meridional. Los análisis de conteos históricos sugieren que la abundancia de *E. carolinus* ha venido disminuyendo sostenidamente por más de un siglo. Se propusieron varias hipótesis para explicar la disminución. Esta especie depende de humedales arbolados a lo largo del año, por lo tanto la pérdida y degradación de estos habitats—particularmente en el área de distribución de invierno—representan la principal sospechosa. Los programas de control de *E. carolinus* pueden haber contribuido. En décadas recientes, la alteración de hábitat, el calentamiento global y la contaminación ambiental en la zona boreal pueden haber tenido un grave efecto en las poblaciones reproductivas. En el 2005 se formó el Grupo Internacional de Trabajo de *E. carolinus* (IRBWG por sus siglas en inglés) para desarrollar esfuerzos de investigación para lograr entender la misteriosa disminución. Esta sección especial presenta los resultados de las investigaciones del IRBWG—el primero para la especie sobre uso de hábitat reproductivo y de invierno, éxito reproductivo, prevalencia parasitaria, patrones de muda, y conectividad migratoria. Los datos de los niveles de metilmercurio en tejidos y el rol del manejo forestal en el éxito reproductivo son intrigantes. Subrayamos la necesidad de investigación para evaluar los roles de los distintos factores en la causa de la disminución de las poblaciones de *E. carolinus*.

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INTRODUCTION

It is difficult to know the size of the global population of the Rusty Blackbird (*Euphagus carolinus*). The species is broadly distributed during the breeding season across North America's vast boreal forest, from New England and the Maritime Provinces to the tree line in northern Alaska, and it winters throughout the southeastern U.S. The only published estimates, based on inference from the number detected along North American Breeding Bird Survey routes, holds that between 158 000 and 2 million Rusty Blackbirds remain (Rich et al. 2004, Savignac 2006), suggesting the species is still reasonably common. However, the species has experienced a profound decline rangewide, cumulative to a reduction in population size of 88% or more over the past four decades, with additional qualitative evidence that this decline has been continuing for a century or more (Greenberg and Droege 1999, Niven et al. 2004, Sauer et al. 2008, Greenberg et al. 2011). The severity and persistence of the decline has recently drawn attention to the plight of the Rusty Blackbird and placed the species on a number of notable lists of conservation concern including the IUCN's Red List of Threatened Species (IUCN 2010), the U.S. Fish and Wildlife Service's Birds of Conservation Concern (U.S. Fish and Wildlife Service 2008), and the Committee on the Status of Endangered Wildlife in Canada's Species of Special Concern (Savignac 2006).

Despite this attention, the magnitude of decline has remained the best-known aspect of the Rusty Blackbird's ecology, with literature on its natural history and resource requirements restricted to brief narrative descriptions in avifaunal accounts that were first summarized by Bent (1958) and later updated by Avery (1995) and Savignac (2006). The single published field study designed and focused entirely on the natural history of this species was conducted nearly a century ago by Fred H. Kennard (1920). The Rusty Blackbird escaped serious study because of a combination of its breeding in remote boreal wetlands, its unassuming behavior, its wintering in forested wetlands difficult of access, and its weak association in winter with other blackbirds that have been the focus of research on pest control in agricultural fields or at evening roosts (Avery 1995, Greenberg et al. 2011). As a result, even basic information on the Rusty Blackbird's ecology and resource requirements are sorely needed to understand, let alone reverse, its dramatic decline (Greenberg and Droege 1999, Greenberg et al. 2011).

It was this need that prompted both the formation of the International Rusty Blackbird Working Group in 2005 and the initiation of a series of collaborative research studies by the group's ten founding members to understand and reverse the species' decline (Greenberg 2008, Greenberg et al. 2011). This special section includes nine papers that summarize the initial research findings of various members of the working group, which now includes over 60 members, and provides the first quantitative look of the ecology and possible factors contributing to the decline of the Rusty Blackbird. In this commentary, we provide a brief summary of evidence of the Rusty Blackbird's decline and the factors that we and other have hypothesized are contributing to it (Greenberg and Droege 1999, Greenberg et al. 2011). We then put into a broader ecological perspective the findings of the nine papers included in this special section and end by emphasizing the critical next steps that need to be taken to understand and reverse the species' mysterious decline.

EVIDENCE OF POPULATION DECLINE

The decline of the Rusty Blackbird, first alluded to by Avery (1995) and explicitly posited by Greenberg and Droege (1999), generally comes as no surprise to birders and field ornithologists familiar with the species—their overwhelming perception is that the species is observed much less frequently now than in years or decades past (Greenberg and Droege 1999). Because of the inaccessibility of most of its breeding range and myriad problems of surveying the species in the winter (e.g., difficulty of detection, poorly understood movements within the season, and annual variation in distribution), databases that can be used to evaluate the decline are few and less than ideal. The North American Breeding Bird Survey (BBS) and Christmas Bird Count (CBC) provide the only broad-scale and reasonably long-term data with which the possibility of a global decline in the species can be assessed. The BBS trend is –9.3% per year (95% CI –11.7 to –1.5%) for the period 1966–2008. But this trend is based on data from only 110 routes concentrated in the southern boreal zone (Sauer and Link 2011). All Bird Conservation Regions across the breeding range show evidence of decline (Sauer et al. 2008), and on the basis of rangewide estimates of annual decline the cumulative decline is 93%.

The CBC, although based on a protocol less standardized than the BBS, has advantages of more data and broader coverage. Over a period 5 years shorter than that of the BBS (winter 1965–1966 to 2002–2003), Rusty Blackbirds were recorded in up to ~1600 count circles per year across the species' entire winter range. Such extensive coverage is particularly important in the winter as the species' distribution changes markedly within and between winters according to the weather (Hamel and Ozdenerol 2009). On the basis of the CBC Niven et al. (2004) estimated the rangewide trend at −5.1% per year (95% credible interval −6.6% to −2.4% per year). The decline is over the entire winter range and particular strong for the four Bird Conservation Regions where the species' relative abundance is highest: Central Hardwoods (–6.2%), West Gulf Coastal Plain (–3.9%), Southeastern Coastal Plain (–5.1%), and Mississippi Alluvial Valley (–6.5%; Niven et al. 2004). Although of slightly smaller magnitude than the trend based on the BBS for the same period, the rangewide decline based on the CBC is considerable and tantamount to a total decline of approximately 88% through 2007.

The Rusty Blackbird's downward turn appears to be rooted in historical changes of North America's avifauna, as our qualitative analysis of descriptions of the species' abundance since the late 19th century implies the species had been declining before the advent of the BBS. In 56% of state or provincial ornithological overviews published before 1920 the Rusty Blackbird was considered to be very common to abundant. This percentage declined to 19% in accounts published from 1920 to 1950 and to only 6.7% in those published from 1951 to 1997. These and similar data suggest that a long and severe decline may have haunted populations well before the recent 88–98% decline estimated from the BBS and CBC (Greenberg and Droege 1999). In addition to the long-term decline, recent surveys in central and western Canada suggest a range contraction from areas traditionally occupied in the south (K. Hobson, S. Van Wilgenburg, J. Morrisette, and A. Smith, unpubl. data), and recent work in Maine indicates that the species' breeding range in that state has contracted 65–160 km northward over the past century (Powell 2008). Limited data from more remote northern regions of the boreal forest suggest that range retractions or general declines have not been as pronounced (Machtans et al. 2007, Cadman et al. 2009).

POSSIBLE REASONS FOR DECLINE

Reasons for the Rusty Blackbird's sharp downturn in numbers largely have remained a mystery. Anthropogenic habitat change is often a primary cause of songbirds' population declines (Terborgh 1989). Unlike other blackbirds, the Rusty Blackbird depends on wooded wetlands throughout the year and is therefore vulnerable to the many forces that affect wetlands throughout North America. It has faced a continuous decline of potential habitat since European settlement especially in winter, with as much as 75–80% of bottomland hardwood forests in the United States converted to agriculture. More recent losses have been the result of logging or conversions to pine plantations or urban development (Hefner and Brown 1984, Hefner et al. 1994, Twedt and Loesch 1999, Hamel et al. 2009). Gross loss of wooded wetlands in the southeastern United States would be consistent with a severe long-term decline in any species that depends on these habitats. Indeed, since the 1950s regional declines in both the Rusty Blackbird's abundance and area of forested wetlands are roughly equivalent in the species' two primary wintering areas, the Mississippi Alluvial Valley and the Southern Coastal Plain (Greenberg and Droege 1999, Hamel et al. 2009). Conversion of bottomland forests to agriculture has progressed from drier to wetter sites over time; therefore, habitat conversion in the last half of the 20th century may have had a particularly detrimental effect because the species generally winters in wetter sites (Hamel et al. 2009). Across the winter range many wooded wetlands and bottomland forests now exist as small fragments (Twedt and Loesch 1999), and such fragmentation may further degrade habitat suitability by exposing Rusty Blackbirds to increased predation and increased competition with the Common Grackle (*Quiscalus quiscula*) and other species of blackbirds.

Historically, boreal wetlands were less affected by human activities than were forested wetlands across the species' winter range. Even so, many species that breed primarily in boreal wetlands, including the Horned Grebe (*Podiceps auritus*), Lesser Scaup (*Aythya affinis*), White-winged and Surf Scoters (*Melanitta fusca* and *M. perspicillata*), Lesser Yellowlegs (*Tringa flavipes*), and Solitary Sandpiper (*T. solitaria*), have experienced some of the highest rates of decline among North American birds (Austin et al. 2000, Hanna 2004, North America Waterfowl Management Plan Committee 2004, Sauer et al. 2008, U.S. Fish and Wildlife Service 2009, Greenberg et al. 2011). Declines of the Rusty Blackbird and other boreal wetland species may be associated with exploitation and development of natural resources, which have accelerated in recent decades, particularly in the southern and eastern portions of the boreal zone. Agricultural development, peat production, timber harvests, oil and gas exploration and development, and reservoir formation have contributed both to large-scale direct losses of boreal wetlands and profound changes in hydrology (Greenberg and Doege 1999, Savignac 2006, Greenberg et al. 2011). Apparent range retractions at the southern edge of the boreal forest may provide prima facie evidence that global warming is taking its toll, although climate change is also drying wetlands in the northern boreal forest (Klein et al. 2005, Riordan et al. 2006), drying that appears to affect the chemistry of water and abundance of macroinvertebrates (Corcoran et al. 2009).

Other environmental factors of extrinsic origin are affecting boreal wetlands negatively. An increase in atmospheric deposition of industrial pollution, particularly in the eastern breeding range, may affect trophic resources through an insidious combination of lower pH and higher load of mercury. In acidic wetlands, mercury is readily converted to its toxic form, methylmercury. In eggs of the Common Grackle, methylmercury kills the embryo at relatively low concentrations (Heinz et al. 2009). Given the Rusty Blackbird's preference for feeding on predatory aquatic invertebrates and small fish (Beal 1900, Martin et al. 1951), its risk of accumulating methylmercury may be higher than that of other passerines.

Habitat loss and degradation on the breeding and winter range, climate change, and contaminant exposure are the usual suspects for the decline of a migratory bird. Given our general ignorance about the population dynamics of the Rusty Blackbird, however, researchers need to be open to other possibilities. For example, in the 1970s, already declining populations may have been particularly hard-hit by large-scale pest-control programs that focused on reducing the numbers of blackbirds and European Starlings (*Sturnus vulgaris*) that congregated at large evening roosts in several states within the Rusty Blackbird's winter range (Heisterberg et al. 1987, Dolbeer et al. 1997). Rusty Blackbirds were generally found in only small numbers in these large mixed-species roosts and thus are thought not to have been greatly affected by these control programs (Avery 1995, Greenberg et al. 2011), but negative effects may be cumulative. Such large-scale control programs have ceased, but continued small-scale programs to control blackbird populations may have long-term effects during the nonbreeding season. The importance of disease in regulating bird populations has become increasingly apparent (Marra et al. 2004, LaDeau et al. 2008) and should not be overlooked as a factor contributing to the Rusty Blackbird's decline. The dramatic increases in many raptor populations during the post-DDT era (Sauer et al. 2008) may also be hampering the recovery of the Rusty Blackbird.

IMPORTANT FINDINGS OF THE SPECIAL SECTION

The first task of the International Rusty Blackbird Working Group in 2005 was to identify and implement critical studies to understand the species' natural history and factors contributing to its decline across its annual cycle. This special section presents the findings of the majority of the initial recommended studies. Hobson et al. (2010) examined levels of deuterium in feathers of wintering Rusty Blackbirds and found strong isotopic evidence for separate Mississippi and Atlantic flyways: birds that breed from Alaska through central Canada winter in the Mississippi Alluvial Valley, and birds that breed in eastern Canada winter along the Atlantic Coastal Plain. These findings allow scientists to now link research, monitoring, and management to the appropriate flyway, an approach effective in the management of North American waterfowl (North American Waterfowl Management Plan Committee 2004). Hobson et al. (2010) also identified a geographically restricted and potentially smaller Atlantic flyway population that appears to be particularly susceptible to the extirpations observed in New England, the Maritime Provinces, and the southern boreal zone (Powell 2008, Greenberg et al. 2011; Maritime Breeding Bird Atlas, unpubl. data).

The special section updates substantially our understanding of the species' nesting ecology and habitat requirements in te breeding season, topics previously known from brief descriptions of sixteen nests found in New England by Kennard (1920). Matsuoka et al. (2010a) and Powell et al. (2010a) respectively surveyed and radio-tracked breeding Rusty Blackbirds and found that the generally low breeding densities observed over much of the species' range are linked to specialized use of shallow-water habitats for foraging and large home ranges, which typically include multiple wetlands used for foraging and nesting. Matsuoka et al. (2010b) and Powell et al. (2010b) analyzed data from >450 nests across the breeding range and showed that the species' widespread use of small stunted conifers, primarily spruce (*Picea* spp.), for nest sites is selective and leads to relatively high rates of nest survival when nests are placed in undisturbed wetlands in Alaska and New England. In New England, however, when Rusty Blackbirds nested in young spruce or balsam firs (*Abies balsamea*) regenerated from recent logging of wetlands or adjacent uplands, they experienced a nearly 70% reduction in nest survival because of high nest predation. Thus, buffers from logging around wetlands ought to be explored as a conservation measure to protect nesting Rusty Blackbirds from these negative consequences (Powell et al. 2010b). Average rates of nest success in Alaska (56%; Matsuoka et al. 2010b) and New England (62%; Powell 2008) are not at chronically low levels that could be linked to long-term declines, so factors reducing survival of adults or juveniles are likely limiting population growth (Matsuoka et al. 2010b).

Luscier et al. (2010) conducted the first formal surveys targeting wintering Rusty Blackbirds and modeled occupancy to show that birds wintering in the lower Mississippi Alluvial Valley are commonly found in a variety of forested wetlands but often are observed in adjacent agricultural fields, where they sometimes feed in loose association with other blackbirds. The species appears to depend on forest wetlands with open water but may use nearby disturbed sites, possibly to feed on waste grains and weed seeds to supplement its principal winter diet of aquatic and terrestrial invertebrates (Beal 1900) and acorn masts and pine (*Pinus* sp.) seeds (Meanley 1995). Other studies are currently underway in various parts of the winter range to fill critical gaps in our understanding of the species' winter foraging ecology and the relative importance of various habitats for foraging and daytime and evening roosts (N. W. Dias, C. Mettke-Hofmann, and P. Newell; unpubl. data).

The cross-seasonal investigation by Edmonds et al. (2010) shows that methylmercury levels in Rusty Blackbirds are an order of magnitude greater in breeding than in wintering populations, in part as a result of a trophic shift from an omnivorous diet during winter to a diet of predatory invertebrates during summer. Methylmercury is higher in birds breeding in New England and the Maritime Provinces than in those in breeding in Alaska, likely because of both lower pH in eastern wetlands and higher rates of atmospheric deposition of mercury from industrial emissions. Barnard et al. (2010) found wintering birds in the Mississippi Alluvial Valley to have an unexpectedly high prevalence of infections with hematozoa, equivalent to levels found in birds breeding in Alaska and Maine. In temperate regions, winter is a time when insect vectors are dormant, so the presence of hematozoa in the peripheral circulatory system of birds is typically rare but can be brought on by stress. These findings present the intriguing hypothesis that in winter Rusty Blackbirds are prone to parasite and microbial infections because of stress induced by degradation of winter habitat. Researchers are currently testing whether the rate of hematozoan infections of populations wintering along the Atlantic Coastal Plain is also high (W. H. Barnard and P. Newell, unpubl. data).

Mettke-Hofmann et al. (2010) examined patterns of molt, finding that Rusty Blackbirds in fresh basic plumage in their first fall can be distinguished in the field from older birds on the basis of a distinct pale eye ring and chin. However, a previously undocumented pre-alternate molt during winter is concentrated on the head feathers and obscures most of these age-related differences by late winter. Aging birds during this time remains possible by in-hand inspection. Patterns of molt are useful in aging birds during fall and early winter and for identifying feathers to be collected for isotopic studies of diet or migration.

WHAT MORE WE NEED TO KNOW

The papers in this special section have advanced our understanding of the rangewide ecology of the Rusty Blackbird and have provided both important clues into the factors limiting populations and field-tested methods that can now be applied to more focused studies. Research to date has not delivered the much-needed answer to the mysterious question: what is causing the Rusty Blackbird's decline? The negative trend continues, and considerable research challenges remain before we can reverse it. Here we provide our recommendations for what we need to know to make meaningful progress in restoring Rusty Blackbird populations to historical levels. We emphasize our urgent need to understand factors that limit population growth as well as our still basic need to identify important regions, habitats, and resources for targeted conservation during the nonbreeding season.

BREEDING SEASON

Critical advances have been made in understanding breeding populations at the northwestern and southeastern extremes of the species' boreal range. Studies are needed in the vast regions in between. Such efforts would be most useful if focused on populations breeding in areas of known decline and range retraction and were designed to evaluate various hypotheses for the decline. For example, researchers could repeat previous surveys or atlases of breeding Rusty Blackbirds (e.g., Powell 2008) and compare habitats, patterns of land use, levels of acidification or contamination, and climatic characteristics among sites that retain breeding blackbirds and sites at which the species bred formerly (Machtan et al. 2007, Matsuoka et al. 2010a).

Birds breeding in New England and the Maritime Provinces appear to be particularly threatened by high levels of mercury contamination. Research is needed to understand the geographic extent of this contamination (Edmonds et al. 2010) and how it varies by habitat and by distance to sources of atmospheric pollution, natural occurring sources of mercury, or geologic formations that increase wetlands' pH (i.e., limestone) and thereby minimize methylation of mercury into toxic methylmercury (M. Cadman, pers. comm.). Experiments that identify concentrations of methylmercury that kill Rusty Blackbird embryos (e.g., Heinz et al. 2009) would help determine whether levels of methylmercury exposure at the southeastern edge of the breeding range affect reproduction rates at the population level (Edmonds et al. 2010). Studies that quantify sublethal effects of mercury exposure on nestlings' growth and health and survival of adults and juveniles remain of paramount importance.

Studies also are needed to determine whether the ecological trap proposed by Powell et al. (2010b) is geographically widespread or applies to disturbances other than logging in and near wetlands where Rusty Blackbirds breed. Studies that use the before–after, control–impact (BACI) design (Smith 2002) may give insight on this front, but their spatial scale will need to be relatively large, given the generally low densities at which the species breeds. The availability of shallow water and its aquatic macroinvertebrates (particularly Odonata) as prey appears to be central both in selection of breeding sites (Matsuoka et al. 2010a) and in successful reproduction. Understanding how the composition, densities, and phenology of macroinvertebrates influence clutch size, nestling growth, and mass at fledging will be important in inferring mechanisms governing habitat choice and reproductive success and for assessing how climate change will affect populations by altering the phenology or reducing the availability of prey by desiccating wetlands (Matsuoka et al. 2010a).

Any effort to protect or restore habitats for breeding Rusty Blackbirds will need to take into account the large area they require (Powell et al. 2010a), to buffer against negative edge effects on nest survival (Powell et al. 2010b), and to recognize that alternative habitats may be equally important after fledging (Faaborg et al. 2010), a period that remains to be studied.

NONBREEDING SEASON

Population dynamics and demography during the nonbreeding season have proven to be difficult to study. The Rusty Blackbird is notorious in the extent to which winter populations fluctuate within a year and in successive years. Particularly outside of the core wintering area in the lower Mississippi Alluvial Valley, it is difficult to establish sites of long-term study and to monitor the fate of individuals. Three approaches may facilitate winter research. First, understanding movements of individual birds will provide insight into how Rusty Blackbirds respond to fluctuations in weather, hydrological conditions, and mast-crop production. Hydrogen-isotope data have elucidated a major migratory divide between the western and eastern boreal forest (Hobson et al. 2010), and this pattern is supported by a small number of band recoveries (Hamel et al. 2009). Short-range transmitters have revealed individuals' space use and roost locations over a few weeks (C. Mettke-Hofmann, unpubl. data), but more advanced tracking technology is necessary to clarify how blackbirds move during migration and in winter. Second, we need to locate and determine the spatial consistency of the remaining concentrations of the species. Establishing locations of nonbreeding "hot spots" and comparing landscape and local attributes of these spots to areas with only small numbers of blackbirds may disclose key factors for roosting and feeding. In an attempt to harness the largely untapped power of myriad birders who comb the countryside daily, the International Rusty Blackbird Working Group and eBird have established a Rusty Blackbird Winter Hotspots Blitz to locate and monitor areas of high concentrations. Once an array of sites for comparison is established, standardized protocols for assessing hydrological conditions, weather, and mast-crop abundance need to be instituted.

A few studies focusing on the winter distribution of the Rusty Blackbird in various habitats are underway. Researchers are using counts (Luscier et al. 2010), a variety of measures of condition (C. Mettke-Hofmann and P. Newell, unpubl. data), and age and sex ratios to compare sites. Refining these measures should continue. In particular, wintering Rusty Blackbirds are often difficult to capture and have proven almost impossible to recapture. The seemingly simple task of developing reliable techniques for trapping continues to be a high priority for winter work. Ultimately, our ability to estimate apparent survival within a winter and in successive winters will be critical if we hope to develop year-round models of population dynamics, models that could be a primary tool for evaluating the causes of decline. To date, small-scale attempts to obtain survivorship data have met with failure because of the mobility of the birds and the low rate of resighting of color-banded individuals. Progress will come when efforts at banding and resighting become more regional or if appropriate tracking technology is developed.

Research on the population dynamics of songbirds has focused increasingly on the role of habitats in which the birds stop over during migration. Stopover habitat may be particularly critical in spring, when migration is more contracted and selective pressure to arrive on the breeding grounds early and in good physical condition is high (Rotenberry and Chandler 1999). With more information on habitat use and movement, it may be possible to look for cross-seasonal effects, where conditions during winter and spring migration affect reproductive performance (Norris et al. 2006).

The emerging picture is that two resources appear to be critical to the success of nonbreeding Rusty Blackbirds: semi-flooded wetlands where blackbirds forage for aquatic arthropods and fish and the mast of small-seeded oaks and domesticated pecans. Aquatic arthropods and fish provide a protein-rich diet, but they are available only from unfrozen water. Mast provides energy easily procured regardless of weather. The relative importance of wetland conditions and the distribution and abundance of mast need to be assessed through correlational and experimental studies. For example, experiments in which water in impoundments is drawn down may be useful for testing how habitats can be managed to benefit the species.

CROSS-SEASONAL PERSPECTIVE

As for all declining migratory species, ultimately what is needed is a model of annual population growth that connects demographic processes throughout the year so that the relative importance of various factors on fecundity, survival, and recruitment can be integrated into models of population dynamics. The cross-seasonal approach may be particularly needed to understand when and where deficits in juveniles' or adults' survivorship limit population growth because nesting success is not clearly limited (Matsuoka et al. 2010b).

Studies might focus particularly on the Rusty Blackbird's Atlantic flyway population, which likely is smaller than the Mississippi flyway population and which appears to be at higher risk of extirpation from a combination of higher mercury contamination during the breeding season and more habitat loss and alteration throughout the annual cycle. Analysis of potential genetic differentiation between Mississippi and Atlantic flyway populations is underway and may provide important fuel to future debates as to whether this population deserves protective status under the U.S. or Canadian endangered species acts.

CONCLUSIONS

The attention now paid to a "common" species with a plunging population underscores a sea change in the approach to bird conservation over the past two decades. The mantra, first uttered by Rosalie Edge in 1932 (Furmansky 2009), that "the time to save a species is while it is common; the only way to save a species is to never let it become rare" is now widely appreciated among conservation biologists. Such a proactive approach has been a philosophical underpinning of the Partners in Flight program to conserve migratory birds (Rich et al. 2004) and the motivation of International Rusty Blackbird Working Group to undertake the research presented in this special section.

The Rusty Blackbird, a formerly common species, has suffered both a chronic long-term decline and an acute recent decline. Most losses attracted no notice or comment. Like that of many birds breeding in North America's boreal forest, the basic natural history of the Rusty Blackbird is poorly known. Research over the past five years has been an exercise in catching up, so we may systematically evaluate causes of the decline. We have accumulated a number of plausible hypotheses for the decline, so the phase of testing hypotheses has begun in earnest. The Rusty Blackbird has a number of attributes that make even the simplest research difficult: most of the breeding range is inaccessible, breeding populations are often sparse and patchy, migratory and wintering populations are unpredictable and often hard to detect, and during the winter the birds are difficult to catch and often almost impossible to recapture. But in many ways the Rusty Blackbird is typical of other common yet declining species. Although there has been a philosophical shift in conservation to focus on protecting species while they are still common, the effort and resources required to determine the factors underlying the decline of any particular species are often daunting. However, the research is critical to any attempt at population recovery. The most important looming question is do we have the will and the resources to address the mystery of the Rusty Blackbird's decline.

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