SPECIAL SECTION: RANGEWIDE ECOLOGY OF THE DECLINING RUSTY BLACKBIRD

NESTING ECOLOGY OF THE RUSTY BLACKBIRD IN ALASKA AND CANADA

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Abstract. We examined the nesting ecology of the Rusty Blackbird (*Euphagus carolinus*) from 162 nests monitored for nest survival in Alaska and 252 incidental records from Alaska and Canada to identify important habitats for nesting and to test whether low rates of nest success are contributing to populations declines in Alaska. In coastal Alaska and throughout Canada, nests were primarily in conifers (85% of 212 nests). All conifer nests in Alaska and 80% of those in Canada were placed in spruce (*Picea* spp.), primarily black spruce (*P. mariana*). In Alaska use of small spruces (<8 cm dbh) was selective and resulted in high reproductive success—nest survival increased with black spruce density, and success of nests in spruce (79%) was higher than that of nests in deciduous vegetation (52%). Survival of nests in taller spruce declined, possibly from predation by red squirrels (*Tamiasciurus hudsonicus*). Rusty Blackbirds nested near water in interior ($\overline{x} = 8$ m) and south-central Alaska ($\overline{x} = 30$ m), and small spruces near water appear to be important over much of the species' range. In interior Alaska, however, most nests were in willows (78%), which dominated the vegetation near water. Nest success in Alaska averaged 56%, similar to rates over the same period in New England but higher than those of other North American blackbirds (30–39%). Studies are needed to verify whether nest survival is also high in Canada and to investigate where and why deficits in survival of adults or juveniles may be limiting population growth.

Key words: Alaska, *Canada*, Euphagus carolinus, *nesting ecology*, *nest-site selection*, *nest success*, *nest survival*, *Rusty Blackbird.*

Ecología de Nidificación de *Euphagus carolinus* en Alaska y Canadá

Resumen. Examinamos la ecología de nidificación de *Euphagus carolinus* a través del monitoreo de 162 nidos para obtener datos de supervivencia de nidos en Alaska y de 252 registros adicionales de Alaska y Canadá para identificar habitats importantes para la nidificación y evaluar si las bajas tasas de éxito de nidos contribuyeron a las disminuciones poblacionales en Alaska. En la costa de Alaska y a lo largo de Canadá, los nidos se encontraron principalmente en coníferas (85% de 212 nidos). Todos los nidos en coníferas de Alaska y el 80% de los de Canadá estuvieron ubicados en ejemplares de *Picea* spp., principalmente *P. mariana*. En Alaska se identificó un uso selectivo de ejemplares pequeños de *Picea* (<8 cm DAP), resultando en un alto éxito reproductivo—la supervivencia de los nidos incrementó con la densidad de *P. mariana*, y el éxito de nidos en ejemplares de *Picea* (79%) fue mayor que el de los nidos ubicados en vegetación decidua (52%). La supervivencia de nidos en ejemplares más altos de *Picea* disminuyó, posiblemente debido a la depredación por parte de *Tamiasciurus hudsonicus*. Los individuos de *E. carolinus* nidificaron cerca del agua en el interior ($\overline{x} = 8$ m) y en el sur centro de Alaska ($\overline{x} = 30$ m), y los ejemplares pequeños de *Picea* parecieron ser importantes dentro de la mayor parte del área de distribución de la especie. Sin embargo, en el interior de Alaska, la mayoría de los nidos se ubicaron en ejemplares de *Salix* (78%), los que dominaban la vegetación cercana al agua. El éxito de nidos en Alaska promedió el 56%, similar a las tasas del mismo periodo en Nueva Inglaterra pero mayor que las de otras especies de *Euphagus* de América del Norte. Son necesarios estudios para verificar si la supervivencia de nidos es alta también en Canadá y para investigar dónde y cómo el déficit en la supervivencia de adultos o juveniles puede estar limitando el crecimiento poblacional.

INTRODUCTION

The Rusty Blackbird (*Euphagus carolinus*) breeds across North America's vast boreal forest, where it is often associated with forested wetlands and open fresh water (Avery et al. 1995, Matsuoka et al. 2010, Greenberg et al. 2011). Until the early 20th century ornithologists had often described the Rusty Blackbird as common or abundant—since then it has suffered one of the steepest rangewide declines of any bird in North America (Link and Sauer 1996, Greenberg and Droege 1999, Niven et al. 2004). The causes of the decline remain unknown (Greenberg et al. 2011). Despite the species' broad range, steep decline, and high conservation concern (Rich et al. 2004, Greenberg et al. 2011), the nesting ecology of the Rusty Blackbird is known only from a small number of nests placed primarily in small spruce (*Picea* spp.) and balsam fir (*Abies balsamea*) trees in the extreme southeastern portion of the species' breeding range in New England (Kennard 1920, Ellison 1990, Powell et al. 2010). Information on nest survival in New England has only just become available (Powell et al. 2010), and even information as basic as the length of the incubation and nestling periods remains unconfirmed (Kennard 1920, Avery 1995). Therefore, a much broader assessment of the species' nesting ecology is needed to document basic attributes of its life history, identify habitats important for nesting, and evaluate whether chronically low reproductive success is contributing to the decline (Greenberg et al. 2011).

In this study we evaluated the nesting ecology of Rusty Blackbirds from nests found across the boreal zone in Alaska from 1995 to 2008 and in Canada from 1887 to 2008. Specifically, we first analyze data from nests to describe the species' general nesting chronology and to test for spatial variation in clutch size, nest-site vegetation, and nest height. Second, we examine data from six study areas in Alaska to test whether clutch initiations and daily nest survival varied spatially or temporally. We then analyze data from the subset of nests monitored on military lands in Alaska to identify habitat features associated with nest-site selection and to test whether daily nest survival varied with habitat features. Finally, we discuss our findings from Alaska and Canada in relation to those from New England (Kennard 1920, Ellison 1990, Powell et al. 2010) to provide a rangewide perspective on the nesting ecology of the least studied and northernmost of North America's blackbirds (Avery 1995).

METHODS

STUDY AREA

We obtained data on nesting Rusty Blackbirds from across the species' breeding range outside of New England, primarily from the boreal forest region of Alaska and Canada, with a few records from the temperate rainforest region of Alaska. From Canada, we obtained data from 1887 to 2008 on 230 nests from Project NestWatch (Bird Studies Canada 2009), which included records of Rusty Blackbird nests from all Canadian provinces and territories except Nunavut: the Yukon Territory (*n* = 14 nests), British Columbia (*n* = 44), Northwest Territories (*n* = 7), Alberta (*n* = 7), Saskatchewan (*n* = 5), Manitoba (*n* = 3), Ontario (*n* = 52), Quebec (*n* = 34), Newfoundland (*n* = 7), Nova Scotia (*n* = 38), and New Brunswick (*n* = 19). In Alaska, most of the data (*n* = 162 nests) are from six study areas collectively surveyed for nests from 2006 to 2008 in interior and south-central regions of the state. Other data came from incidental observations of nests from 1995 to 2008 in interior (*n* = 20 nests) and southeast Alaska (*n* = 2 nests; Fig. 1).

In interior Alaska, we studied the Rusty Blackbird in four areas within the expansive floodplain of the Yukon River and its major tributaries: from west to east the Innoko National Wildlife Refuge (Innoko; 63° 34′ N, 158° 16′ W; R. M. Corcoran data), Fairbanks (64° 52′ N, 147° 45′ W; D. Shaw, 2006 data; N. A. Rojek, 2008 data), the Tanana Flats Training Area of the U.S. Army's Fort Wainwright (Tanana Flats; 64° 45′ N, 147° 45′ W; D. Shaw data), and Tetlin National Wildlife Refuge (Tetlin; 62° 39′ N, 141° 3′ W; D. Shaw data; Fig. 1). These study areas comprise complex mosaics of poorly differentiated wetlands with lesser amounts of upland habitats. Willow (*Salix* spp.) and alder (*Alnus* spp.) are the common wetland shrubs >1 m in height; balsam poplar (*Populus balsamifera*), paper birch (*Betula papyrifera*), black spruce (*Picea mariana*), and white spruce (*P. glauca*) are the dominant trees in forested wetlands. We reached the study sites in Innoko and the Tanana Flats by motor boat and searched for nests in wetlands along 22 km of Hather Creek (Innoko) and 11.25 km^2 of floodplain adjacent to the Tanana River (Tanana Flats; Matsuoka et al. 2010). Study sites in Fairbanks and Tetlin were reached by road and included wetlands with open water on the perimeter of the city of Fairbanks and two lakes and their adjacent forested and shrubby wetlands near the Alaska Highway (Tetlin).

In south-central Alaska, study areas included boreal wetlands within Elmendorf Air Force Base and adjacent Fort Richardson near Anchorage (Anchorage; 61° 15′ N, 149° 41′ W; S. M. Matsuoka data) and a large complex of wetlands in the temperate rainforest zone in the upper Copper River Delta (Copper River; 60° 23′ N, 145° 18′ N; P. M. Meyers data; Fig. 1). The study area in Anchorage was located in a primarily upland landscape. Wetlands of various sizes were generally isolated and dispersed; we searched for nests in all wetlands that were seasonally or permanently flooded (*n* = 33) and in the adjacent 50 m of upland habitats (Matsuoka et al. 2010). The dominant trees and shrubs within wetlands in Anchorage are similar to those in interior Alaska except that willows are uncommon. The Copper River study area is located in a large network of freshwater sloughs and wetlands where woody plants >1 m in height, dominated by willow and alder, grow on the banks of sloughs; young Sitka spruces (*P. sitchensis*) are sparse. Plant communities in this area are still undergoing rapid succession as a result of substantial uplifting from the Good Friday earthquake of 1964 (Stover and Coffman 1993).
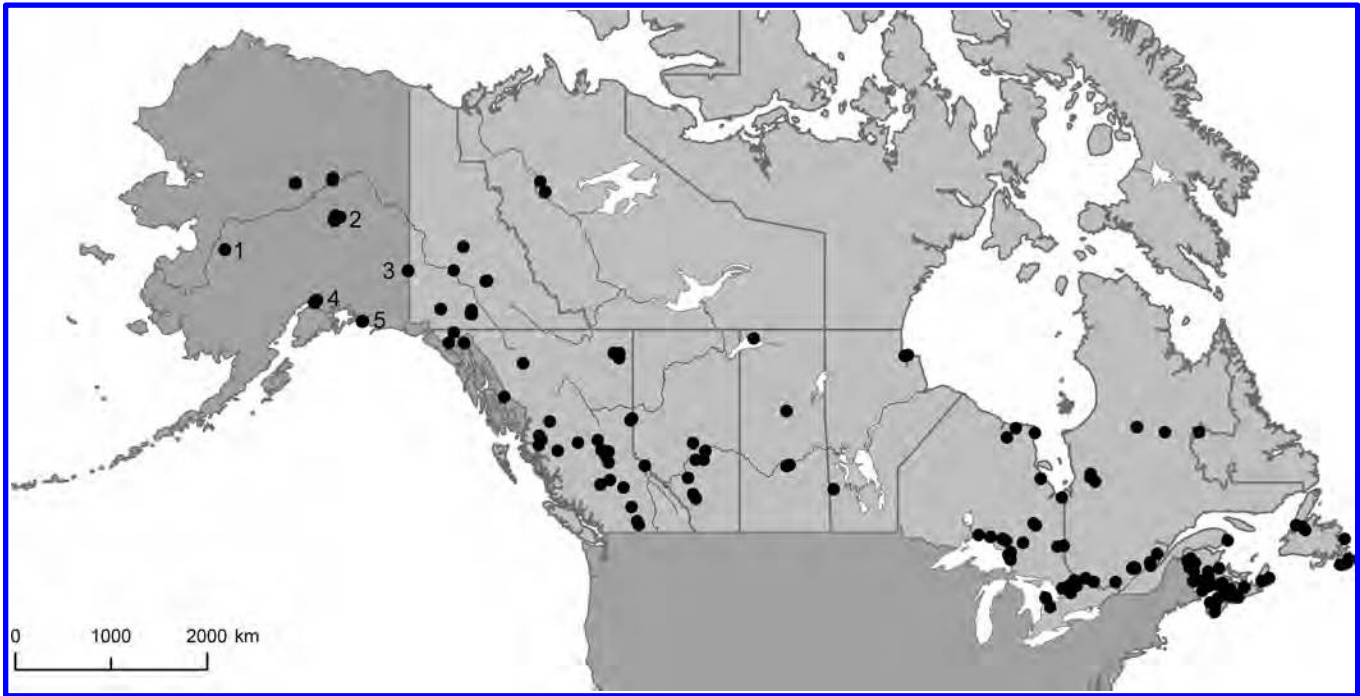
FIGURE 1. Distribution of Rusty Blackbird nests found in Alaska ($n = 184$) and Canada ($n = 230$). Records of nests in Canada date from 1887 to 2008 and were submitted to Project NestWatch (Bird Studies Canada, unpubl. data). Most nests in Alaska are from studies of the Rusty Blackbird from 2006 to 2008 in (1) Innoko National Wildlife Refuge (NWR), (2) Fairbanks and adjacent Tanana Flats Training Area, (3) Tetlin NWR, (4) Elmendorf Air Force Base and adjacent Fort Richardson near Anchorage, and (5) Copper River delta.

FIELD SAMPLING

All nests from Canada and a small number from Alaska were found incidental to other field work. Most of these nests were visited one or two times and thus do not provide information from which nest survival can be assessed. Each nest record is accompanied by a date and typically includes the number of eggs or nestlings, the plant species used for nesting, and the height of the nest (m). In Alaska, the dates of field work varied by the six study areas where we intensively searched for and monitored nests: Anchorage (10 May–5 July 2007 and 2008), Copper River (25 May–21 June 2006), Fairbanks (13 May–28 June 2006 and 2008), Innoko (3–18 June 2006), Tanana Flats (10 May–5 July 2007 and 2008), and Tetlin (19 May–19 June 2008). In each study area, field observers systematically surveyed wetlands for territorial Rusty Blackbirds either by foot or from the water by canoe (Anchorage and Tetlin), kayak (Copper River), or motor boat (Innoko). We searched blackbird territories for nests by observing adults from a distance and following them back to their nests as they carried nest materials or returned to incubate their eggs or feed their mates or young. In Anchorage and Copper River, when we found nests during incubation, we estimated the stage of incubation by candling the eggs and comparing the observed stage of embryo development to known stages of development in eggs of the Red-winged Blackbird (*Agelaius phoeniceus*; Fig. 2

in Lokemoen and Koford 1996). In all study areas, when we found nests with nestlings we estimated their age from their size and feather development. We monitored each nest every 2–7 days to determine survival, intervals of egg laying, and lengths of the incubation and nestling periods. When we did not observe activity we inspected nests to verify failure or fledging (Martin and Geupel 1993).
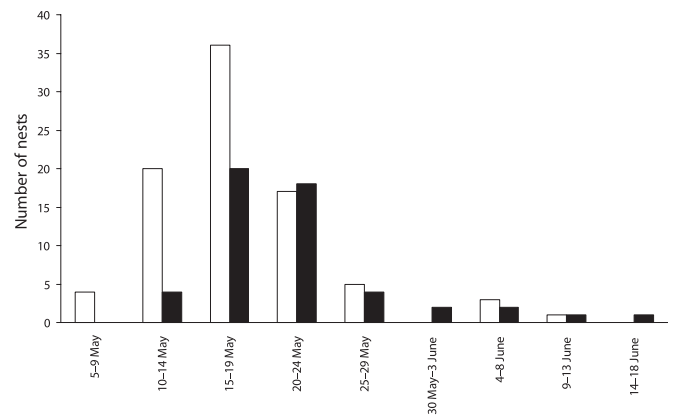

FIGURE 2. Dates of clutch initiations among Rusty Blackbirds nesting in interior (□, $n = 86$ nests) and south-central Alaska (■, $n = 52$ nests), 2006–2008.

We typically monitored activity at nests from a distance with binoculars, but we examined the contents of nests, either directly or with the aid of a mirror mounted on a telescoping pole, once during laying to determine date of clutch initiation, once during incubation to determine final clutch size, on the estimated date of hatching to estimate the incubation period and the number of eggs hatched, and 4 days before estimated fledging to band, weigh, and measure nestlings, and count them before they fledged. Thereafter, we checked nests from a distance until we verified fledging or failure. We captured a subset of adults in mist nests (2.6 × 6.0 m or 2.6 × 12.0 m; 36-mm mesh) placed near their nests and banded each bird with a unique combination of one U.S. Geological Survey aluminum band and three colored leg bands (Anchorage, Innoko, and Tanana Flats). We considered nests to have been successful when we observed adults feeding newly fledged young within 100 m of the nest. This distance was less than half the average distance between nests (see Results) and was within the distance that banded adults have been observed feeding newly fledged young in both Alaska (S. M. Matsuoka and D. Shaw, unpubl. data) and New England (L. L. Powell, pers. comm.). We considered nests to have failed from predation when nest contents disappeared before the chicks had adequate time to fledge, when we found an empty nest with the materials pulled apart, or when we found eggshell fragments below an empty nest. We considered nests to have been abandoned because of our activities when we found a clutch of cold eggs on the visit after we banded the adults. During all visits we searched for additional nests when we encountered new pairs. Following each nest failure, we searched the associated territory for renesting and monitored replacement nests as described above.

There were notable exceptions to these protocols. In Anchorage and Tanana Flats, 2008, we inserted iButtons (model DS1992L) into a subset of nests and onto nearby trees or shrubs to record nest and ambient temperatures at 10-min intervals and thereby provide precise dates for fledging and failures, which we assumed occurred when nest temperatures dropped and remained at ambient levels (Hartman and Oring 2006). In Anchorage, 2008, we could not visually inspect the contents of two nests in the canopy (>4 m above the ground). We therefore determined activity at these nests by repeatedly observing adults at nests through binoculars or a spotting scope. We assumed these nests to be in the incubation stage if we observed a female sitting continuously on the nest for >20 min and if we repeatedly observed adults approaching an unattended nest with no food in their bills. We assumed that a nest contained nestlings if we observed adults carrying food to an unattended nest and subsequently leaving the nest with an empty bill or fecal sac (Martin and Geupel 1993, Martin et al. 1997).

After each nesting attempt in Alaska, we recorded the nest's location in a global-positioning system and sampled the nest's microhabitat for variables that included the plant species used for nesting, height of the nest above the ground or water

(m), and whether tree or shrub containing the nest was alive or dead. In Anchorage and the Tanana Flats, we also measured more specific attributes of the nest sites that were not consistently measured at other study areas in Alaska. This included the diameter at breast height (cm at 1.37 m, dbh) and the height (m) of the tree or shrubs used for nesting. When more than one tree or shrub stem supported the nest, we measured the dbh of each stem and the height (m) of the tallest supporting stem. At these two study areas we also estimated the concealment of the nest by foliage from 1 m above and 1 m from the side from each of the cardinal directions by quartiles (0–25%, 26–50%, 51–75%, and 76–100% concealment); we used the minimum of the five nest-cover scores for each nest as a conservative index of its vulnerability to potential predators. In Anchorage and Tanana Flats, where we thoroughly searched the sampled areas for nests in order to estimate nest densities (Matsuoka et al. 2010), we used a GIS to measure the distance from each nest to the nearest neighboring nest (m). In Anchorage, Tanana Flats, and Tetlin we measured the dimensions of nests and noted the materials used in their construction.

After the nesting season from late June to mid July, we also measured vegetation in Anchorage and the Tanana Flats within a 20- × 20-m plot centered on each nest (nest area), and within a 20- × 20-m plot located at a random distance (40–60 m) and cardinal direction from each nest but not in open water. We chose plots of 20 × 20 m because this size sampled an area similar to that of other standard studies of nesting passerines (James and Shugart 1970, Martin et al. 1997); we chose the square shape because determining whether trees and shrubs near the plot boundary are within the area to be sampled is easier with a square plot than with a circular plot (Husch et al. 2003). Within each nest area and plot of available habitat, we counted the number of stems of standing trees and shrubs by species, dbh class (2.5–8 cm or ≥8 cm), and whether the tree or shrub was live or dead. On the Tanana Flats, when we encountered dense willows or alders, we restricted our stem counts to a plot of 10 × 10 m then multiplied them by 4 to standardize them to the 0.04-ha area sampled within the 20- × 20-m plots. At 39 intercept points systematically distributed at 1.5-m intervals along three 20-m transects spaced 6 m apart, we measured canopy cover by looking directly overhead through a sighting tube to determine the proportion of points with foliage above 3 m (James and Shugart 1970, Ganey and Block 1994). We estimated water cover as the proportion of the intercept points landing on surface water. Although multiple observers sampled vegetation, we trained them before sampling in order to minimize variation by observer in measurement and ocular estimation of cover (Block et al. 1987).

STATISTICAL ANALYSES

We analyzed different subsets of the nest data to address different aspects of the Rusty Blackbird's nesting ecology. At the largest scale we evaluated all nests from Alaska and Canada to

describe the species' basic nesting ecology and to determine whether clutch sizes or substrates used for nesting varied spatially. We examined the data from nests in Alaska to test whether clutch-initiation dates, clutch sizes, and nest survival varied temporally and spatially. Finally, we analyzed data from our intensive studies on military lands in Alaska to evaluate nest-site selection and to test whether nest survival varied with habitat.

Nesting chronology and clutch size across Alaska and Canada. We first screened all data from Alaska and Canada and extracted the subset of nests with more than one observation within the nest-building, egg-laying, incubation, or nestling periods to describe the timing and lengths of each period. We pooled all data because samples from any one location were small. We estimated the interval at which eggs were laid by examining data from nests with more than one observation during laying to determine whether the number of eggs and number of days between observations differed. We determined when incubation began relative to clutch completion from our observations of females at nests during laying in Alaska and by comparing nest temperatures to ambient temperatures for three nests in Anchorage fitted with iButtons before clutch completion.

Clutch initiations in Alaska. We estimated clutch-initiation dates for 138 nests in Alaska that we either observed during egg laying or had multiple observations of the final clutch size and had accurate information on the date of hatching or the date of fledging. We did so by backdating on the basis of our observations of the interval between eggs, the clutch size, the modal number of days from clutch completion to the beginning of hatching, and the modal number of days from the beginning of hatching to fledging. We then used analysis of variance (ANOVA) and developed eight models of clutch-initiation date that included the intercept only, the univariate effects of year, location, and region, the bivariate effects of location plus year and location plus region, and the full-factorial effects of location plus year and location plus region. We compared the relative fit of these models with Akaike's information criterion adjusted for small sample sizes (AIC_c) and rescaled to AIC_c differences (Δ_i) and model probabilities (w_i). To assess the overall evidence that the variable was associated with the clutch-initiation date, we summed w_i of models sharing a common explanatory variable (Σw_i, Burnham and Anderson 2002).

Nesting substrates across Alaska and Canada. We examined all data available on the plant species used for nesting (nest substrates; $n = 184$ nests in Alaska, $n = 149$ nests in Canada) to test for spatial variation of nest substrate across six regions: interior Alaska, coastal Alaska (south-central and southeast Alaska), western Canada (BC, NT, and YT), central Canada (AB, SK, MB, and ON), eastern Canada (QC and interior NL), and maritime Canada (NB and NS). We pooled data from adjacent provinces to minimize counts of fewer than five nests per substrate, a general recommendation for comparison of proportions based on counts (Zar 1984). We

did not include nests from Canada that were found after the chicks had fledged ($n = 28$ nests) because we were not certain that these were the nests from which the chicks had fledged. We first assigned each nest to a general class of substrate: conifer, deciduous tree, deciduous shrub, and other; the latter including nests placed in grasses, sedges (*Carex* sp.), cattails (*Typha* sp.), or on the ground. We then used a log-linear model with a Poisson distribution to test whether the proportional use of substrates in the six regions varied. We did so by first developing a main-factor-effects model with region and nest substrate, which allowed numbers of nests to vary by region and substrate. We then used AIC_c to compare the fit of this model to that of the full-factorial model, which allows proportions of nests in each substrate to vary by region.

We tested whether nest heights varied regionally or by nest substrate in the subset of 157 nests from Alaska and 133 nests from Canada that included information on both nest height and nest substrate. Specifically, we used ANOVA and resultant AIC_c values to compare the relative fit of five models of average nest height that included the intercept only and the univariate effects of region and nest substrate, the bivariate effects of region plus nest substrate, and full-factorial effects of region and nest substrate.

Use and selection of habitats on military lands in Alaska. We then examined the habitat data on 107 nests on military lands in Alaska to (1) test for differences in the use of microhabitats between the two areas of intensive study (Anchorage and Tanana Flats) and (2) to identify habitat variables that distinguished nest sites from nearby random sites in each study area. First, we used ANOVA and compared the study areas in the average distance of nests from surface water, distance to the nearest nest, height of nests above ground or water, number of supporting stems, dbh, and height of substrates used as nest sites. Using AIC_c, we compared the relative fit of models with and without the effects of study area. Next, we tested for selection of nest substrate by comparing the frequencies that Rusty Blackbirds used each substrate for nest sites versus the proportional availability of the substrate within the 20- × 20-m nest area. We pooled samples across nests and nest areas separately because of small sample sizes. We further pooled counts of substrates for each study area as follows because of low counts of nest use or availability: in Anchorage, alders plus paper birch, black plus white spruce; on the Tanana Flats, alders plus willows, paper birch plus balsam poplar, black plus white spruce. We then used log-linear models with a Poisson distribution and log-link function to test for departures of use from availability for each study area separately (Manly et al. 1993). Following Manly et al. (1993:141), we used the parameters estimated from the resulting log-linear models to calculate the ratios of proportional use to proportional availability.

We then used univariate logistic regression with a matched-pairs design (Hosmer and Lemeshow 2000) to test whether individual habitat variables could distinguish 20- × 20-m nest areas from nearby 20- × 20-m random areas not used for

nesting. We ran separate analyses for Anchorage and Tanana Flats because we did not expect selection to be the same, owing to large differences in habitats (Matsuoka et al. 2010). We did not construct multivariate logistic regressions because in the univariate analyses we found few effects of covariates. The habitat attributes were chosen prior to analysis and included distance to water, distance to nearest nest, percent of the 20- × 20-m area with surface water, canopy cover, and tree- and shrub-stem densities by dbh class. For the latter, we combined counts of live and dead stems for each plant species to minimize redundancies due to correlations ($r > 0.4$) and because we found Rusty Blackbirds to nest commonly in both live and dead vegetation (see Results). We compared the fit of the univariate logistic regressions within a study area by AIC_c.

Clutch sizes in Alaska and Canada. For nests in Alaska ($n = 104$) and Canada ($n = 28$) with multiple observations of the final clutch, we used ANOVA to test for mean differences in clutch size between Alaska and Canada. We did not include nests observed only once because we sometimes found nests during egg laying. From the Alaska data on clutches we developed nine ANOVA models of clutch size that included the intercept only, the null model with a covariate effect for clutch-initiation date, and all univariate, bivariate, and full-factorial models for the effects of year, location, and region within Alaska. We did not include location and region in the same models. We compared these models' relative fit with AIC_c. We calculated egg viability in Alaska as the proportion of eggs surviving the incubation stage that hatched. We pooled data from Alaska because of small sample sizes.

Nest survival in Alaska. We calculated maximum-likelihood estimates of daily nest survival and proportion of nests fledging at least one nestling (nesting success) according to Dinsmore et al. (2002), who used a logit link to modeled survival as a function of covariates. The sample comprised 39 nests from Anchorage, 14 from the Copper River Delta, 24 from Fairbanks, 5 from Innoko, 60 from Tanana Flats, and 8 from Tetlin, 150 nests total, excluding 12 that were abandoned during construction from unknown causes, 4 abandoned early in incubation after we banded the female, and 4 of unknown fate. We assessed nest survival across the six study areas in two stages. We first controlled for temporal variation by comparing the fit of 18 models of nest survival that included the intercept only and all combinations of either (1) the linear or quadratic effects of nest age (age and age[2]), (2) the linear or quadratic effects of date (date and date[2]), and (3) the categorical effects of year (Grant et al. 2005). Models with quadratic effects were second-order polynomials that included both the linear and squared effects of age or date (Grant et al. 2005). To both identify years with low or high nest survival and to minimize the number of estimated parameters, when we found evidence for year effects we assessed the resulting coefficients for each year and combined years with coefficients whose 95% confidence intervals overlapped. We then tested for spatial variation in nest survival controlled for temporal

variation by using the temporal model with the lowest AIC_c and then adding the single effects of region (interior vs. south-central Alaska), study area, and the full-factorial effects of region plus year and study area plus year.

Nest survival in relation to habitat on military lands in Alaska. We then examined the subset of 99 nests on military lands in Alaska (Anchorage and Tanana Flats) to determine if nest survival was related to specific habitat attributes used for nesting. This analysis excluded 8 nests with either unknown fate or that were abandoned after the adults were banded. We used the methods above and first developed 18 models of temporal variation in nest survival. We then used the temporal model with lowest AIC_c and added to it individual nest-habitat characteristics. Nest-microsite variables included the categorical effects of minimum nest concealment (≤50% concealed vs. >50% concealed), nest substrate (shrub, conifer, other), status of the nest substrate (live or dead), and the linear or quadratic effects of nest height and nest-substrate height. On a broader scale, we considered distance to surface water, distance to nearest nest, and numbers of stems of willows or black spruce within the 20- × 20-m nest area. For the latter, we restricted stem densities to willows and black spruce because they were the dominant substrates used for nesting (black spruce in Anchorage, shrubby willows on the Tanana Flats).

For all models of nest survival we included each categorical covariate as a series of indicator variables; we rescaled each continuous habitat variable with a z-transformation (Dinsmore et al. 2002, Rotella et al. 2004). We compared the relative fit of models with AIC_c and used the delta method to calculate the standard error associated with our estimates of daily nest survival (Cooch and White 2009). Because we found substantial evidence for effects of age[2] and date, we calculated nest success as the product of the daily estimates over the modal length of the nesting period from clutch initiation to the fledgling of young (29 days). We used the delta method to calculate the variance and 95% confidence intervals associated with our estimates of nest survival and nest success (Cooch and White 2009).

We used ArcGIS version 9.0 (ESRI 2005) to map the location of nests and study areas, program MARK version 5.0 (White and Burnham 1999, Cooch and White 2009) to analyze data on nest survival, and SAS version 9.2 (SAS Institute 2008) to fit generalized linear models. We developed sets of candidate models prior to data analyses, considered models with $\Delta_i < 2.0$ to be best supported by the data (Burnham and Anderson 2002), and present all statistics ± SE.

RESULTS

NESTING CHRONOLOGY AND CLUTCH SIZE

In Alaska and Canada, Rusty Blackbirds constructed new nests for each nesting attempt and often placed their nests near old nests from previous years. We observed one pair of Solitary Sandpipers (*Tringa solitaria*) that hatched young from an old

Rusty Blackbird nest in Anchorage in 2008. In Alaska, we observed 27 nests the female constructed while closely guarded by her apparent mate; we observed copulations of five of these pairs, but we never saw males assisting females in building. Most of our observations of nest building in Alaska were from 11 to 24 May ($n = 25$ nests), but in Anchorage we noted two late nests under construction on 4 and 9 June 2007. The interval between the start of building and the laying of the first egg was three days for one nest and four days for four nests in Alaska.

The ranges of dates over which nests with eggs (Alaska: 9 May–26 June, Canada: 4 May–30 June) and nestlings (Alaska: 25 May–8 July, Canada: 23 May–16 July) were observed in Alaska and Canada were similar. In Alaska, we estimated clutches to have been initiated from 6 May to 14 June, most (91% of 138 nests) from 10 to 24 May (Fig. 2). A model of clutch-initiation dates that included region of Alaska was best supported by the data (log likelihood $[L] = -273.7$, $n = 138$ nests, number of parameters $[K] = 3$, $AIC_c = 553.6$, $w_i = 0.44$). This model indicated that clutches were initiated an average of 4 days earlier in interior ($\bar{x} = 12.7 \pm 0.6$ days, $n = 96$ nests) than in south-central Alaska ($\bar{x} = 16.6 \pm 0.9$ days, $n = 52$ nests; day 1 = 6 May; Fig. 2) and had better fit than the model that included study area ($\Delta_i = 2.8$) and much better fit than the models with the effect of year or no effects ($\Delta_i \geq 10.5$). The fit of the univariate models with region or study area was not improved when year or an interaction term was added, so we found no evidence that average dates of clutch initiation varied by year.

In both Canada and Alaska, in 21 nests observed multiple times during egg laying ($n = 25$ intervals between visits), one egg was laid per day. In one nest in Canada, the first egg was laid before the female had finished lining the nest with fine grasses. In Alaska, females were often observed on eggs prior to clutch completion (on 7 of 21 visits during laying), but during these observations the eggs were not typically warm to the touch like incubated eggs in completed clutches. We fitted three nests with temperature-data loggers on the day the second egg was laid. In two nests, daytime temperatures were consistent with ambient temperatures until the clutch was completed. In the third nest, daytime temperatures remained higher than ambient through egg laying. In all three nests, evening temperatures were consistently higher than ambient prior to clutch completion. Both day and evening nest temperatures were consistently higher than ambient from clutch completion to fledging or failure.

In Alaska, the modal number of days from the laying of the last egg until the hatching of the first egg was 12 days ($\bar{x} = 11.8 \pm 0.2$ days, range = 10–13 days, $n = 18$ nests). Males did not incubate eggs but often delivered invertebrate prey to females, which typically flew from the nest to a nearby tree or shrub where they gave begging calls, quivered their wings, and accepted the food. Chicks hatched over 1–2 days ($n = 5$ nests). In all six study areas in Alaska, researchers noted that multiple pairs of blackbirds often mobbed them during their visits to a nest, particularly during the later stages of the nestling phase. The modal number of days from the onset of hatching to the fledging of young was 12 days ($\bar{x} = 11.5 \pm 0.2$ days, range 10–13 days, $n = 13$ nests). In both Alaska and Canada males and females were observed feeding nestlings and newly fledged young.

NESTS AND NEST SITES

Nest characteristics in Alaska. The average dimensions of nests from Anchorage ($n = 31$ nests), Tanana Flats ($n = 63$), and Tetlin ($n = 7$) were total outside diameter = 14.1 ± 0.2 cm, total height = 11.5 ± 0.2 cm, cup width = 9.6 ± 0.2 cm, and cup depth = 5.9 ± 0.1 cm. The outer frame and rim of these nests were constructed primarily of spruce, willow, or birch (*Betula* sp.) branchlets and coarse grasses, which were often woven into the stems and branches of the tree or shrub supporting the nest. Lesser materials included mosses, the stems of horsetail (*Equisetum* sp.) and fireweed (*Epilobium angustifolium*), and plant down from cottongrass (*Eriophorum* sp.) and fireweed. The inner cup consisted of mud, mosses, or organic shoreline detritus, which were typically wet during construction and hardened when dried. The nest cup was often thinly lined with fine grasses or sedges; hair of the moose (*Alces alces*) commonly lined nests in Anchorage and Tanana Flats but was not observed in Tetlin.

Use of nesting substrates across Alaska and Canada. Across Alaska ($n = 184$) and Canada ($n = 149$) nests were placed primarily in conifers ($n = 199$) and deciduous shrubs ($n = 114$); few were placed in deciduous trees or other substrates ($n = 20$ nests; Fig. 3). A log-linear model that allowed the proportion of nests in each substrate to vary by region
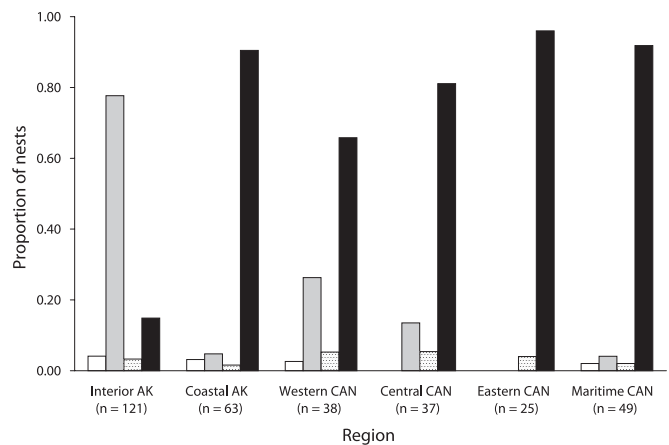

FIGURE 3. The proportion of Rusty Blackbird nests in each region of Alaska and Canada (CAN) that were placed on the ground or in grasses, sedges, or cattails (□, $n = 9$ nests), deciduous shrubs (▨, $n = 114$), deciduous trees (▧, $n = 11$), and conifers (■, $n = 199$). Regions included interior Alaska, coastal Alaska (south-central and southeast Alaska), western Canada (British Columbia, Northwest Territories, and Yukon Territory), central Canada (Alberta, Saskatchewan, Manitoba, and Ontario), eastern Canada (Quebec and interior Newfoundland), and maritime Canada (New Brunswick and Nova Scotia).

($L = -34.2$, $n = 333$ nests, $K = 19$, $AIC_c = 109.0$, $w_i = 1.0$) had substantially better fit than the model in which the proportion of nests in each substrate in each region was constant ($K = 13$, $\Delta_i = 186.4$). This model indicated that Rusty Blackbirds in all boreal regions but interior Alaska were most likely to nest in conifers (Fig. 3).

In coastal Alaska and central, eastern, and maritime Canada, Rusty Blackbirds placed nearly all of their nests (81–96%) in conifers. In western Canada, a majority (66%) did so. In contrast, in interior Alaska a much smaller proportion of nests (15%) was placed in conifers and a much larger proportion (78%) was placed in shrubs (Fig. 3). In interior Alaska, 93 shrub nests were placed in willows, which were often dead ($n = 26$ nests); one additional shrub nest was located in a dead alder. Small numbers of willow ($n = 13$) and alder shrubs ($n = 6$) were used as nest sites across the other regions (Fig. 3).

Of the nests placed in conifers, all in Alaska ($n = 75$ nests) and the majority in Canada (80% of 124 nests) were located in spruces. In Canada, small numbers of Rusty Blackbirds nested in other conifers, including balsam fir ($n = 14$ nests in Ontario, Quebec, Newfoundland, and New Brunswick), northern white cedar (*Thuja occidentalis*; $n = 4$ nests in Ontario, Quebec, and New Brunswick), and unidentified conifers ($n = 6$ nests). Most spruce nests were in black spruce ($n = 76$ nests), which was used across all regions except the coastal rainforest zone in Alaska, where 15 nests in the Copper River delta and one nest near the Stikine River were placed in live Sitka spruce. Small numbers of white spruce were also used over a broad area that included interior Alaska ($n = 11$ nests), south-central Alaska ($n = 7$ nests in Anchorage), the Yukon Territory ($n = 2$ nests), and Ontario ($n = 5$ nests). Most nests in unidentified spruces (62% of 58 nests) were located in the zone of introgression between the black and red spruce (*P. rubens*) in Quebec, New Brunswick, and Nova Scotia (Gordon 1976). In interior Alaska and Anchorage, 39% of the 59 spruces used for nest sites were dead.

Eleven nests were also found in deciduous trees including paper birch (four nests in Anchorage, Quebec, and Tanana Flats), balsam poplar (three in British Columbia and Tanana Flats), red maple (*Acer rubrum*; one in Nova Scotia), and pin cherry (*Prunus pensylvanica*; one in Ontario). Two nests were located in grasses (Tanana Flats), and six nests were located in emergent sedges (*Carex* sp.) and cattails (*Typha* sp.) in Anchorage, Nova Scotia, and the Tanana Flats. A single nest in British Columbia was found on the ground on a beaver (*Castor canadensis*) dam.

Across Alaska and Canada, the average height of nests was 1.6 ± 0.1 m ($n = 321$ nests), but it varied by substrate used for nesting ($L = -164.6$, $n = 290$ nests, $K = 5$, $AIC_c = 339.2$, $w_i = 1.0$). Nest heights from lowest to highest were grass/sedges/cattails/ground = 0.23 ± 0.06 m (range 0–0.5 m; $n = 9$ nests), shrubs = 1.0 ± 0.1 m (range 0–4.1 m; $n = 93$ nests), deciduous trees = 1.3 ± 0.4 m (range 0.3–5.0 m; $n = 10$ nests), and conifers = 2.0 ± 0.2 m (range 0–16.2 m, $n = 178$ nests). The model of nest height with an intercept only was not well supported by the data ($\Delta_i = 21.0$).

Use and selection of habitats on military lands in Alaska. We found 21 and 23 nests in Anchorage in 2007 and 2008, respectively, and 32 and 31 nests on the Tanana Flats in 2007 and 2008, respectively. Reflecting regional patterns (Fig. 3), in Anchorage Rusty Blackbirds placed 93% of 44 nests in spruces ($n = 32$ nests in black spruce and 7 in white spruce); on the Tanana Flats they placed 76% of 63 nests in shrubs ($n = 47$ nests in willows and 1 in alder). All models of nest-microsite characteristics that included study area had far better fit ($w_i = 1.0$) than their equivalent models without study area ($\Delta_i \geq 11.4$). Substrates used for nesting in Anchorage were on average nearly 2 times taller and 3 times greater in dbh than those on the Tanana Flats; they had one third the number of stems supporting nests. Nests in Anchorage were also nearly 2 times higher, 3.5 times farther apart, and 3 times farther from surface water than nests on the Tanana Flats (Table 1). Evidence

TABLE 1. Comparisons of characteristics [mean ± SE (range) or proportion] of sites of Rusty Blackbird nests in Anchorage and Tanana Flats, Alaska, 2007–2008. Most nests in Anchorage were placed in black spruce ($n = 32$); most nests on the Tanana Flats were placed in willows ($n = 47$).

Variable[a]	Anchorage	n	Tanana Flats	n
Number of supporting stems	1.5 ± 0.1 (1–4)	42	4.3 ± 0.3 (1–11)	58
Height of supporting stems (m)	6.6 ± 0.7 (0.9–19.8)	42	3.6 ± 0.3 (0.4–9.5)	57
Nest height (m)	3.2 ± 0.5 (0.1–16.2)	43	1.3 ± 0.2 (0.2–12.0)	61
Diameter at breast height (cm)	9.8 ± 0.8 (1–24)	42	3.2 ± 0.3 (0.7–13.2)	50
Distance to surface water (m)	30.6 ± 6.3 (0–185)	44	8.2 ± 2.7 (0–150)	63
Distance to nearest nest (m)	866 ± 213 (24–5437)	44	246 ± 19 (26–699)	62
Proportion of nests >50% concealed[b]	0.46	44	0.06	62

[a]We did not measure dbh or count supporting stems for nests that were placed in grasses, sedges, or cattails ($n = 2$ nests in Anchorage and 5 nests on the Tanana Flats); we did not measure dbh for nests in trees or shrubs shorter than breast height (1.4 m; $n = 8$ nests on the Tanana Flats). For other variables sample size varies because of missing values.
[b]Percent nest concealment visually estimated by quartile at each nest from 1 m above, below, and from each cardinal direction. We present the proportion of nests that were at least 50% concealed from all directions.

of colony nesting was limited, as only four pairs of nests were within 50 m of each other (two each in Anchorage and Tanana Flats). Nests on the Tanana Flats were less concealed by vegetation (6% of 62 nests were more than 50% concealed) than were those in Anchorage (46% of 44 nests were more than 50% concealed).

When we compared the proportions of nests in shrubs, deciduous trees, and conifers to the proportional availability of these substrates, we found evidence that the blackbirds used these substrates selectively in both Anchorage ($L = -13.1$, $n = 42$ nests and 4154 stems, $K = 5$, $\text{AIC}_c = 36.3$, $w_i = 1.0$) and the Tanana Flats ($L = -19.0$, $n = 58$ nests and 4840 stems, $K = 7$, $\text{AIC}_c = 52.0$, $w_i = 1.0$). Ratios of use to availability ($\beta > 1$ indicates selection, $\beta < 1$ indicates avoidance) indicated that in Anchorage Rusty Blackbirds nested in black and white spruce in proportion to their availability ($\beta = 1.3 \pm 0.5$) and avoided nesting in alders and paper birch ($\beta = 0.1$), the reference category. On the Tanana Flats they nested selectively in black and white spruce ($\beta = 5.0 \pm 1.2$), used willows and alders in proportion to availability ($\beta = 1.5 \pm 0.4$), and avoided nesting in paper birch and balsam poplar ($\beta = 0.3$), the reference category.

Areas in which Rusty Blackbirds nested in Anchorage were characterized by a predominance of black spruce and a scarcity of willows, but the opposite was true on the Tanana Flats. In both areas the canopy around nests was sparse (Table 2). We compared habitat characteristics of nest areas and paired random areas not used for nesting and found evidence for nest-site selection in Anchorage but not on the Tanana Flats, where the addition of none of habitat covariates improved the logistic regression with an intercept only ($L = -43.7$, $n = 63$ matched pairs of nests and random areas, $K = 2$, $\text{AIC}_c = 87.3$, $\Delta_i = 1.0$) by 2 AIC_c values ($K = 3$, $\Delta_i = 0.0$–3.1; Table 2). In Anchorage, the model of nest-site selection that included the total number of small black spruces (dbh 2.5–8 cm) was best supported by the data ($L = -26.9$, $n = 44$ matched pairs of nests and random areas, $K = 3$, $\text{AIC}_c = 58.1$, $w_i = 0.60$). This model indicated that Rusty Blackbirds nested in areas with densities of small black spruce higher than at matched random sites ($\beta = 0.019 \pm 0.008$); other models of nest-site selection were not well supported by the data ($\Delta_i = 3.6$–7.1; Table 2).

FECUNDITY AND NEST SUCCESS

Clutches in Alaska and Canada. Among nests with multiple observations of the final clutch size, 48 nests had 6 eggs, 62 nests had 5, 21 nests had 4, and one in Canada had 3. One additional nest on the Tanana Flats was found with 7 nestlings. An ANOVA model that compared mean clutch size in Alaska to that in Canada ($L = 54.7$, $n = 132$ nests, $K = 3$, $\text{AIC}_c = -103.2$) had substantially better fit than the model with only an intercept ($\Delta_i = 20.2$), indicating that clutches in Alaska ($\bar{x} = 5.3 \pm 0.1$ eggs, mode = 5 eggs, $n = 104$ nests) were larger than those in Canada ($\bar{x} = 4.6 \pm 0.1$ eggs, mode = 4 eggs, $n = 28$ nests). For the subset of nests from Alaska, clutch size was best described

TABLE 2.   Habitat characteristics of areas used by nesting Rusty Blackbirds in comparison[a] to matched random areas not used for nesting in Anchorage and Tanana Flats, Alaska 2007–2008.

Variable[b]	Diameter (dbh) class (cm)	Anchorage ($n = 44$ matched pairs)			Tanana Flats ($n = 63$ matched pairs)		
		Nests	Random	Δ_i	Nests	Random	Δ_i
Alder	2.5–8	15.6 ± 4.2	8.6 ± 2.7	4.9	26.1 ± 5.9	25.3 ± 7.6	3.1
	≥8	0.9 ± 0.6	0.3 ± 0.2	6.5	0.7 ± 0.2	1.0 ± 0.5	2.2
Willow	2.5–8	0.0 ± 0.0	0.0 ± 0.0	*	73.7 ± 8.5	57.0 ± 9.3	0.9
	≥8	0.0 ± 0.0	0.0 ± 0.0	*	7.0 ± 1.3	5.1 ± 1.2	1.8
Paper birch	2.5–8	2.9 ± 1.6	2.1 ± 1.3	5.5	13.5 ± 2.8	12.4 ± 2.6	2.8
	≥8	1.1 ± 0.3	3.6 ± 1.4	3.6	8.2 ± 1.5	9.8 ± 2.0	2.0
Balsam poplar	2.5–8	0.0 ± 0.0	0.0 ± 0.0	*	0.4 ± 0.3	0.5 ± 0.3	3.1
	≥8	0.0 ± 0.0	0.0 ± 0.0	*	0.3 ± 0.2	1.8 ± 1.1	0.0
Black spruce	2.5–8	55.9 ± 7.3	36.3 ± 6.6	0.0	0.3 ± 0.3	0.0 ± 0.0	2.1
	≥8	8.9 ± 1.4	6.2 ± 1.5	4.4	0.2 ± 0.2	0.0 ± 0.0	0.3
White spruce	2.5–8	1.7 ± 0.5	1.3 ± 0.6	6.8	1.0 ± 0.3	2.2 ± 1.2	1.5
	≥8	1.6 ± 0.5	1.9 ± 0.8	7.1	0.5 ± 0.2	0.8 ± 0.3	1.4
Canopy cover		20.5 ± 2.6	17.1 ± 3.9	6.4	25.2 ± 2.4	24.1 ± 3.5	3.0
Surface-water cover		12.4 ± 3.3	15.3 ± 3.8	6.9	22.4 ± 3.0	25.0 ± 3.5	2.6
Intercept only				5.1			1.0

[a]For each study area separately, we used univariate logistic regression with a matched-pairs design to compare habitat variables of nest areas and paired random areas not used for nesting. We compared the relative fit of models within each study area with Akaike's information criterion adjusted for small sample sizes (AIC_c) and rescaled as AIC_c differences (Δ_i; an asterisk indicates that the tree or shrub species occurred at a density too low for habitat selection to be modeled).
[b]Shrub and tree densities are numbers of live and dead stems within 20- × 20-m vegetation plots (0.04 ha). Canopy cover and surface water cover were the percent of 39 points intercepting vegetation > 3 m in height and surface water, respectively.

by a model that included clutch-initiation date ($L = 55.2$, $n = 104$ nests, $K = 3$, $AIC_c = -104.4$), indicating that clutch size declined as the nesting season progressed ($\beta_0 = 5.87 \pm 0.15$, $\beta_{intiation\ date} = -0.04 \pm 0.01$). Other models with the effects of region, study area, year, or an intercept only were not well supported by the data ($\Delta_i \geq 9.9$).

Nest losses in Alaska. Within Alaska, egg viability was high and partial reductions of broods were quite rare. Among the 69 nests that survived through incubation period, $90 \pm 2\%$ of 373 eggs hatched. Among the subset of 63 of these nests that fledged young, $96 \pm 2\%$ of 312 hatchlings fledged. Of the 150 nests in Alaska whose survival we monitored, 96 fledged young, 54 failed, and four had an unknown fate. Among failed nests, 48 were lost to predators (89%), four failed from unknown causes, and one nest in sedges and one nest in cattails sank into water. We observed one instance of predation, a red squirrel (*Tamiasciurus hudsonicus*) taking eggs from a nest during incubation. Although we rarely witnessed nest predation, we often observed adult Rusty Blackbirds mobbing Gray Jays (*Perisoreus canadensis*) or Black-billed Magpies (*Pica hudsonia*) in our study areas. Less commonly, we observed blackbirds mobbing Common Ravens (*Corvus corax*) and a variety of raptors including the Bald Eagle (*Haliaeetus leucocephalus*), Northern Harrier (*Circus cyaneus*), Sharp-shinned Hawk (*Accipiter striatus*), Northern Goshawk (*A. gentilis*), Red-tailed Hawk (*Buteo jamaicensis*), and Merlin (*Falco columbarius*). We even observed adult blackbirds on single instances chasing Solitary Sandpipers, Wilson's Snipe (*Gallinago delicata*), or American Robins (*Turdus migratorius*). We never observed pairs to renest after successfully fledging young, but we observed two color-marked females in Anchorage renesting 57 m and 196 m from their failed first nests.

Nest survival in Alaska. All models of daily nest survival in Alaska that included the effects of year indicated that nest survival was similar in 2007 and 2008. For parsimony, we therefore reduced models with year effects to 2006 versus 2007 and 2008 combined. With years reduced in this manner, daily nest survival averaged 0.947 ± 0.012 in 2006 [nest success (S) = 0.21 (95% CI 0.08–0.37)], 0.985 ± 0.002 in 2007 and 2008 [S = 0.64 (95% CI 0.54–0.72)], and 0.980 ± 0.003 for all three years combined [S = 0.56 (95% CI 0.47–0.64)]. Daily nest survival, however, was best described by a temporal model that included age^2, date, and year ($L = -192.5$, $K = 5$, $AIC_c = 395.0$, $w_i = 0.42$), indicating that daily nest survival declined with date, first declined and then increased with nest age, and was lower in 2006 than in 2007 and 2008 combined (logit scale; $\beta_0 = 6.89 \pm 1.32$, $\beta_{age} = -0.32 \pm 0.15$, $\beta_{age^2} = 0.016 \pm 0.009$, $\beta_{2007-2008} = 1.16 \pm 0.30$; Fig. 4). Standardizing to the median nest-initiation date of May 16 (date = 7 in the model), we calculated the product of the daily estimates of nest survival over the modal nesting period (29 days) and found that nest success was 0.34 in 2006 (95% CI 0.17–0.67) and 0.71 in 2007 and 2008 combined (95% CI 0.59–0.85). This model had better fit than the second-best model, which included the
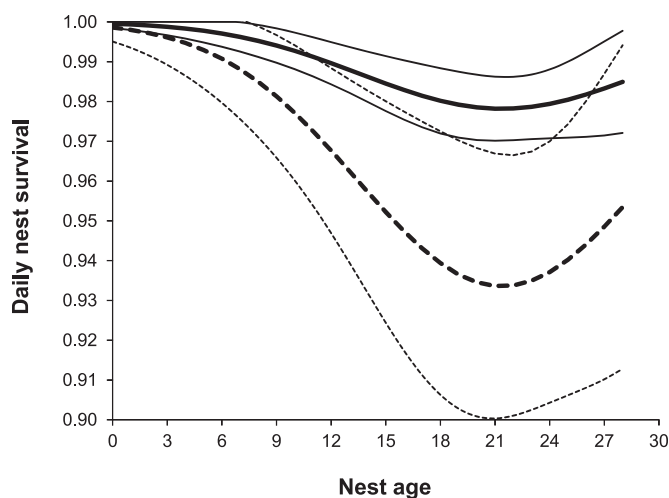

FIGURE 4. Daily survival rate and associated 95% CI of Rusty Blackbird nests ($n = 150$) in Alaska in relation to nest age (days) and year (dashed line, 2006; solid line, 2007 and 2008 combined). Estimates of daily nest survival on day 0, when the first egg was laid, are standardized to May 17 and are based on a model with covariates for date, year, and the quadratic effects of nest age.

effects of age^2, $date^2$, and year ($K = 6$, $\Delta_i = 2.0$, $w_i = 0.16$) and the third-best model with age^2 and year ($K = 4$, $\Delta_i = 2.3$, $w_i = 0.14$). Summing model weights we found the most support for models with year effects ($\Sigma w_i = 1.0$), age^2 ($\Sigma w_i = 0.72$), and date ($\Sigma w_i = 0.62$); we found less support for models with the linear effects of age ($\Sigma w_i = 0.13$) and the quadratic effects of date ($\Sigma w_i = 0.22$) and no support for the model with the intercept only ($\Delta_i = 27.6$, $w_i < 0.001$). The best temporal model was not improved by the addition of the effects of study area, study area times year, region, or region times year ($\Delta_i = 0.2$–2.7).

Nest survival in relation to habitat on military lands Alaska. On military lands in Alaska, we found the most support for a temporal model that included age^2 ($L = -117.1$, $K = 3$, $AIC_c = 240.2$, $w_i = 0.32$). As in the model in Fig. 4, daily nest survival first declined from ages 0 to 21 days and then rose thereafter. The next four best-fitting models, in decreasing order of relative fit, included age^2 in combination with either date, year, $date^2$, or date plus year ($\Delta_i = 0.9$–2.9). Summing model weights we found the most support for models with age^2 ($\Sigma w_i = 0.83$), far less support for models with age, date, $date^2$, or year ($\Sigma w_i = 0.14$–0.34), and no support for the model with the intercept only ($\Delta_i = 17.7$, $w_i < 0.001$). The model with age^2 ($\Delta_i = 3.8$) was improved by more than two AIC_c values by the addition of the substrate used for nesting ($K = 5$, $\Delta_i = 0.0$), the quadratic effect of the height of the plant used for nesting ($K = 5$, $\Delta_i = 0.8$), the density of black spruce stems in the area used for nesting ($K = 4$, $\Delta_i = 1.1$), or the quadratic effect of nest height ($K = 5$, $\Delta_i = 1.5$). None of these models was improved by more than one AIC_c value by the addition of the effects of study area. The model with age^2 was not improved by the addition of the linear effects of nest height, the linear effects

of the height of vegetation used for nesting, or the effects of study area, nest cover, whether the plant supporting the nest was live or dead, densities of willow stems, distance to water, or distance to nearest nests ($\Delta_i = 2.2$–5.7).

Reducing nesting substrates to conifers versus all others substrates combined further improved the model with age^2 and nesting substrates by 1.5 AIC_c values (logit scale; $\beta_o =$ 9.8 ± 2.9, $\beta_{age} = -0.63 \pm 0.31$, $\beta_{age^2} = 0.015 \pm 0.008$, $\beta_{conifer} = 1.00 \pm 0.38$). When we calculated the product of the survival rates for each nest age with this model, we found that nest success in conifers was 0.78 (95% CI 0.64–0.96) and in other substrates combined was 0.52 (95% CI 0.33–0.80). The fit of the model with age^2 and nesting substrates was not improved by reducing substrates to shrubs versus all other substrates combined.

The model with age^2 and the quadratic effect of the height of the plants used for nesting (logit scale; $\beta_o = 11.1 \pm 3.0$, $\beta_{age} = -0.69 \pm 0.31$, $\beta_{age^2} = 0.016 \pm 0.008$, $\beta_{substrate\ height} = 0.53 \pm 0.23$, $\beta_{substrate\ height^2} = -0.19 \pm 0.07$) indicated that daily nest survival first increased as nests were placed in vegetation up to 6 m in height and then began to decline with increases in vegetation height above 11 m. This model's estimated coefficients were nearly identical to those of the model with age^2 and the quadratic effect of nest height because of the high correlation ($r = 0.57$) between nest height and the height of the plant supporting the nest. Finally, the model of nest survival that included age^2 and the density of black spruce indicated that nest survival increased with increases in the density of black spruce in the area used for nesting ($\beta_{black\ spruce} = 0.42 \pm 0.23$).

DISCUSSION

In our analysis of Rusty Blackbird nests from across Alaska and Canada, we found that (1) the species has a widespread affinity for conifers, particularly spruces, for nest sites, (2) that selectivity for spruces on military lands in Alaska was adaptive in terms of relatively high reproductive success, and (3) that nest survival across Alaska varied within the year and in successive years but was generally high and not at chronically low levels that would strongly contribute to the species' long-term and rangewide decline. Across the coastal region of Alaska and the boreal region of Canada, 85% of 212 nests were placed in conifers, primarily spruces (100% in Alaska, 80% in Canada). This pattern is quite similar to that in New England where 93% of 65 nests were in conifers and 64% of conifer nests were placed in spruces (Kennard 1920, Ellison 1990, Powell et al. 2010). The use of black spruce as a nest site was particularly widespread through all regions of Alaska and Canada except in the coastal rainforest zone of Alaska, the only area where Rusty Blackbirds nested in young Sitka spruce, the principal conifer available. As we found, Erskine (1977), on the basis of Breeding Bird Censuses across boreal Canada, described the Rusty Blackbird as characteristic of

black spruce bogs. DesGranges and Houde (1989) also found Rusty Blackbirds breeding at 75% of 63 lakes in districts with black spruce in Quebec, and 74% of the Rusty Blackbirds encountered by Machtans et al. (2007) in the Northwest Territories were in black spruce muskegs, often near standing water and lakes. Thus, black spruce near emergent vegetation, ponds, and particularly lakes (Matsuoka et al. 2010) may be a favored combination of habitat features for breeding across much of the species' range.

Our nest monitoring on military land in Anchorage indicated that the Rusty Blackbird's use of spruce is selective and results in relatively high rates of nesting success. In this area, Rusty Blackbirds nested in areas of relatively high density of small black spruce and placed their nests primarily in such trees. Birds nesting in dense spruce benefited reproductively, as nest survival increased with black spruce density. We suspect that in areas of high density of the small black spruce in which Rusty Blackbirds typically nest, predation rates may be lower because the number of potential nest sites that predators have to search is higher, in accordance with the potential-prey-site hypothesis (Martin 1993). Nesting in spruce trees, particularly small ones, had additional advantages, as nest success in both Anchorage and the Tanana Flats was slightly higher for nests placed in spruces (78% of nests fledged young) than for those in deciduous vegetation (52% of nests fledged young) and survival of nests placed in trees > 11 m tall was lower. In Alaska, deciduous vegetation tended to leaf out after Rusty Blackbirds began to incubate their eggs and so may have provided less direct cover from predators than did conifers. However, we did not find nest survival to be associated with level of nest concealment. All trees taller than 9 m in which Rusty Blackbirds nested were spruces. Taller spruces are more likely to produce cones (Greene et al. 2002) and attract foraging red squirrels, the major predator of passerine nests in the boreal forest (Rangen et al. 1999, Bayne and Hobson 2002, Willson et al. 2003, Ball et al. 2009) and the one species we observed preying on Rusty Blackbird eggs. Therefore, nesting in small spruces may be in part an adaptation to reduce nest predation by red squirrels, which range across North America's boreal forest (Steele 1998). Nesting in wetlands may also be advantageous because their densities of red squirrels and corvids are low (DeSanto and Willson 2001) and nest-predation rates are lower than in uplands (Robertson 1972, DeSanto and Willson 2001).

In New England, as we found in Alaska, Rusty Blackbirds nest in small spruces and firs where growth of these conifers is dense (Kennard 1920, Ellison 1990, Powell et al. 2010). Although the use of such habitat resulted in high rates of nest survival in undisturbed wetlands in Alaska, it does not in human-altered landscapes in New England, where Rusty Blackbirds often nest in dense young conifers regenerating from recent logging adjacent to wetlands (Ellison 1990, Powell et al. 2010). In regenerating forest in New England, the Rusty

Blackbird's rates of nest success were much lower (33% of 30 nests fledged young) than in undisturbed wetlands with older but stunted conifers (100% of nine nests fledged young). Habitat characteristics of harvested sites and undisturbed wetlands were quite similar with the exception of landscape (upland and wetland, respectively) and the average age of the small conifers used for nesting (14 and 28 years, respectively). Thus, recent harvests appear to attract nesting Rusty Blackbirds into upland habitats that they would otherwise avoid; once in the upland habitats they suffer high rates of nest predation (Powell et al. 2010).

Although in New England the Rusty Blackbird seems to be sensitive to logging, the species appears to be adaptable to natural disturbances that occur frequently and at large scales in the boreal forest (Blais 1983, Johnson 1992, Matsuoka et al. 2006). We often observed Rusty Blackbirds nesting in willows and spruces in Alaska that had been recently killed by flooding or outbreaks of bark beetles (*Dendroctonus rufipennis* or *Ips* sp.). In New England, the species has also been observed nesting in dead spruces (Kennard 1920) and areas flooded by beavers (Ellison 1990). Unlike that of the Red-winged Blackbird, survival of Rusty Blackbird nests in dead vegetation is no lower than in live vegetation (Dinsmore and Dinsmore 2007). With respect to fire, Machtans et al. (2007) found no changes in Rusty Blackbird abundance or occupancy from 1975 to 2006 despite fires during that period in the forests surrounding 13 of 45 sampled lakes. The black spruce forests that nesting Rusty Blackbirds favor are quite flammable, with a mean fire-return interval of 79 years on the Kenai Peninsula, Alaska (DeVolder 1999). Fires may benefit the Rusty Blackbird by reducing densities of nest predators (Robertson and Hutto 2007) such as the red squirrel (Koprowski et al. 2006).

The only region we studied where spruce was not the dominant nest sites was interior Alaska, where Rusty Blackbirds instead placed 78% of 121 nests in shrubs, nearly all willows. Within this region on the Tanana Flats, willows numerically dominated the vegetation in the areas where the blackbirds nested, and the blackbirds placed their nests in willows in proportion to their availability. We observed this same pattern with spruce in south-central Alaska in Anchorage. Both on the Tanana Flats and in Anchorage, nests were on average quite close to surface water (8 and 30 m, respectively) so in both areas the birds may have simply been using the dense vegetation that was near water. But although spruces were quite rare on the Tanana Flats, they were used as nest sites more often than expected from their availability. Furthermore, alders were also common in nest areas in Anchorage, the Tanana Flats, and Maine (Powell et al. 2010) but were almost never used as nest sites (2% of 333 nests in Alaska and Canada; 0% of 63 nests in New England, Kennard 1920, Ellison 1990, Powell et al. 2010). Alders may be avoided because of an intrinsic preference for conifers (Parrish 1995) or willows or because they lack the structure to support Rusty Blackbird nests, which are quite large and typically woven into multiple stems and branches. For similar reasons, grasses, sedges, and cattails are likely avoided as nests sites. One nest in sedges and one nest in cattails failed as they sank into water, and low nesting in general may be avoided because it runs a higher risk of flooding.

In Alaska, we found that daily survival rates of Rusty Blackbird nests varied temporally, being highest during laying, declining through hatching, and increasing slightly during the last 8 days of the nestling period (Fig. 4). This pattern is similar to that of the Red-winged Blackbird in Connecticut (Robertson 1972) and Missouri (Cao et al. 2008) and grassland sparrows in North Dakota (Grant et al. 2005): nest survival is low during hatching and increases as adults become increasingly defensive as fledging approaches (Robertson 1972, Grant et al. 2005). The Rusty Blackbird's nest survival also declined linearly through the breeding season, in parallel with the seasonal decline in clutch size. This decline in fecundity might explain why the species has not been found to renest after successfully fledging young in Alaska (this study) or New England (Kennard 1920, Powell et al. 2010). Second broods may further be precluded because, before fall migration, juveniles must undergo a nearly complete first prebasic molt that is much more costly, in terms of time and energy, than the first prebasic molt typical of passerines, which does not include the remiges (Pyle et al. 1997).

Although nest success was relatively low in Alaska in 2006 (21%) and low in regenerating clearcuts in New England from 2005 to 2008 (Powell et al. 2010), the overall pattern developing from studies of nesting in Alaska and New England does not support a hypothesis that the Rusty Blackbird is suffering from chronically low rates of nest success. In Alaska, nest success did vary by year but was high in both 2007 and 2008 (64%) and averaged 56% across the three years combined. The average rate is quite similar to that of Rusty Blackbirds nesting in New England (62%, Powell 2008) and much higher than that of the Red-winged, Yellow-headed, and Brewer's Blackbirds (30–39%; Martin 1995). We found no relationship between the distance between nests and nest survival in Alaska. Thus, density-dependent limitations on nest survival may now be minimized because of the species' decline. We also recognize that low-quality nest sites may have previously contributed to the species' decline but are no longer used because nest densities are now much lower. We cannot explain why nest survival in Alaska was so low in 2006, though most nest losses we noted were due to predation (89% of losses) and rates of predation of Red-winged Blackbird nests are also quite variable (Beletsky and Orians 1996, Dinsmore and Dinsmore 2007). Additional years of data from Alaska would help provide a stronger test of whether low reproductive success currently limits populations of Rusty Blackbirds. However, we believe that the need for information on nest survival is more urgent in southern Canada, where the evidence for both

long-term decline and landscape change is stronger than in Alaska (Greenberg et al. 2011).

In Alaska, clutches averaged 5.3 eggs, slightly larger than in Canada (4.6 eggs) or New England (4.5 eggs; Powell et al. 2010) and much larger than those of Red-winged Blackbirds breeding in the temperate zone, whose average clutch size in 20 studies ranged from 2.4 to 3.7 eggs (Yasukawa and Searcy 1995). This pattern follows the latitudinal increase in clutch size common among passerines (Kulesza 1989) and thought to be a function of greater food availability (Ricklefs 1980), lower nest-predation risk (Martin 1995), or lower probability of adults' annual survival (Martin et al. 2000) in northern latitudes. However, our sample of clutch sizes from Canada was small, and additional data would help clarify spatial patterns in the species' clutch size. Starvation of nestlings was particularly rare in Alaska; nests that fledged young successfully reared 96% of their hatchlings.

Like nest survival, the viability of Rusty Blackbird eggs in Alaska was also quite high, with 90% of the eggs that avoided predation and flooding hatched. This rate is similar to that in New England, where only two eggs among 43 Rusty Blackbird nests studied by Powell et al. (2010) failed to hatch. We had expected the incidence of nonviable eggs to be higher in New England because the level of methylmercury in the blood of adult Rusty Blackbirds was three times higher in New England, Nova Scotia, and New Brunswick than in birds sampled on our study areas in Alaska. Levels in New England and the maritime provinces were equivalent to the levels killing embryos in other species of birds (Edmonds et al. 2010). Across this region, Rusty Blackbirds are both contracting in range (Powell 2008) and declining at particularly high rates (Sauer et al. 2008; Maritime Breeding Bird Atlas, unpublished data). The high levels of methylmercury that are accumulating from the atmospheric fallout of industrial pollution (Driscoll et al. 2007) may be reducing fitness by lowering physiological condition and survival of Rusty Blackbirds rather than by killing embryos; however, we cannot rule out that some adults may have been sterile. Likewise, if events during the nonbreeding season, such as losses or degradation of bottomland forests, are contributing disproportionately to the species' decline (Greenberg and Droege 1999), such effects will likely be reflected in lowered body condition or lower survival rates (Greenberg et al. 2011). Therefore, studies that examine survival of adults and juveniles are needed, particularly since nest success is not clearly limited. Such studies would help put into perspective the rates of nest survival that are necessary to support viable populations and would be most useful if they were incorporated into carefully designed cross-seasonal investigations aimed at distinguishing the effects of events in the breeding season from those in winter on the Rusty Blackbird's physiological condition, survival, and population growth rate (Sillett and Holmes 2002, Greenberg et al. 2011). Such investigations of migratory species are few but sorely needed both to understand the mechanisms and address the causes of migratory birds' declines (Greenberg and Marra 2005, Holmes 2007).

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