AN ABSTRACT OF THE THESIS OF

David M. Loomis for the degree of Master of Science in Wildlife Science presented on May 31, 2013.

Title: Reproductive Success and Foraging Ecology of the Rusty Blackbird on the Copper River Delta, Alaska.

Abstract approved:

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Katie M. Dugger

The Rusty Blackbird (*Euphagus carolinus*) has suffered significant population declines across its entire geographic range and the mechanisms associated with this decline are poorly understood. Although much of the Rusty Blackbird breeding habitat in Alaska has remained relatively unaltered by anthropogenic activities, this species continues to decline by an estimated 5% annually. As part of a collaborative effort to obtain data on the reproductive ecology, breeding success, and habitat requirements of this species throughout their range, a total of 42 nests were found and monitored for two consecutive breeding seasons (2009 – 2010) on the Copper River Delta in south-central Alaska. Nests were monitored every 2-4 days to calculate nest success, survival rates, clutch initiation date, clutch size, egg viability, and fledging rates. In 2010, chick provisioning rates, chick diet, and aquatic invertebrate availability in Rusty Blackbird foraging habitats were also investigated. Mean clutch size ranged from 5 to 7 eggs both years (2009 = 5.41 ± 0.15, 2010 = 5.67 ± 0.13). Daily nest survival rate averaged over both seasons was high, at 0.9913 ± 0.0043 (95% CI 0.9772-0.9967) and most eggs were viable (N = 31 nests), with 0.8922 ± 0.0275 of

eggs over both seasons hatching. Approximately 85% of clutches were initiated within a two week period for both years of the study. Clutch-initiation date (CID) was significantly different between years (p-value < 0.0001), with mean CID of 10 May ($\bar{x}$ = 10.476 ± 0.95) in 2010 and May 18 ($\bar{x}$ = 18.421 ± 1.13) in 2009. The mean provisioning rate was 0.84 (± 0.06; 95% CI: 0.72 to 0.95) invertebrate food items per chick per hour. Large odonate nymphs, specifically dragonflies, made up the bulk (97.2%) of the observed food items provisioned to chicks. Weekly pond sampling revealed four taxonomic groups of invertebrates that were of the size observed provisioned to chicks (Coleoptera, Hirudinea, Zygoptera, Anisoptera) and Anisoptera were among the rarest collected (16.2%) of this size. Although the least common large invertebrate collected, Anisoptera nymphs were present in all weekly samples. The week with the most abundant Anisoptera collection coincided with the week of peak hatching during 2010 of the study. Thus, availability of dragonfly nymphs appear to be important to Rusty Blackbird reproductive success on the Copper River Delta and may have contributed to the high nest success observed in this study.

Reproductive Success and Foraging Ecology of the Rusty Blackbird on the Copper
River Delta, Alaska

by
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APPROVED:

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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David M. Loomis, Author

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Reproductive Success and Foraging Ecology of the Rusty Blackbird on the Copper River Delta, Alaska

CHAPTER 1 – GENERAL INTRODUCTION

The Rusty Blackbird (*Euphagus carolinus*) breeds in forested wetlands across the boreal forest from New England and the Maritime Provinces of Canada into Alaska (Avery 1995). Rusty Blackbirds migrate to their breeding territories from over-winter sites found primarily in the bottomland forested wetlands of the Mississippi Alluvial Valley and the Atlantic coastal Plain (Avery 1995 Hobson et al. 2010). The entire population has declined by at least 88% across its range since 1966 and the species continues to decline by a rate of 5% or more per year (Greenberg and Matsuoka 2010, Sauer et al. 2012). This species is suffering one of the most rapid population declines of any bird in North America and the World Conservation Union (IUCN) considers the Rusty Blackbird vulnerable to extinction in the wild (Sauer et al. 2012, Birdlife International 2008). This staggering rate of decline went relatively unnoticed until researchers combined anecdotal reports from the ornithological literature, Breeding Bird Survey (BBS), and Christmas Bird Counts (CBC) data to document declines that date back to the early 20th century (Greenberg and Droege 1999, Sauer et al. 2012). Most of the published accounts of Rusty Blackbirds prior to 1920 recorded them as "common" or "abundant" and there were no accounts of them being uncommon prior to 1950; however, records suggesting they were becoming more and more

"uncommon" increased steadily throughout the remainder of the century (Greenberg and Droege 1999).

Many factors have been suggested as potential causes for this decline including, breeding habitat loss, mercury exposure, boreal wetland drying, wintering habitat degradation, acid rain, historic and ongoing blackbird control programs, and increased competition with other blackbird species (Greenberg and Droege 1999, Greenberg et al. 2011). However, because of its remote breeding habitat, inconspicuous behavior, and lack of economic impact this species has received little study, and its basic ecology remains poorly understood in many portions of its range (Avery 1995, Matsuoka and Greenberg 2010). The International Rusty Blackbird Technical Group (IRBTG) was formed to increase awareness of the species and implement a strategy to recover populations. The IRBTG is represented by federal, state, academic, and non-profit agencies across the U.S. and Canada. This group has emphasized the need to identify demographic limitations, important habitats, and key geographic areas for the species' throughout its annual cycle (Greenberg and Matsuoka 2010, Greenberg et al 2011).

Although Alaska has experienced less anthropogenic landscape changes than many eastern regions of their breeding range, the nesting success of Rusty Blackbirds in New England was found to be higher than Alaska in congruent studies that spanned similar time periods (Powell 2008, Matsuoka et al. 2010). These results are puzzling when considering that methylmercury levels were found to be three times higher in New England, Nova Scotia, and New Brunswick compared to Alaska (Edmonds et al.

2010, Sauer et al. 2012). To further confound these results it has been estimated that this eastern population has experienced a significant breeding range reduction and continues to suffer from higher rates of population decline than those documented in Alaska (Powell 2008, Sauer et al. 2012). By examining deuterium levels in feathers of wintering Rusty Blackbirds, researchers found isotopic evidence for separate Mississippi and Atlantic flyway populations (Hobson et al. 2010). This evidence indicates that birds wintering in the Mississippi Alluvial Valley breed from Alaska through central Canada, and birds that winter along the Atlantic Coastal Plain breed in eastern Canada and New England (Hobson et al 2010). Thus, the smaller Atlantic flyway population could be especially vulnerable to the declines documented throughout breeding areas in the southern boreal zone, New England and the Maritime Provinces (Powell 2008, Hobson et al. 2010). Multiple, wide-spread studies in different portions of the species' geographic range, may be the best way to pinpoint population bottlenecks and reasons for decline. As part of a multi-study area project conducted throughout Alaska, I participated in a coordinated effort with the Cordova Ranger District to investigate the breeding season ecology of Rusty blackbirds in Alaska. The Cordova Ranger District administers approximately 930,777 ha of public land including the Copper River Delta (Figure 1.1), which presents a unique study site for assessing the breeding ecology of the Rusty Blackbird in Alaska. The majority of the Delta (151,256 ha) is national forest land with small pockets of land controlled by the State, native corporations, and private landowners. The wetlands of the Delta are

Figure 1.1: Location of the Copper River Delta in the State of Alaska

Copper River Delta
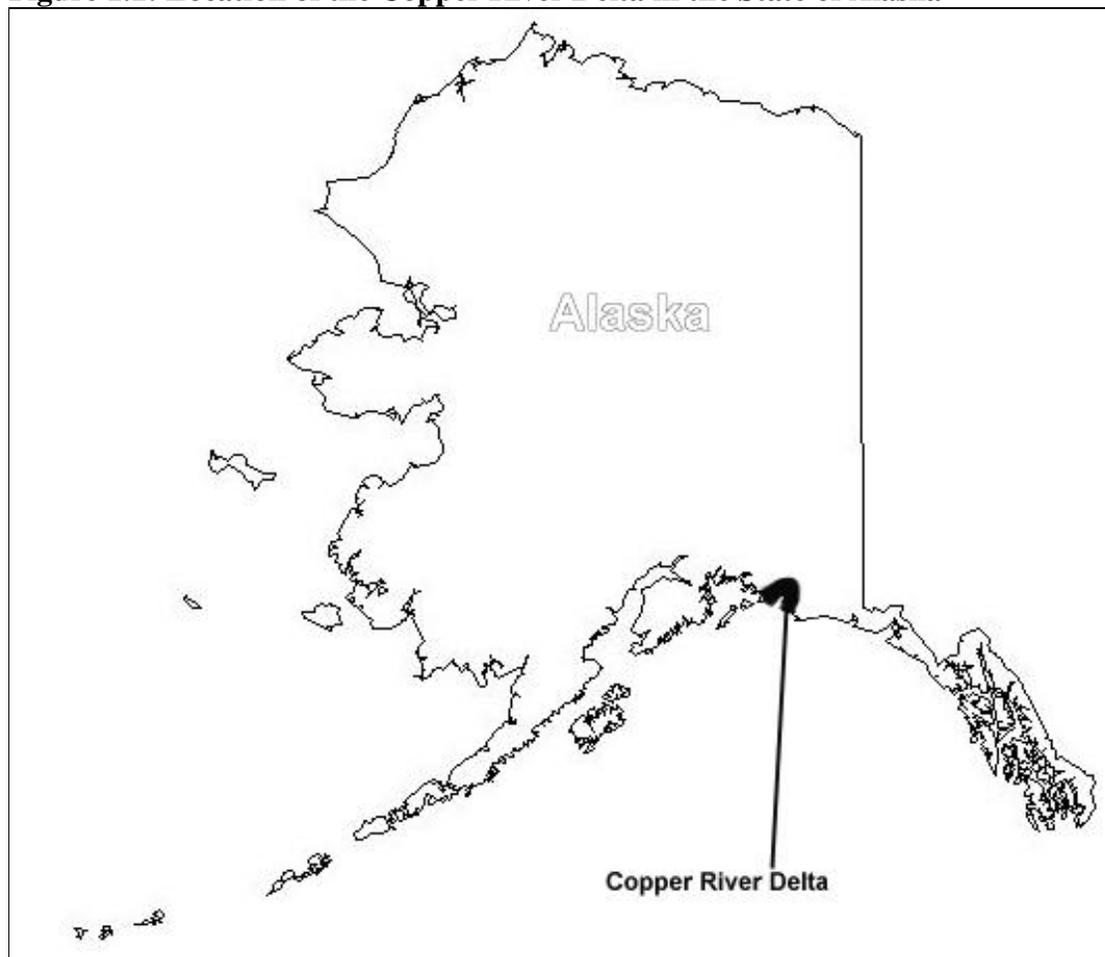
in a state of rapid succession resulting from the creation of freshwater habitat

following uplift caused by the earthquake of 1964 (Crow 1971, Thilenius 1995).

Records from the 1970's indicate that nesting by Rusty Blackbirds rarely occurred on

the Copper River Delta during that time (Isleib and Kessel 1973). Conditions prior to

the 1964 earthquake such as lack of spruce trees, sparse shrubs, and few freshwater

ponds that support invertebrate communities (Crow 1971, DeVelice 2001), suggest

suitable Rusty Blackbird nesting habitat has appeared only within the last 20-25 years

in my study area. Overall, the species has suffered an estimated 4.9% decline in

Alaska for at least the past four decades (Hannah 2005, Sauer et al. 2012), but changes in hydrology and vegetation on the Delta since the earthquake has likely increased the suitable nesting habitat for Rusty Blackbirds in this area. Thus, the Copper River Delta is an important habitat to monitor for breeding success compared to other sites across Alaska and could represent one of the few habitats with increasing Rusty Blackbird populations.

Breeding Bird Survey (BBS) data and the Alaska Landbird Monitoring Survey (ALMS) on the Copper River Delta have only detected two Rusty Blackbirds on one occasion in 1995 (Sauer et al. 2012, Cordova Ranger District, unpublished data). However, the Cordova Ranger District Wildlife Department documented incidental sightings of Rusty Blackbirds from 2006 – 2008, while conducting fieldwork that covers the majority of the West Delta (Cordova Ranger District unpublished data). Since the earthquake, the Delta can be categorized into two general habitat types: outwash plain (OP) vs. uplift marsh (UM) (Davidson 1998, DeVelice et al 2001). Both habitat types contain trees and shrubs along fresh water borders that can be used for nesting, but these areas differ geomorphologically. The UM is categorized as the area primarily consisting of freshwater ponds, levees, freshwater streams, sea cliffs, and tidal creeks (Boggs 2000). The marsh was intermittently flooded by extremely high tides prior to the uplift (Boggs 2000, Thilenius 1995), but the resulting uplifted marsh now supports dense stands of spruce, alder and willow along tidal and beaver sloughs. The OP vegetation types were less affected by the uplift and therefore have remained relatively constant compared to the UM (Boggs 2000). The OP is a glacial

and alluvial outwash with braided glacial rivers, low terraces, sand and gravel bars. (Davidson 1998).

Breeding birds observed in the OP wetland areas of the Copper River Delta have not been reported in high densities (Cordova Ranger District and D. M. Loomis, unpublished data). A pilot project conducted in 2008 (Cordova Ranger District and D. M. Loomis, unpublished data) found only one breeding pair in all of the OP area searched, but no Rusty Blackbirds returned to this area the following season (2009). Nearly all of the BBS and ALMS points fall within the OP area, which is likely why few Rusty Blackbirds were seen on these surveys. In contrast, these birds have been found at breeding densities that allowed researchers to locate ≥20 breeding pairs in only one location of the UM area of the Delta (Cordova Ranger District and D. M. Loomis, WDFW, unpublished data). Given the availability of trees and shrubs for nest placement in both habitats, the question remains as to why Rusty Blackbirds appear to use this UM area for nesting more than the OP?

Dissimilarities in food availability associated with differences in wetland ponds may be the reason birds prefer this area of the UM for breeding. Rusty Blackbird breeding season diet has only been described by Ellison (1990), and no one has reported on the food items provisioned to chicks. The breeding diet of Rusty Blackbirds is thought to include primarily invertebrate foods (Ellison 1990, Avery 1995) and invertebrate sampling across the Delta suggests availability and abundance differs among ponds and sloughs in the UM compared to the OP(Van Duzor 2011). That study determined there is a pattern of reduced Anisoptera availability in UM

ponds compared to OP ponds and Anisoptera were found to be quite rare in many UM ponds, although this study did not report on invertebrate communities in the UM ponds located within my study area (Van Duzor 2011). The objectives of this study were two-fold. As part of a larger collaborative study, I supplemented efforts to examine one possible hypothesis regarding the species' decline, and that is whether reproductive output is limiting population growth in Alaska. Thus my first objective was to document the reproductive success, specifically daily nest survival, in my study area on the Copper River Delta, Alaska for two consecutive breeding seasons spanning 2009 and 2010. Habitat characteristics associated with nest placement were summarized and the potential impacts of these factors on daily nest survival were modeled and evaluated to determine if reproductive rates and associated breeding habitats are bottlenecks to this species.

Second, I wanted to understand the food resources associated with Rusty Blackbird reproductive success in this location and to determine if invertebrate availability is a critical component of high quality breeding habitat on the Delta. The composition of invertebrates available to foraging Rusty Blackbirds throughout the breeding season was of principle concern. I was particularly interested in the specific invertebrate food resources provided to chicks, and the rate at which they were being provisioned.

CHAPTER 2 – HIGH NEST SUCCESS OF A RAPIDLY DECLINING
SPECIES: THE RUSTY BLACKBIRD ON THE COPPER RIVER
DELTA, ALASKA

INTRODUCTION

Since 1966 trends from Christmas Bird Counts (CBC) and the Breeding Bird Survey

(BBS) suggest the Rusty Blackbird (*Euphagus carolinus*) has suffered the steepest

population declines of any passerine in North America, and additional sources of

evidence suggests this species has been in decline since before the 1960's (Greenberg

and Droege 1999, Niven et al. 2004, Sauer et al. 2012). Although historic accounts

have recorded individual flocks in excess of 100,000, it is estimated that the current

rate of decline has reduced the total population by at least 88% across their range since

1966 (Greenberg and Droege 1999, Niven et al. 2004, Greenberg et al. 2011, Sauer et

al. 2012). More recent estimates that rely on new analytical approaches suggest rates

of decline for this species equal a mean annual population trend of -4.8% (95% CI = -

8.0, -1.6) during 1996-2011 and -2.2% (95% CI = -10.5, 9.1) more recently (2001 –

2011; Sauer and Link 2011) Both rates are less than previously predicted (>5% per

year), but still of concern over the long term (Sauer and Link 2011).

The mechanisms resulting in this current population decline have only recently

received scientific attention (Greenberg and Droege 1999, Shaw 2006, Hamel et al.

2009, Barnard et al. 2011, Edmonds et al. 2011, Greenberg and Matsuoka 2011,

Hobson et al. 2011, Matsuoka et al. 2010a, Powell et al. 2010a). There are no known populations exhibiting a positive growth rate (Sauer et al. 2012). Even the relatively pristine breeding habitat found in Alaska has not offered a sanctuary for Rusty Blackbirds. The statewide population has experienced a 5% annual decline over the past 4 decades, although BBS data for this region are scarce prior to the 1980's (Hannah 2005). However, there is evidence that the population breeding on the Copper River Delta may be the exception due to the rapid vegetation succession that has only recently created suitable nesting habitat (Boggs 2000). The Great Alaskan Earthquake or Good Friday Earthquake of 1964 caused the entire delta to uplift 1.8-3.4 m, creating freshwater habitat from brackish wetlands once regularly inundated by seawater (Thilenius 1995, Boggs 2000).

The poor understanding of the basic reproductive ecology of the Rusty Blackbird is primarily a result of the remoteness of the vast boreal forest where these birds breed. When this study was initiated the understanding of the species' breeding ecology was known from only a small sample of nests in New England (Kendall 1920, Ellison 1990). Rusty Blackbirds are often associated with open water habitats and breed in forested wetlands of the boreal forest, but until recently they were often regarded as "common" and most historic accounts were largely pertaining to birds in their winter range (Avery et al. 1995, Greenberg and Droege 1999). In an attempt to gain crucial insight into the factors limiting the Alaska population, a state-wide, multi-agency, collaborative study was initiated in 2009. As part of this larger study I examined whether reproductive output was a factor limiting population growth of

Rusty Blackbirds in Alaska. The objectives of this study were to determine reproductive ecology, specifically daily nest survival, and sources of nest loss, nesting chronology, clutch size, egg viability, and fledging rate on the Copper River Delta, Alaska for two consecutive breeding seasons (2009- 2010). I also summarized the habitat characteristics associated with nest placement and the potential impacts of these factors on daily nest survival to determine whether reproduction and associated breeding habitats were a bottleneck to this species in Alaska.

METHODS

Study Area

The study site is located within the Cordova Ranger District of the Chugach National Forest, approximately 32 km east of the city of Cordova on the West Copper River Delta (CRD) in south central Alaska. The primary study area encompasses an area slightly larger than 10 km^2 and base camp was situated along Walhalla Slough (Lat. -145.32413, Lon. 60.36908). This region receives 203-254 cm of precipitation annually and mean minimum temperatures in January and July are -8.9°C and 8.3°C, respectively (Davidson 2003, Western Regional Climate Center (WRCC) 2013). The Delta stretches from the base of the Chugach Mountains to coastal mudflats leading to the Gulf of Alaska and the Copper River separates the West Delta from the East Delta.

This area is a coastal wetland complex consisting of a wide array of habitat types ranging from mudflats to early successional boreal forest. The Delta was uplifted in the Great Alaskan Earthquake of 1964, radically altering the hydrology of the site and creating new land from formerly intertidal areas (Crow 1971, Boggs 2000). The West Delta has been classified into glacial outwash plain (OP) further inland and uplifted marsh (UM) closer to the coast (DeVelice et. al 2001, Davidson 1998). My study site is positioned within a relatively small portion of the UM area and was chosen because during a 2006 feasibility study no other area in surveyed parts of the West Delta was found with as high a density of breeding Rusty Blackbirds (Cordova Ranger District, unpublished data).

Field Methods

I conducted my research from the third week in May to 30 July during 2009 and 2010, to encompass the majority of the breeding season. The earliest confirmed initiation date of the 17 nests found during the 2006 feasibility study was 16 May, and at other sites in Alaska, Rusty Blackbirds initiated their clutches over a one month period from 7 May to 8 June (Matsuoka et al. 2008). A period of rapid surveys followed by a period of intensive searches was used to first identify possible breeding pair territories and later to focus nest search efforts. I used search techniques similar to those described by Martin and Geupel (1993). The rapid surveys concentrated around fresh water ponds and beaver sloughs and possible nesting sites situated between or adjacent

to these freshwater systems. During rapid surveys the gender, movements, and behaviors of adult Rusty Blackbirds were mapped on aerial photographs. Follow-up intensive searches were then conducted to locate Rusty Blackbird territories and active nests (Appendix A). All bird species encountered during rapid surveys were recorded and inventoried, and incidental sightings of any species I suspected could be a potential nest predators, such as red squirrels (*Tamiasciurus hudsonicus*), Black-billed Magpies (*Pica hudsonia*) and other corvids, were recorded during nest checks. An airboat and/or poke boats were necessary to access the general study area because of the remote, isolated study area location and the extreme tide fluctuations that resulted in nearly dry channels at low tide. Extensive searches within the study area were conducted by walking or wading.

Once nests were located, standardized nest monitoring protocols developed by the University of Montana BBIRD program (Martin et al. 1997, Martin and Geupel 1993) were followed. Several eggs (2-3) from complete clutches were candled using 1.6 cm (5/8 in) pipe insulation to estimate embryonic development stage. I used Red-Winged Blackbird embryonic development (Lokemoen and Koford 1996) as a model for Rusty Blackbird development. Active nests were revisited every 2-5 days to determine clutch size, duration of incubation and nestling periods, nest survival, number of young fledged, and the cause of nest failure. Nests were observed from afar with binoculars unless no activity was witnessed or if it was expected to have hatched since the previous visitation. Nestlings were weighed, measured, and banded at day 9

post-hatch to assess condition prior to fledging, and mark individuals for future re-sighting efforts associated with the state-wide collaborative study.

I attempted an inexpensive technique for remotely monitoring nests in 2009 by inserting iButton temperature loggers (© 2009 Maxim Integrated Products) in each nest to determine the timing of fledging or nest failure and to estimate rates of daily nest survival (Hartman and Oring 2006). The iButtons monitor temperature in the nest and the exact day of abandonment, depredation, or fledging can be determined when the nest goes cold. These temperature loggers are the diameter of a dime and approximately 5 mm thick. However, 3 of the 12 nests (25%) which received an iButton during the egg laying and incubation stages were abandoned in 2009. An additional two nests where ultimately predated, but it is possible these nests were abandoned prior to the predation event. Given 41.7% of these 12 nests failed to reach fledging stage and similar cases of nest abandonment were noted on other studies in Alaska using iButtons (David Tessler, ADFG, personal communication), I chose not to use this technique in 2010.

Habitat characteristics associated with nest placement were assessed by measuring nest height (Nht), nest tree height (Treesize), distance to water (Dist.), and nest concealment (Conceal). The percentage of the nest concealed was visually estimated from a distance of 1m in each cardinal direction, and below and above. The 1 m nest concealment measurements were summed for a total concealment score ranging from 0.0-1.0 (0%-100%). Nest height and nest tree height were measured in meters from the base of the tree to the nest and to the top of the crown for each nest

located. Three individual nest habitat covariates were ultimately investigated and

modeled as potential factors that affect patterns of Rusty Blackbird daily nest survival

in my study: concealment (Conceal), nest height placement (Nht), and nesting tree size

(Treesize) (Table 2.1).

Table 2.1: Acronyms and brief descriptions of variables used to model daily nest
survival of Rusty Blackbirds on the Copper River Delta, Alaska.

Acronym	Description	Predicted Effects
(.)	No effects	
T	Linear time trend over entire nesting season	$\beta_T < 0$
lnT	Pseudo-threshold time effect	$\beta_{lnT} < 0$
TT	Quadratic time effect	$\beta_T > 0$; $\beta_{TT} < 0$
Nage	Age of nest (in days) relative to day 1st egg was laid	$\beta_{Nage} < 0$
Nstage	Nest stage: incubation vs. chick-rearing	$\beta_{Nstage} < 0$
Conceal	Mean from measurements taken in four cardinal directions and above of the percentage of the nest concealed from view at a 1m distance.	$\beta_{Conceal} > 0$
Nheight	Nest location height in the tree (m)	$\beta_{Nheight} > 0$
Treesize	Height of nest tree (m)	$\beta_{Treesize} > 0$
YR	Year effects - 2009 vs. 2010	YR09 > YR10
t	Time-specific survival (daily variation)	$\beta_t < 0$

I predicted that daily nest survival would be higher for nests with higher concealment

scores, or for those nests placed higher in the tree or placed in larger trees. Nest

construction material was examined to determine composition of the base, rim and cup

while taking detailed nest measurements of the cup width, cup depth, nest width and

total nest height.

During the 2009 season several nest measurements were not documented, or

were recorded several weeks post fledge when many nests were beginning to show

signs of structural degradation attributed to exposure to strong wind and heavy rain

common in this region of Alaska. To reflect the most accurate nest dimensions, I

chose to analyze only 2010 nests that were measured promptly after fledging, and excluded one nest that showed signs of significant structural degradation after exposure to a strong rainstorm, which resulted in a total of 22 nests (n=22) remaining for analysis. The vegetation community was visually estimated by marking 5 m in each cardinal direction from the nest and documenting any vegetation type constituting > 5% vegetation cover in the tree and shrub layer or the understory. Distance to water was estimated by pacing or the use of a rangefinder and later calculated using ArcGIS software to confirm field estimates. All nests examined for daily survival estimates were found to be less than 30m from open water over both study years, thus this covariate (Dist) was deemed uninformative and was omitted from analysis.

Data Analysis

The original project design proposed that daily nest survival could be estimated using a Kaplan-Meier known fate framework using iButtons as the monitoring device. However since I felt the iButtons might be increasing the probability of nest abandonment, nest survival was monitored through multiple visits, with nest fate dates and total exposure day the resulting data type. Thus, the extension of the Mayfield estimator developed by Bart and Robson (1982) and available in Program MARK was deemed more appropriate and used to evaluate models and generate daily nest survival

estimates (Dinsmore et al. 2002, Rotella et al. 2004). This approach provides a more flexible and robust estimate of daily nest survival than the traditional Mayfield method because it requires no assumptions about when nests were lost and allows visitation intervals to vary (Dinsmore et al. 2002, Shaffer 2004). In addition, nest success can be modeled as a function of any number of explanatory variables to evaluate potential factors limiting nest survival (White and Burnham 1999).

An information-theoretic approach to model selection was used to evaluate a candidate model set using Akaike's Information Criteria (adjusted for small sample sizes: AIC_c) and Akaike's model weights to assess model performance (Dinsmore et al. 2002, Rotella et al. 2004). The degree to which 95% confidence limits surrounding slope coefficients overlapped zero was used to evaluate the strength and direction of specific effects. All single factor models were part of the *a priori* model set, and several single factor models were combined *a posteriori* to examine potential additive and interactive effects between the covariates occurring in the most competitive models. Final estimates of daily nest survival were generated by model averaging all models in my model set.

In addition to nest habitat covariates I investigated a variety of factors previously reported to explain observed patterns in daily nest survival of passerines including linear seasonal trends (T; lower daily nest survival with increasing time and subsequent exposure days) (Caccamise 1976, Hirsch-Jacobson 2012), pseudothreshold (lnT) and quadratic (TT) seasonal time trends (Hirsch-Jacobson 2012) , nest age effects (Nage; lower daily nest survival with increased nest age; Caccamise 1976, Best

and Stauffer 1980, Grant and Shaffer 2012) and nest stage (NStage; lower survival during chick-rearing compared to incubation; Caccamise 1976, Best and Stauffer 1980, Davis 2003) (Table 2.2). I also tested for nest survival differences between years (YR) and general time effects within season (t) (Grant and Shaffer 2012) (Table 2). Values reported in the results section are means plus or minus standard errors ($\pm$ SE), unless otherwise noted.

A combined total of 42 nests were located over both years of the study, 19 in 2009 and 23 in 2010, and 41 of these were used in assessing nest site selection habitat characteristics. I believed the disturbance associated with the iButton insertion resulted in some nest abandonment, so I did not include these 3 abandoned nests in the daily nest survival analysis (i.e., n=16 in 2009). Of the 23 nests found in 2010, one was discovered during nest construction phase which resulted in flushing the female from the partially complete nest while the male was continually giving alarm calls. I believe this pair abandoned due to researcher disturbance, thus this nest was excluded from DNS analysis since it is generally accepted that most birds will abandon easily if disturbed prior to egg laying (Martin and Geupel 1993). In addition to that abandonment, another 2010 nest was excluded from nest survival analysis and also from the site selection analysis because it was determined to have initiated a clutch 32 days after the mean CID for all other pairs found that season. This later nesting attempt was also the only nest found with less than a 5 egg clutch (4 eggs), was located in an alder shrub, and received little attendance from the male when monitored. The breeding attempt was successful, however the small clutch size, late

CID, nest placement, and modest male nest attendance suggested this was a re-nesting attempt and/or potential extra-pair copulation that was not exhibited by any other nesting pairs monitored. I chose to summarize characteristics of first nest attempts only, as renesting and polygynous breeding are rarely observed for this species (Avery 1995, Matsuoka et al. 2010b). Therefore, a total of 37 nests over two years (n=16 in 2009, n=21 in 2010) were included in the daily nest survival analysis.

RESULTS

Nest Site Selection and Nesting Chronology

Of the 41 Rusty Blackbird nests in my study area utilized for nest site selection analysis, all were found exclusively in Sitka spruce (*P. sitchensis*) in both years, except for one nest found on a branch of an alder (*Alnus* spp.), growing through and concealed by, a larger spruce (100% Sitka spruce nest tree selection). Spruce trees used by nesting Rusty Blackbirds varied widely in size from 1.8-12.0 m (mean=6.8 ± 0.47 m) in height although all nests were placed in live trees, and all but two of the nests (n = 41) were placed directly adjacent to the main trunk of the tree. Mean nest height was 2.7 ± 0.20 m, but ranged from 1.0-6.0 m. Although the nests were generally well concealed at greater distances by surrounding trees and shrubs, 84% of the nests were less than 50% concealed from all directions at 1 m.

Nest dimensions, including nest width ($\bar{x} = 15.64 \pm 0.364$ cm) nest depth ($\bar{x} = 9.09 \pm 0.381$ cm), cup width ($\bar{x} = 8.69 \pm 0.287$) and cup depth ($\bar{x} = 5.5 \pm 0.269$ cm) were measured for 22 nests during 2010. The rim and outer frame of these sturdy cup nests were constructed primarily of spruce branchlets and aquatic horsetail stems (*Equisetem* sp.) intertwined with the branches supporting the nest, and to a lesser extent some also included mixes of grass and/or sedge. The inner cup was constructed of mud and various mixes of grass and/or sedge, detritus, and mosses. Moose (*Alces alces*) hair was the most common nest lining, with a few lined only with grasses or sedge.

The modal nesting interval which includes egg laying, incubation and nestling phase was 29 days (n = 33, $\bar{x} = 29.03 \pm 0.15$, incubation range 11-13 days, hatching to fledging range = 11-13 days). All nesting activity in my study area was highly synchronous in both years, with roughly 85% of nests initiated within a different two week period for both years of the study. Clutch-initiation date (CID) was significantly different between years (p-value < 0.0001) on the west CRD, with mean CID of 10 May ($\bar{x} = 10.476 \pm 0.95$) being eight days earlier in 2010 than in 2009 (May 18, $\bar{x} = 18.421 \pm 1.13$). CIDs ranged from 10 May to 30 May (95% CI, 16 May to 21 May) and 4 May to 21 May (95% CI, 8 May to 12 May) in 2009 and 2010, respectively.

Clutch Size, Hatching Success, Nest Success and Daily Nest Survival

Mean clutch size for Rusty Blackbird first nest attempts on the CRD during the study period was 5.55 ± 0.1 (2009 = 5.41 ± 0.15, 2010 = 5.67 ± 0.13), but ranged from 5-7 eggs (Figure 2.1). Final clutch size was determined by repeated observations for 37 first nest attempts: 18 nests had 5 eggs, 17 had 6 eggs and 2 had 7 eggs (Figure 1). None of the unviable eggs were removed from the nest by adults. Excluding all predated and abandoned nests, most eggs were viable (N = 31 nests), with 0.8922 ± 0.0275 of all eggs laid in successful nests over both seasons hatching. Fledging rate averaged 4.13 ± 0.29 chicks fledged per nest (n = 37), producing 157 total fledglings. Thirty-three of 37 nests fledged chicks for an apparent nest success rate of 89.2%. Of the four unsuccessful breeding attempts, three failed during incubation and one during chick-rearing. Although Rusty Blackbirds were observed mobbing Bald Eagles (*Haliaeetus leucocephalus*) and Northern Harriers (*Circus cyaneus*) on several occasions, and Common Ravens (*Corvus corax*) less frequently, no avian predators believed to be important passerine nest predators (Martin and Joron 2003, Thompson and Burhans 2003, Willson et al. 2003, Thompson 2007) were detected during the rapid area surveys. Potential nest predators observed during nest checks were documented (Table 2.2), but throughout the duration of the study only a single detection of a Black-billed Magpie was recorded.

Figure 2.1: Frequency of Rusty Blackbird nests (n=37) by clutch size on the Copper River Delta, Alaska, during 2009-2010.
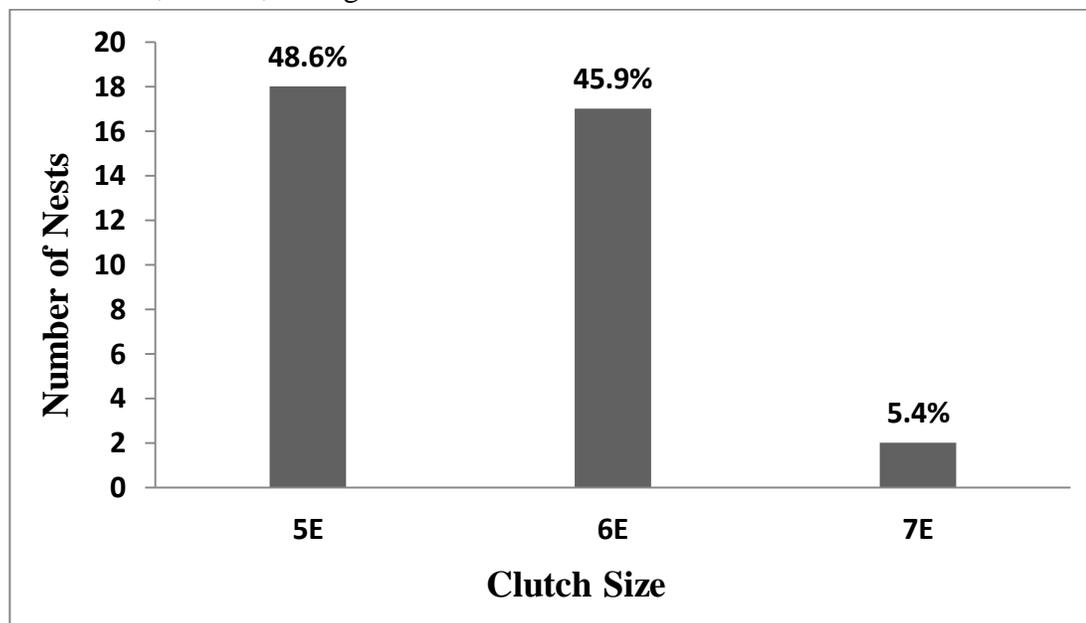
Table 2.2: Inventory of all avian and terrestrial predatory species encountered (with total number of each species) during rapid area surveys and nest visits for all 33days (66 total) of the 2009 and 2010 seasons.

AVIAN		TERRESTRIAL	
Common Raven (7)	*Corvus corax*	Short -tailed Weasel (2)	*Mustela ermine*
Merlin (1)	*Falco Columbarius*	American Mink (1)	*Neovision vision*
Northern Harrier (21)	*Circus cyaneus*		
Black-billed Magpie (1)	*Pica hudsonia*		
Bald Eagle (11)	*Haliaeetus leucocephalus*		
Short-eared Owl (5)	*Asio flammeus*		

The most parsimonious model that best described nest success was the null model S(.) containing no effects. There were several competing models within 2 AIC_C of my most parsimonious model, including a model with an increasing linear time trend on daily survival ($S_{(T)}$), and a trend where survival increases, but then levels off

over time ($S_{(\ln T)}$). There was some evidence that daily survival increased with nest age ($S_{(Nage)}$), nest height ($S_{(Nheight)}$) and nest stage ($S_{(Nstage)}$; increased survival for nestlings compared to eggs) (Table 2.3). A single 2-factor model with an increasing time trend and nest height ($S_{(T+Nheight)}$; survival increased over the nesting interval and with greater nest height) was also within 2 AIC_C. However, none of the slope coefficients for any of these effects included 95% confidence limits that excluded zero (Table 2.4), so these effects are likely of little importance, particularly given the null model had more support, and the direction of effects was generally contrary to what we predicted (Best and Stauffer1980, David 2003, Grant et al. 2005). Five models, including those containing the nest concealment factor, tree height, year, and a single 2-factor model of nest height + nest age, were between 2-3 AIC_C (Table 3), however, 95% confidence limits around slope coefficients for all these models also overlapped zero, suggesting little effect on nest survival(Table 2.4).

Table 2.3: Model selection results for models relating time trends (T, ln, TT), general time effects (t), nest age (Nage), nest stage (Nstage), nest height (Nht), nest concealment (Conceal), and nest tree height (Treeht) on daily survival rates of Rusty Blackbird nests on the Copper River Delta, AK during 2009-2010. Models were ranked according to Akaike's information criterion adjusted for small sample size (AICc). The model deviance ($-2\log(l)$), number of parameters (k), ΔAICc, and AICc weights are given for all models.

Model	ΔAICc	AICc Wts	K	Deviance
$S_{(.)}$	0.00	0.20	1	35.57
$S_{(T)}$	0.83	0.13	2	34.38
$S_{(lnT)}$	0.91	0.11	2	34.47
$S_{(Nage)}$	1.17	0.11	2	34.72
$S_{(Nheight)}$	1.17	0.11	2	34.73
$S_{(Nstage)}$	1.65	0.09	2	35.21
$S_{(T+Nheight)}$	1.88	0.08	3	33.41
$S_{(Conceal)}$	2.01	0.07	2	35.56
$S_{(Treesize)}$	2.01	0.07	2	35.56
$S_{(YR)}$	2.02	0.07	2	35.57
$S_{(TT)}$	2.23	0.06	3	33.76
$S_{(Nheight + Nage)}$	2.38	0.06	3	33.91
$S_{(t)}$	56.54	0.00	33	22.80
$S_{(YR*t)}$	141.69	0.00	67	21.78

[a]Lowest AIC$_c$ = 35.5819

Table 2.4: Slope coefficients $(\hat{\beta})$, with standard errors (SEs) and 95% confidence limits (95% CI) for models within 4 AIC$_c$ of the top model, relating time trends (T, ln, TT), general time effects (t), year (YR), nest age (Nage), nest stage (Nstage), nest height (Nht), concealment of the nest (Conceal), and height of the nest tree (Treeht) to daily survival rates of Rusty Blackbird nests on the Copper River Delta, AK 2009-2010.

Model	$\widehat{\beta}$	SE	95% CI	
			Lower	Upper
S$_{(T)}$	0.088	0.082	-0.073	2.49
S$_{(lnT)}$	0.744	0.623	-0.477	1.965
S$_{(Nage)}$	0.067	0.070	-0.071	0.206
S$_{(Nheight)}$	0.440	0.542	-0.622	1.503
S$_{(Nstage)}$	1.017	1.441	-1.807	3.842
S$_{(T+Nheight)}$	0.093	0.083	-0.070	0.257
S$_{(Conceal)}$	-0.457	4.408	-9.097	8.183
S$_{(Treesize)}$	-0.018	0.176	-0.363	0.328
S$_{(YR)}$	-0.013	1.004	-1.982	1.955
S$_{(TT)}$	0.279	0.235	-0.182	0.740
S$_{(Nheight + Nage)}$	0.433	0.540	-0.626	1.491

Average daily nest survival rate over both seasons from the best model [S(.)] was high, at 0.9913 ± 0.0043 (95% CI 0.9772-0.9967). The probability that any given nest survived the duration of the nesting period (29 days) was 0.7762 ± 0.098. Given my results included a large set of highly competitive models I used a multimodal inference approach to generate best estimates of daily nest survival. I model-averaged

daily survival estimates in Program Mark, which computes a weighted average of the

daily estimates based on model uncertainty across every day within the 33 day study

season (duration from first nest located until the last nest fledged) (Figure 2.2).

Figure 2.2: Model averaged estimates of daily nest survival for Rusty Blackbirds on the Copper River Delta during 2009 and 2010 (n=37) throughout the duration of the 33 day nesting season.
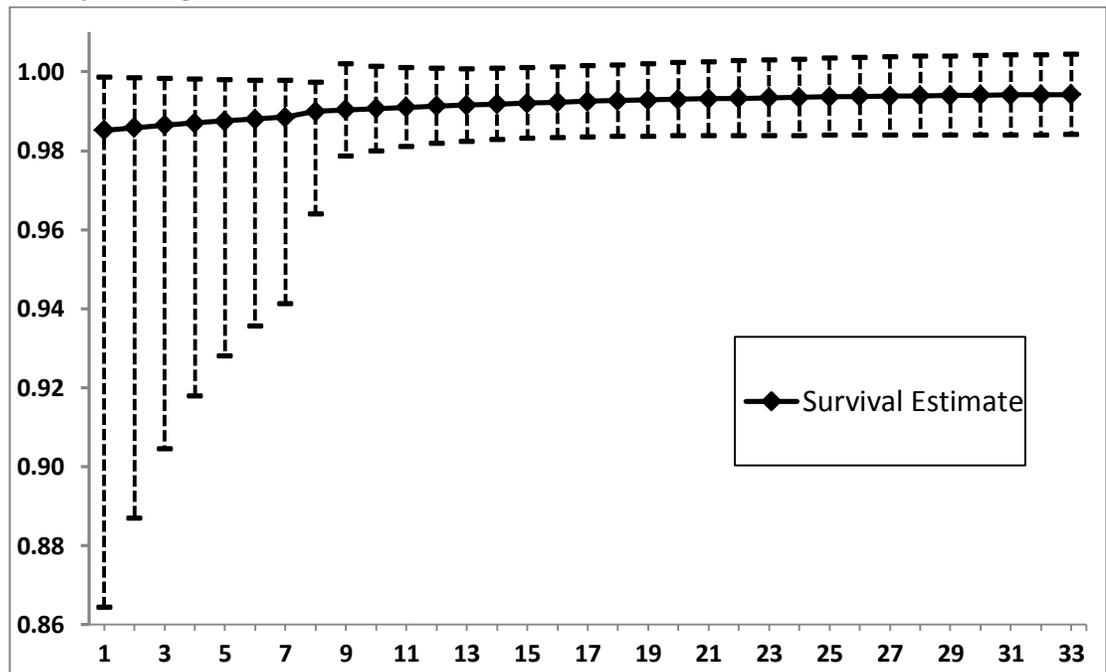
DISCUSSION

The results of this study support recent conclusions that suggest Rusty Blackbird nest

success in Alaska at least, does not appear to be a major force behind long-term

population declines (Matsuoka et al. 2010b). Nesting success (78%) on the CRD was

the highest thus far documented in Alaska and Canada (56%; Matsuoka et al. 2010b),

as well as New England (62%; Powell 2008), and was high in comparison to general nest survival rates reported for other passerines (Thompson 2007). Thus, none of the nest survival rates reported thus far for Rusty Blackbirds would imply poor reproductive success was a cause for population declines, and factors associated with migration and wintering areas are likely driving population declines.

For the first time in history, forested wetlands comprise less than 50% of the total wetland acreage of conterminous United States (Dahl 2011). The loss of forested wetlands in the Mississippi Alluvial Valley and the southeastern United States have undergone profound landscape alterations and much of the bottomland hardwood forests in this region that Rusty Blackbirds are thought to depend on in winter, have been converted to agriculture or other human-dominated landscapes (Avery 1995, Greenberg et al. 2011) . Although conservation measures have slowed the loss of wetlands, between 2004 and 2009 forested wetlands, particularly those in the southeastern United States, sustained their largest losses since the 1985 (Dahl 2011). During winter, the entire Rusty Blackbird population is restricted to a much smaller, more confined area (Avery 1995) thus, a larger proportion of the population is potentially affected by any small scale effects to the landscape and resource availability.

As reported from other sites throughout Alaska, Canada and New England, Rusty Blackbirds on the CRD showed a strong affinity for conifers for nesting (Powell et al. 2010a, Matsuoka et al. 2010b). Most of the well-drained mineral soils that support larger and denser woody vegetation communities have formed along the banks

of tidal sloughs and linear beaver sloughs. The linear beaver sloughs are old tidal channels that were exposed from the uplift caused by the 1964 earthquake and subsequently dammed by beavers. The majority of the spruce trees that were used for nesting have established along these levees, thus most nesting sites are restricted to these areas adjacent to beaver sloughs. Surface water is the most dominant landscape feature on the West Delta and as such, essentially all nests were located within 30 m of water. However it should be noted that Rusty Blackbirds in my study area all used spruce trees located within the dense, linear riparian vegetation zones associated with tidal and freshwater beaver sloughs, even when comparably sized spruce trees were available in adjacent wet meadows and along banks of ponds (D. M. Loomis, personal observation). Of the 42 combined nests sites found, one was suspended over water in a large spruce that had fallen over a beaver slough from windfall and/or bank erosion.

In addition to high nest success, my study documents the largest clutch sizes (5.55 ± 0.1, n = 37) thus far reported of any population of Rusty Blackbirds studied in Alaska (5.3 ± 0.1, n = 104) or Canada (4.6 ± 0.1, n = 28) (Matsuoka et al. 2010b). A latitudinal gradient in clutch sizes (larger at higher latitudes) both within and among taxa, is well documented for passerine birds (Kulesza 1990, Jetz et al. 2008). However this general trend does not explain why mean clutch size was greater on the CRD than other studies reported at similar latitudes. I propose that abundant food resources on the CRD, may account for larger Rusty Blackbird clutch sizes (Loomis 2013, Chapter 3). Proximate causes of seasonal and spatial variation in clutch size, egg quality and chick growth of altricial birds has long been linked to food availability (see Martin

1987 for review). The hypothesis that food availability to nestlings may limit clutch size was first proposed by Lack (1947), an idea that evolved from earlier migration theories of Rowan (1926) and Baker (1938). Many subsequent studies support the idea (Arcese and Smith 1988, Bryant and Tatner 1988, Perrins and McCleery 1989, Nilsson 1991, Martin 1995, Decker et al. 2012), while others have reported a lack of significant evidence (Murphy 1986). Thus, clutch size may be constricted by nestling food availability in some bird species (but not others), and these effects are perhaps most apparent in birds like Rusty Blackbirds, with greater migration distances, truncated breeding seasons, specialized diets, and greater seasonal variability in food abundance (Ashmold 1963, Slagsvold 1982, Kulesza 1990, Decker et al. 2012).

Rusty Blackbirds were highly successful breeders in my study area and the large clutch size may also have been a response to low predation pressure. When the risk of nest predation is low, there is a reduced chance the female will need to invest energy in producing a second clutch, and populations with high survival rates have been shown to respond by laying larger initial clutch sizes (Slagsvold 1982, Kulesza 1990, Martin 1995, Doligez and Clobert 2003). Decreased predation risk for passerines (Kulesza 1990, Jetz et al. 2008), and ground-nesting shorebirds has been confirmed in relation to latitude (higher latitudes associated with decreased predation risk; McKinnon et al. 2010), so this may be an important factor facilitating the high nest success observed on my study area. However, as Alaska in general might be expected to have reduced predation rates relative to lower latitudes, this hypothesis only explains my results within Alaska breeding sites if my study area has decreased

predation pressure compared to other study areas in Alaska. I did not quantify predator

populations directly, but the CRD is in a rapid state of succession. Thus, red squirrels,

Steller's Jays (*Cyanocitta stelleri*) and Northwestern Crows (*Corvus caurinus*) do not

appear to have colonized my study areas yet (D. M. Loomis, personal observation),

and Grey Jay's (*Perisoreus canadensis*) that were observed being mobbed by Rusty

Blackbirds in other study sites, do not inhabit the CRD (ALMS, BBS, D. M. Loomis,

personal observation). Succession models of the Delta predict that most of the area

will become forested wetland (DeVelice et al. 2001), which would provide suitable

habitat for several avian predators currently not a common threat to birds nesting on

the Delta.

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CHAPTER 3 –SPECIALIZED PROVISIONING BY THE RUSTY BLACKBIRD ON THE COPPER RIVER DELTA, ALASKA

INTRODUCTION

The plight of the Rusty Blackbird (*Euphagus carolinus*) has only recently received

rigorous scientific study when Breeding Bird Survey and Christmas Bird Count data,

in comparison to historic accounts, suggested that this species had declined by at least

85% rangewide (Greenberg 1999, Niven et al. 2004, Sauer et al. 2012). Although the

global population is currently estimated to be anywhere from 158,000 to 2 million

birds, this represents the steepest documented population decline experienced by any

passerine since the 1960's, and populations have potentially been suffering reductions

for even longer time periods (Greenberg and Droege 1999, Rich et al. 2004, Savignac

2006, Greenberg et al. 2011). This species breeds in remote wetland areas of the

boreal forest and was until recently, classified as an agricultural pest along with other

blackbird species; thus, the declining population went relatively unnoticed. There has

been much speculation as to the causes for such dramatic reductions in total

population size of this species, and methylmercury, PCB, or other toxicant exposure,

and anthropogenic habitat change are often cited as likely causes (Avery 1995,

Greenberg and Matsuoka 2010). However, little research exists linking Rusty

Blackbird population declines to any of these factors. Even the relatively pristine

breeding habitats Rusty Blackbirds exploit in Alaska have not provided a buffer

against regional population reductions, as estimated declines of 5% annually have been reported statewide (Hannah 2005), and recent estimates that rely on new analytical approaches suggest the trend to be only slightly less with, 4.9% declines annually between 1996-2007 (95% CI = -9.7 to-0.1; Sauer et al. 2012).

Recent studies published by those associated with the Rusty Blackbird Working Group in Alaska (Edmonds et al. 2010, Matsuoka et al. 2010a, Matsuoka et al. 2010b,), Canada (Hobson et al. 2010, Matsuoka et al. 2010a), New England (Powell et al. 2010a, Powell et al. 2010b,) and over-wintering sites in the southern U.S. (Barnard et al. 2010, Edmonds et al. 2010, Hobson et al. 2010, Luscier et al. 2010) have recently added valuable insight to rangewide reproductive ecology, habitat utilization, migratory connectivity, parasite prevalence, and toxicity exposure of this poorly understood species. However, little is known about the foraging ecology of breeding Rusty Blackbirds although they have been observed searching for and gleaning invertebrates at water margins (Ellison 1990). Jaw musculature and bill morphology reinforce observations that Rusty Blackbirds primarily forage for aquatic prey (Beecher 1951, Ellison 1990, Avery 1995). In addition, the importance of aquatic invertebrate availability as a high energy forage base for breeding adults and to provision rapidly developing nestlings has been well documented in other wetland nesting blackbirds of North America (Wilson 1978, Orians 1980, Whittingham and Robertson 1994), but little species-specific information exists for Rusty Blackbirds, particularly in Alaska.

As part of a statewide collaborative effort I investigated some aspects of the foraging ecology of breeding Rusty Blackbirds on the West Copper River Delta (CRD), Alaska. Limited observations obtained during a 2008 pilot study suggested that aquatic invertebrates, particularly dragonfly nymphs (Order Odonata: Suborder Anisoptera) could be an important food source for Rusty Blackbird chicks. Previous studies determined that abundances of Anisoptera can vary considerably at different pond locations around the West CRD (Van Duzor 2011). My primary objectives were to determine chick provisioning rates and the specific food resources that were being fed to Rusty Blackbird chicks on the West CRD. Another goal was to inventory aquatic invertebrates in known Rusty Blackbird foraging locations and to determine availability of invertebrate taxa throughout the chick provisioning period. Understanding these factors and the effect they have on Rusty Blackbird habitat use and productivity is a key component to understanding breeding population distributions and status in Alaska.

METHODS

Study Area

The study site is located within the Cordova Ranger District of the Chugach National Forest, approximately 20 miles east of the city of Cordova on the West Copper River

Delta (CRD) in south central Alaska. The primary study area was approximately 10 square kilometers and was centered on Walhalla Slough (Lat. -145.32413484, Lon. 60.36907995). This region receives an average of nearly 230 centimeters of precipitation annually, and mean minimum temperatures in January and July are -8.9°C and 8.3°C, respectively (Davidson 2003, WRCC 2013). The West Delta and the East Delta are separated by the Copper River that terminates into several braided channels and tidal sloughs. This area is a coastal wetland complex consisting of a wide array of habitat types ranging from mudflats to early succession boreal forest. The Delta was uplifted in the Great Alaskan Earthquake of 1964, radically altering the hydrology of the region and creating new land from formerly intertidal areas (Crow 1971, Boggs 2000). The West Delta has been classified into two landscape types: glacial outwash plain (OP) further inland, and uplifted marsh (UM) closer to the coast (DeVelice et. al 2001, Davidson 1998). Study sites were located within a relatively small portion of the uplifted marsh area and were chosen because high densities of breeding Rusty Blackbirds were observed here during a 2006 feasibility study designed to identify potential study locations for a general reproductive ecology study on this species (Cordova Ranger District, unpublished data).

The uplifted marsh habitats are categorized primarily by freshwater ponds and streams, levees, cut banks, and tidal creeks (Boggs 2000). Extremely high tides flooded the marsh periodically prior to the uplift (Boggs 2000). As salt leached out and dissipated from the uplifted marsh soils, freshwater plant species that were formerly unable to tolerate the sporadic influx of salt water began to colonize the area

(Crow 1971). Prior to 1964, UM vegetation was primarily sedge (*Carex spp.*) and mixed grass/forb communities (Boggs 2000). The UM vegetation currently consists of a wide variety of herbaceous, shrub and tree species (Boggs 2000, DeVelice et al. 2001). Because the Delta is in a state of rapid succession, many of the water bodies are changing. Non-metric multidimensional scaling (nMDS) incorporating mean water temperatures, aquatic invertebrate community composition, and secondary production revealed strong differences between OP and UM ponds, and there was greater variability in these parameters within OP ponds than within UM ponds (Van Duzor 2011). Much of the wetland area consists of poorly drained soils, but silt and organic matter depositions along beaver sloughs have also created some well-drained areas. These soils support thick willow, alder, and spruce communities (Boggs 2000). Succession models indicate that much of the area will evolve to resemble a wetland boreal forest (DeVelice et al. 2001), which is the preferred nesting habitat of Rusty Blackbirds (Avery et al. 1995, Greenberg et al. 2011). Linear patches of mixed shrub/spruce forest that have developed along some of these beaver channels are currently being used as nest sites by breeding Rusty Blackbirds (Chapter 2).

Field Methods

This remote study site was accessed by airboat and all survey areas were traversed by a combination of paddleboats and walking. In other parts of Alaska, Rusty Blackbirds initiated their clutches over a one month period from 7 May to 8 June (Matsuoka et al. 2008) and of the 17 nests found during the 2006 feasibility study on CRD, the earliest confirmed clutch initiation date was 16 May. Based on this information, fieldwork was conducted from the third week in May to 30 July during 2009 and 2010 to encompass the majority of the breeding season. A period of rapid surveys followed by a period of intensive searches was used to first identify possible breeding pairs and later to focus nest search efforts. I used search techniques similar to those described by Martin and Geupel (1993). These surveys were conducted to map the sex, movements, and behaviors of adult Rusty Blackbirds on aerial photographs and aided to focus efforts during the follow up more intensive searches used to find territories and nests (Appendix A). A subset of the total nests found in 2010 was selected for chick provisioning rate observations. Only nests that were not visually obscured from all sides, and/or for which an observation station could be located at such a distance or with suitable concealment to avoid altering the foraging behavior of the adults, were used for observations.

During a pilot study in 2008, camera traps were positioned 2-4 m from nests to test the effectiveness of this technique to remotely monitor nests and document prey

items provisioned to chicks. I created one camera trap by using a digital single-lens reflex camera contained within a pelican case fitted with an infrared motion sensor that depressed the shutter when anything with a heat signature passed in front of the sensor. The sensor was placed approximately 1 m from the nest. The other three manufactured products included two Sony Cybershot point-and-shoot digital cameras with specialty designed housing (Cam Trakker Digital Ranger) and one self-contained camera trap unit (Reconyx RM45 RapidFire Digital Game Camera). The three professionally manufactured camera traps were also triggered by an infrared motion sensor.

The cameras traps were all placed as close to the nest as possible to obtain a clear view of the nest without causing the birds to alter their behavior. Cameras were moved to alternate nests if it was found that the placement location did not offer a clear view of the nest or when adults continued to mob the camera after deployment and all investigators had vacated the nesting site. The three camera trap designs deployed on a total of four nests during the pilot study in 2008 were found to be of limited effectiveness. Only one of the four recorded any images of adults provisioning chicks and the camera produced only 24 images from a single nest with picture quality such that I could identify the type of invertebrate taxonomically classify the invertebrate and estimate size as invertebrate body length (>1 bill length or <1 bill length) relative to the bill length (~1.5 cm) of the adult Rusty Blackbird. Cam Trakker cameras were also used on four nests during 2010.

During the 2010 season, I observed males and females provisioning chicks to determine the taxonomic identity of the food item, and rate at which invertebrates were being fed to young. My goal was to identify provisioned invertebrates to the Order level or lower. Preliminary data from the 2008 pilot study to determine the effectiveness of camera traps to produce an image for identification of food items, and personal observations with binoculars and scopes indicated that most invertebrates provisioned to nestlings were brought as single, large, individual items that could be identified using scopes and binoculars (Cordova Ranger District and D. M. Loomis unpublished data). Thus, observations during 2012 were made with the aid of spotting scopes and binoculars to identify individual invertebrates as they were brought back to the nest. Observers used shrubs, branches, and camouflage clothing to conceal their presence from distances of 25 m or greater from the nest during observations of adults provisioning chicks.

I defined provisioning rate as the number of individual food items (some trips resulted in >1 food item) brought per nest per hour, which was then adjusted to the number of individual invertebrates fed per chick per hour by accounting for the precise number of chicks within the nest during observations. Working in teams of two, provisioning rate data were recorded by one observer while the other visually documented the invertebrate species being fed. Mean provisioning rate per chick per hour was calculated during the nestling phase for each nest located prior to hatch at three stages of chick development, including Early:1-4 days, Middle:5-8 days, and Late:9-12 days. One way ANOVA was used to check for differences in means and

unpaired t-tests compared means between each phase. Observers recorded the number of individual provisioning trips (i.e., the number of times adults returned to the nest to feed chicks), the number and type of invertebrates carried by adult during each visit, and the size of each item relative to the adult's bill length, for all provisioning events in 1-hr blocks throughout the daylight hours. Provisioning rate sampling was not strictly randomized in regard to the specific nest and/or time of day during which nests were observed because of the remoteness of my nest sites and other data collection needs associated with this study. I attempted to include all the active nests with chicks and to make observations across the entire range of daylight foraging hours but early morning and late evening were not possible due to the long day length in June. These data were used to determine the types of invertebrates being fed to chicks as well the abundance and biomass of food items required to successfully fledge chicks.

To determine the types of aquatic invertebrates available to breeding Rusty Blackbirds, invertebrate sampling was conducted at five ponds (four shallow, and one linear dammed beaver slough) within the study site where birds were observed foraging. Five samples were collected every Friday, from the first week of chick hatching through fledging (from May 21 to June 11). Rusty blackbirds have been observed foraging by leaf flipping, probing and plunging their bills or entire head in the shallow pond margins and emergent vegetation where they can capture aquatic prey (Beecher 1951, Ellison 1990, Avery 1995, D. M. Loomis, personal observation). Thus, all sampling efforts focused on shallow water areas and emergent vegetation.

Aquatic invertebrate samples were standardized by collecting two consecutive

samples weekly from each of the same five ponds by sweeping emergent vegetation with a D-frame aquatic sweep net (0.3 m wide, 595 mm mesh) (Turner and Trexler 1997, Wissinger et al 2009). Sweep net samples were taken for 30 s, covering approximately 3 m^2, through the two dominant emergent vegetation types in associated pond ensuring that benthic habitats that are inaccessible to blackbirds were not sampled. Invertebrate samples were sorted to remove detritus and vegetation, replicate pond samples were pooled to represent one sample per pond, and then preserved in ethyl alcohol for later identification and measurements in the lab by collaborators at Loyola University Chicago. Invertebrates were primarily identified to taxonomic order but often to family or more specifically if possible. These samples were used to assess the chronology of invertebrate species available for foraging adults and nestlings throughout the breeding season and to provide baseline data on invertebrate species available as potential food resources for nesting rusty blackbirds. The double 30 s sweeps in emergent vegetation along pond margins were not originally intended to quantify the absolute number of invertebrates found in the Rusty Blackbird foraging areas, but simply to assess which invertebrate taxa were available to provisioning adults and relative abundance within samples in comparison to the assemblage I observed being provisioned to nestlings.

RESULTS

Camera Traps

All of the useable photographs from camera traps documented a long, robust-bodied invertebrate in excess of 2 cm in length. Twenty-one of these 24 images (87.5%) were clearly of dragonfly nymphs (Suborder Anisoptera). The remaining three images are of the correct size to also be Anisoptera nymphs, but obstructions or poor image quality did not allow for more definitive identification. It should be noted that several of the documented invertebrate food items recorded by the camera were of the same provisioning visit and as such include some replicates of the same item(s).

Aquatic Invertebrate Availability

 Five major taxonomic groups were identified as species that could potentially be provisioned to nestlings (Table 3.1). Other species in my samples not observed in chick diets were generally very small or fast swimming, and were thus combined into a single miscellaneous category. The miscellaneous group included 981 individual organisms, representing the majority (71.2%) of all invertebrates (Table 3.1). This group was numerically dominated by scuds (Order Amphipoda, family Gammaridae) and midges (Order Diptera, Family Chironomidae).

Table 3.1: Relative abundance as the total number of individuals in each taxonomic group and the percent of the total number of individuals in the sample (n=1377) in four weekly samples collected from freshwater ponds adjacent to nesting Rusty Blackbirds between May 21 – June 11, 2010 on the Copper River Delta, AK.

Taxonomic Order	Description	Total (%)
Coleoptera	predaceous diving, whirligig, & crawling water beetles	90 (6.5)
Hemiptera	water boatmen & water striders	149 (10.8)
Hirudinea	leeches	25 (1.8)
Odonata	dragonflies (31) & damselflies (62)	93 (6.8)
Trichoptera	caddisflies	39 (2.8)
Miscellaneous	amphipods, midges, copepods, clams & snails	981 (71.2)

Of the other five taxonomic groups identified, Hemiptera was the most common, comprising approximately 10.8% of all invertebrates collected (Table 3.1). Coleoptera and Odonata were nearly equally represented in the samples at approximately 6.5% and 6.8%, respectively (Table 3.1). Weekly samples varied substantially in the total number of individuals collected and the proportions of each taxonomic group in those samples (Table 3.2). The highest number of individuals was collected during week 2, but the largest proportion of odonates was observed during week 1 sampling (Table 3.2).

Table 3.2: Relative abundance as the total number of individuals in each taxonomic group and the percent of the total number of individuals in each weekly sample of aquatic invertebrates collected in freshwater ponds adjacent to nesting Rusty Blackbirds between May 21 – June 11, 2010 on the Copper River Delta, AK.

	Total (%)			
Taxonomic Order	Week 1 (n=217)	Week 2 (n=604)	Week 3 (n=202)	Week 4 (n=354)
Coleoptera	7 (3.2)	18 (3.0)	18 (8.9)	47 (13.3)
Hemiptera	35 (16.1)	51 (8.4)	23 (11.4)	40 (11.3)
Hirudinea	7 (3.2)	2 (0.3)	9 (4.5)	7 (2.0)
Odonata	25 (11.5)	39 (6.5)	10 (5.0)	19 (5.4)
Trichoptera	14 (6.5)	11 (1.8)	8 (4.0)	6 (1.7)
Miscellaneous	129 (59.5)	483 (80.0)	134 (66.3)	235 (66.4)

Provisioning Rates and Diet

Fourteen nests were observed for a total of 39 hours, and 162 provisioning trips were documented. For a majority of the observed foraging trips (97.6%), adults delivered a single item to nestlings, but on four occasions, adults offered two Anisoptera nymphs to nestlings during a single provisioning trip, comprising 7.4% of the identified provisioning event. The observed provisioning trips resulted in 166 individual food items brought to chicks and 108 of these items were identified to Order or lower (65.1%; Table 3.3). All but one identified provisioned items were aquatic invertebrates in excess of 2 cm in length, and 105 of these 108 items (97.2%) were

Anisoptera nymphs. Every invertebrate provisioned (100%) was greater than 2 cm in length. The mean provisioning rate of Rusty Blackbirds in my study was 0.84 ($\pm$ 0.06; 95% CI: 0.72 to 0.95) invertebrate food items/chick/hour and ranged from 0.33 – 2.0 provisions per hour. Though mean provisioning rate varied by nest phase (Figure 3.1), differences were not significant. Running simulations that doubled and tripled sample sizes also did not result in a significant difference in provisioning rates by phase at the α=0.05 significance level.

Table 3.3: Relative abundance as the total number of positively identified invertebrates provisioned in each taxonomic group and the percent of the total number of individuals observed being fed to chicks by nesting Rusty Blackbirds between May 21 – June 11, 2010 on the Copper River Delta, AK.

Taxonomic Order (Suborder)	Description	Total (%)
Odonata (Anisoptera) Nymph	dragonfly nymph (aquatic stage)	105 (97.2)
Odonata (Anisoptera) Adult	dragonfly adult (terrestrial stage)	1 (0.9)
Odonata (Unknown) Nymph	unidentified Odonata nymph	1 (0.9)
Coleoptera Larvae	Predaceous diving beetle larvae	1 (0.9)

Figure 3.1: Mean number of individual invertebrate prey items per chick per hour with 95% confidence limits for the entire combined chick rearing period, and the "early" (1-4 days), "mid" (5-8 days) and "late" (9-12 days) chick rearing periods for Rusty Blackbirds breeding on the Copper River Delta, AK during 2010.
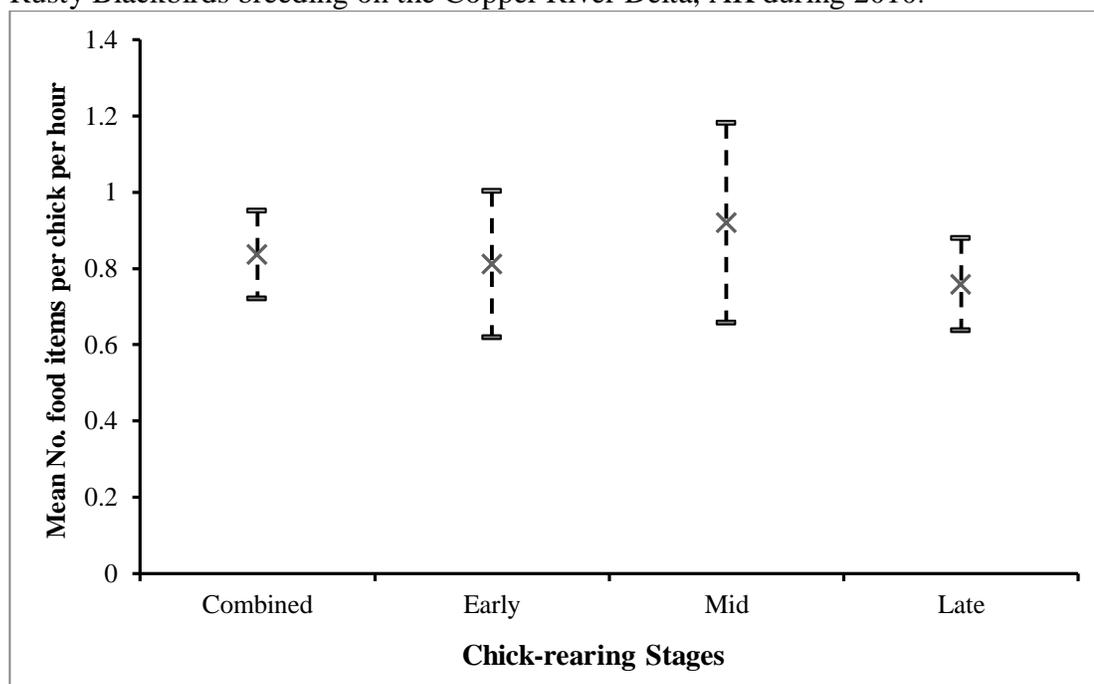
Only a subset of the species I collected in aquatic samples occurred in the size range I observed Rusty Blackbirds feeding to chicks (>2 cm) and this included odonates, Coleoptera and Hirudinea (leeches) (Table 3.4). Thus, several invertebrate species identified as candidate food resources for Rusty Blackbird chicks could be eliminated from weekly invertebrate samples. I focused on items in each weekly sample that represented the size class observed being provisioned to chicks (Table 3.4). Although >97% of the observed invertebrates adults used to provision chicks were large odonate nymphs, damselfly (suborder Zygoptera) nymphs were twice as numerous in my samples but were not fed to chicks during any of my observations. When relative abundances of sampled invertebrates were further investigated by

focusing on species reflecting observed prey sizes offered to chicks, twice the number

of Zygoptera nymphs were collected compared to Anisoptera nymphs (Table 3.4). In

addition, although dytiscids were the most abundant large species in aquatic samples,

even when the highly mobile and hard-bodied adults were excluded and only larvae

were considered, these items were rarely fed to chicks (Table 3).

Table 3.4: Relative abundance as the total number of individuals in each group and the percent of the total number of individuals in the sample (n=192) of aquatic invertebrates that typically average >2cm, the item size fed to Rusty Blackbird chicks from four weekly samples collected from freshwater ponds adjacent to nesting Rusty Blackbirds on the Copper River Delta, AK in 2010.

Taxonomic Classification	Description	Total (%)
Coleoptera	Dytiscidae (pred. diving)	74 (38.5)
Hirudinea	Leeches	25 (13.0)
Odonata	Zygoptera (damselflies)	62 (32.3)
Odonata	Anisoptera (dragonflies)	31 (16.2)

Anisoptera were the least abundant of any invertebrate in this restricted sample

subset from ponds. These large odonates only comprised 16.2% of the total

individuals sampled from ponds that were of the size seen provisioned to nestlings,

and Anisoptera nymphs were observed in the highest numbers in samples collected

during the two weeks that coincided with the highest Rusty Blackbird nest hatch rates

in my study site. This standardized invertebrate sampling technique allowed us to

present weekly availability trends which suggests a temporal relationship between the

number of Anisoptera nymphs available to provisioning blackbirds and the total

number of nests that hatched weekly (Figure 3.3). In contrast, weekly mean number of

the two most abundant large-sized invertebrate groups in my samples, Zygoptera

(Figure 3.4) and larval dytiscids (Figure 3.5), displayed no temporal pattern consistent

with the pattern in the proportion of nests hatched throughout the season.

Figure 3.2: Mean number of Anisoptera per weekly sample (with 95% Confidence limits) and the proportion of Rusty Blackbird nests hatched per week out of the total number of nests that hatched (n=21) during 2010 on the Copper River Delta, AK.

Figure 3.3: Mean number of Zygoptera (with 95% Confidence limits) and the proportion of Rusty Blackbird nests hatched per week out of the total number of nests that hatched (n=21) during 2010 on the Copper River Delta, AK.

Figure 3.4: Mean number of larval dytiscids (with 95% Confidence limits) and the proportion of Rusty Blackbird nests hatched per week out of the total number of nests that hatched (n=21) during 2010 on the Copper River Delta, AK.
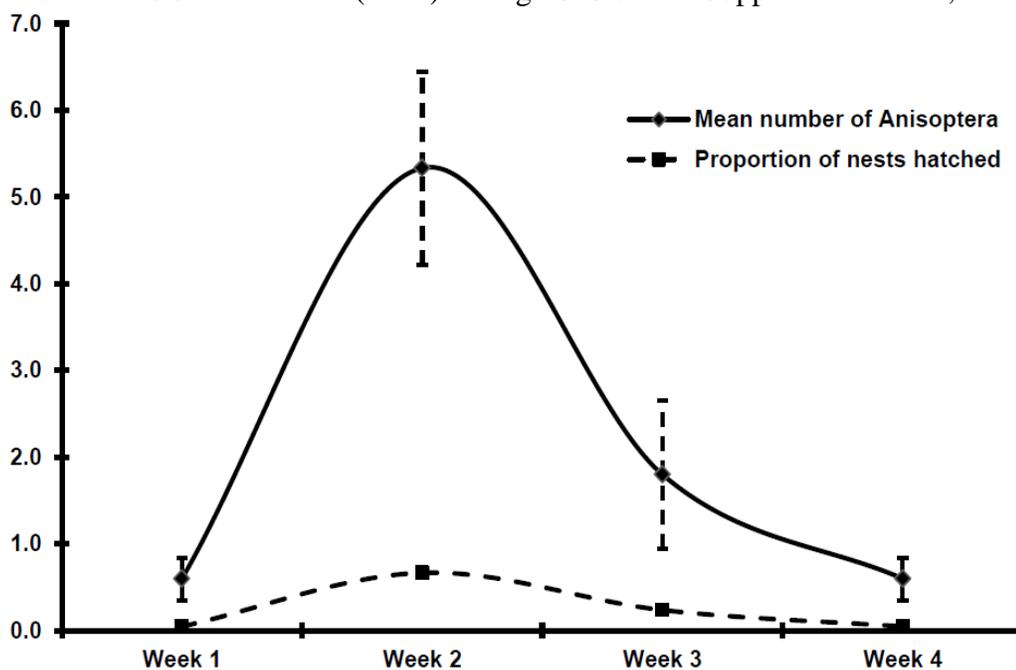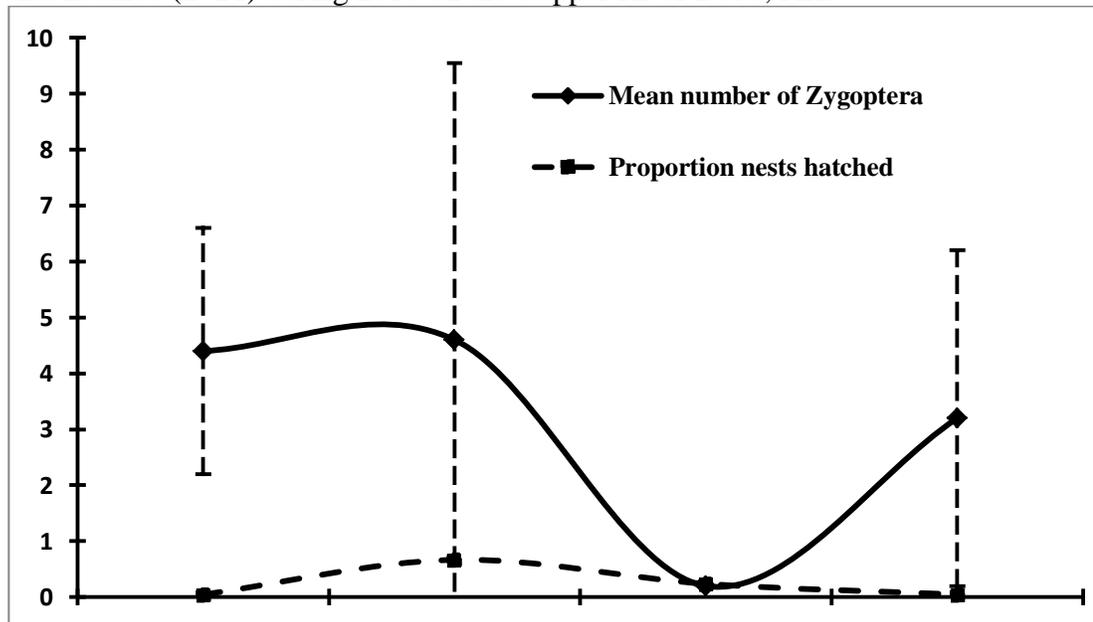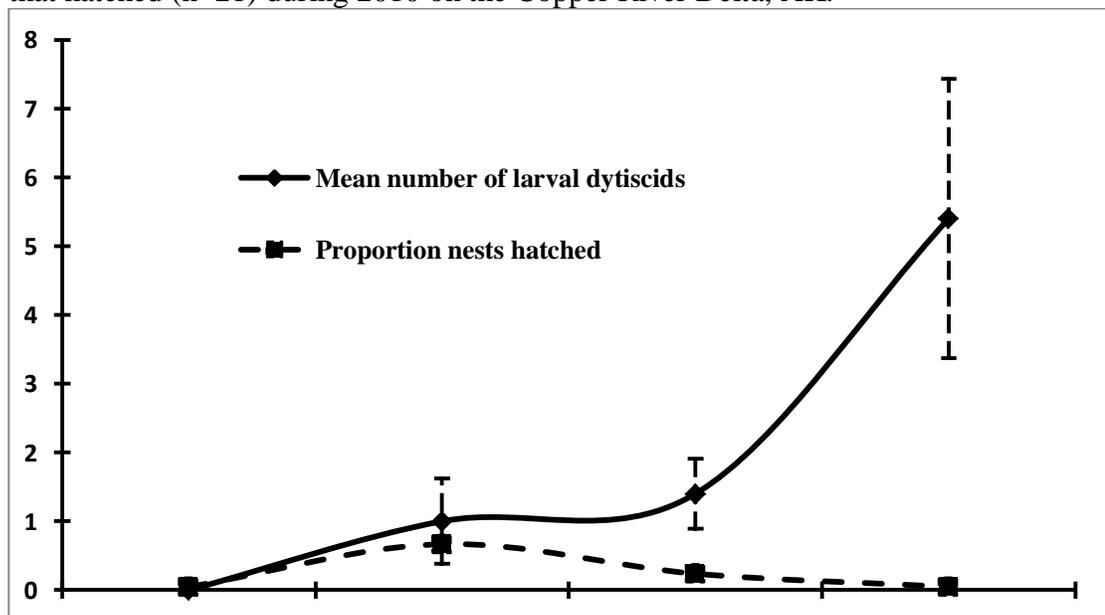
DISCUSSION

A shift from a primarily granivorous to insectivorous diet in some passerines, particularly marsh-nesting blackbirds, has been well documented and hypothesized to facilitate delivery of an easily digested high-protein diet to rapidly developing nestlings (Morton 1973, Wilson 1978, Orians 1980). My results indicate that not only are Rusty Blackbirds highly insectivorous throughout the breeding season, but that Anisoptera nymphs represent the most important food item provisioned to nestlings throughout all chick-rearing phases in this study. Female Red-Winged Blackbirds have been proposed to maximize provisioning efficiency by selecting for larger food items and choosing nymphs/larva that were soft bodied, and thus potentially easier to digest or slower moving making them easier to capture (Wilson 1978). Anisoptera are large, soft-bodied, and in theory, simple to capture if they can be located, in relation to free-swimming invertebrate prey. This particular prey item is cryptic and was among the least common invertebrate found in weekly aquatic sampling, suggesting Rusty Blackbirds do not select prey in relation to availability (apostatic prey selection) when foraging for chicks (Allen and Weale 2005) but instead exhibit prey selectivity (anti-apostatic selection).

Larger, more mature nestlings should require more calories per day than newly hatched individuals, though my provisioning rate results do not reflect this pattern. The number of food items/chick/hour was relatively constant across all phases of the chick-rearing cycle, whereas I predicted provisioning rate would increase with chick

age. These results may have been an artifact of the irregularity of nest observations. Each nest in the study was only observed for a 1-hr interval for each of the three phases. Most observations were made between mid-morning and mid-day, thus early morning and evening when birds are known to be most active may have been the most frequent provisioning times. Adults were observed provisioning > 1 food item/chick/hour during 1-hr observations (range 0.33 – 2.0), even though the mean rate was much less. This does confirm that Rusty Blackbirds on the CRD have the ability to provide food at greater rates than my observed mean. Providing additional food items just prior to dark and again after sunrise is plausible considering that the nestlings do not feed during the night. When compared to day-length limited Great Tits (*Parus major*) in central Europe, Great Tits in northern Europe were found to provision for more hours daily but had more varied distributions of feeding visits (Sanz et al. 1998) and in the far north with 24hrs of daylight, Great Tits did not utilize all available hours to provision (Sanz 2000). Similarly, Tree Swallows (*Tachycineta bicolor*) in central California that provisioned for longer portions of the day provided food at slower rates than birds that provisioned for a shorter duration of the day (Rose 2009). Thus, birds appear to have the ability to adjust daily time budgets to balance energetic requirements of raising offspring against available food resources and day length needed to forage. We did not investigate daily time budgets in this study, so total provisioning effort relative to clutch size and nestling age could not be determined.

A nestling's weight increases by 700% through the first nine days of growth (Robertson 1973), and it has been estimated that a blackbird would have to provision a total 2940 cal of food to each nestling for the first nine days of chick growth to meet this demand (Wilson 1978). Although Anisoptera were among the least numerous of any invertebrate collected during sampling, they provide on average 400 cal per individual, while Zygoptera for example, and only provide 50 cal each (Orians 1980). Thus, Rusty Blackbirds feeding Anisoptera can raise a brood of 5 chicks over 9 days with approximately 37 total provisioning trips or 4.1 trips per day (2940/400 cal per Anisoptera=7.4 items per chick x 5 chicks = 36.7 items), vs. the 58.8 foraging trips per chick or 294 total trips necessary over 9 days if feeding Zygoptera. So while both odonate groups should occupy similar niches and occur in similar habitats in the CRD, the total foraging trips necessary to provide for rapidly developing nestlings would increase dramatically if chicks were provided with the much energetically reduced content of Zygoptera.

Caloric availability alone does not explain why Anisoptera were so highly selected to provision nestlings. Dytiscid beetle larvae were consistently the most common large invertebrate collected in weekly pond samples, and large dytiscids can provide up to 370 cal (Orians 1980). However dytiscid larvae were only seen being fed to nestlings once out of 108 identified food items. Dytiscids are generally free swimming predators in both adult and larval forms, often actively pursuing their prey, but they can also ambush prey with lie-in-wait tactics, resting at depths and potentially inaccessible to Rusty Blackbirds (Larson et al. 2000, Yee 2010). Therefore they are

likely most vulnerable to Rusty Blackbird predation when their larval form crawls into shallow vegetative mats to pupate, which may account for their small contribution to observed provisions.

Vegetation composition of the Delta prior to the 1964 earthquake did not provide suitable nesting habitat for Rusty Blackbirds in the study area. Until recent successional changes created a tree and shrub layer, they were believed to only occupy the CRD during migration stops or possibly overwinter during mild conditions (Isleib and Kessel 1973). The brackish water present on most of the delta prior to uplift would not have permitted odonates to colonize the coastal ponds, and most of the UM ponds where Rusty Blackbirds have since been found is newly created freshwater habitat that did not exist before 1964 (Crow 1968, Davidson 2003, Van Duzor 2011). Thus, rapid colonization of these new freshwater habitats by odonates and other aquatic invertebrates likely facilitated colonization by breeding Rusty Blackbirds into these new habitats once some tree and shrub cover became established. Interestingly, the most common Anisoptera in my samples received an abundance rank of rare or absent in other UM ponds (Van Duzor 2011). Higher abundances of Anisoptera in my study site may be one contributing factor driving nest site selection and resulting food resources for blackbirds are likely partially responsible for the high nest success on the CRD (Loomis 2012, Chapter 2).

Predators generally show apostatic (nonselective) selection, selecting items by density dependence in relation to availability, particularly when all prey have similar nutritional value (Allen 1972, Allen 1988, Marini and Weale 1997, Bond and Kamil

1998). Anti-apostatic selection has been observed when many prey types are crowded, and therefore occur at high density with high encounter rates (Allen and Anderson 1984, Landeau and Terborgh 1986, Allen 1988, Church et al. 1994). When prey occurs at high densities, prey selectivity can result in pursuit of the odd prey type within a group (Srygley 1999). Rusty Blackbirds are not selecting food in relation to its availability, instead they exhibited anti-apostatic selection and this is likely because Anisoptera are characterized by: 1) high caloric content, and 2) ease of capture. Thus, being selective has strong advantages, and in fact ease of capture may ultimately make Anisoptera "more available" than some of the other large-bodied species (such as dytiscid beetle larvae).

The timing of Anisoptera availability may be another important factor that contributes to high nest success and potentially affects the breeding chronology of this Rusty Blackbird population on the CRD. Odonates are particularly vulnerable during the period of emergence, when they migrate to shallow emergent vegetation and are then completely exposed as they crawl out of the water onto vegetation for 1 – 2 hours to fully emerge, dry and eventually fly (Corbet 1999). Breeding birds that time nest hatching to coincide with peak Anisoptera availability would minimize foraging effort and time away from nests during a period when males are responsible for most of the foraging for chicks (D Loomis, pers. observation). Females were rarely observed provisioning chicks until they were 3-4 days old and never left a nest exposed in inclement weather conditions; thus in addition to providing all the nutrients required by the rapidly developing nestling and defending his territory, the male may also

continue provisioning the female during these times. This would be advantageous because chicks of this age are vulnerable to exposure and cannot survive without the shelter and heat provided by the female, especially at these high latitudes. Maximizing foraging efficiency by correlating peak hatch dates with peak Anisoptera availability could result in delivery of a valuable energy source while minimizing time away from the nest, potentially contributing to higher nest success. Empirical evidence suggests that avian breeding chronology is influenced by food supply and birds time breeding to allow chick hatching to coincide with peak invertebrate food availability (Greenlaw 1978, Murphy 1986, Perrins and McCleery 1989, Van Noordwijk et al. 1995, Decker et al. 2012).

Unlike recent studies by Matsuoka et al. (2010) that reported finding no significant difference in breeding chronology between years, in a congruent study I found the eight day clutch initiation date (CID) difference in our study to be highly significant (2010, $\bar{x} = 10.476 \pm 0.95$; 2009, $\bar{x} = 18.421 \pm 1.13$) ($p < 0.0001$) (Chapter 2). Temperature and weather conditions prior to and during the breeding season alone do not explain the earlier CID in the second year of the study (Figure 3.6). Using mean daily temperatures to forecast nesting chronology I would have predicted a later breeding season in 2010 than in 2009, however my results reflect the opposite pattern. This is potentially related to Anisoptera availability, but lack of aquatic invertebrate survey data in 2009 only allows us to speculate.

Figure 3.5: Mean temperature in ˚F for 2009 and 2010 with 9 previous years averaged for reference.
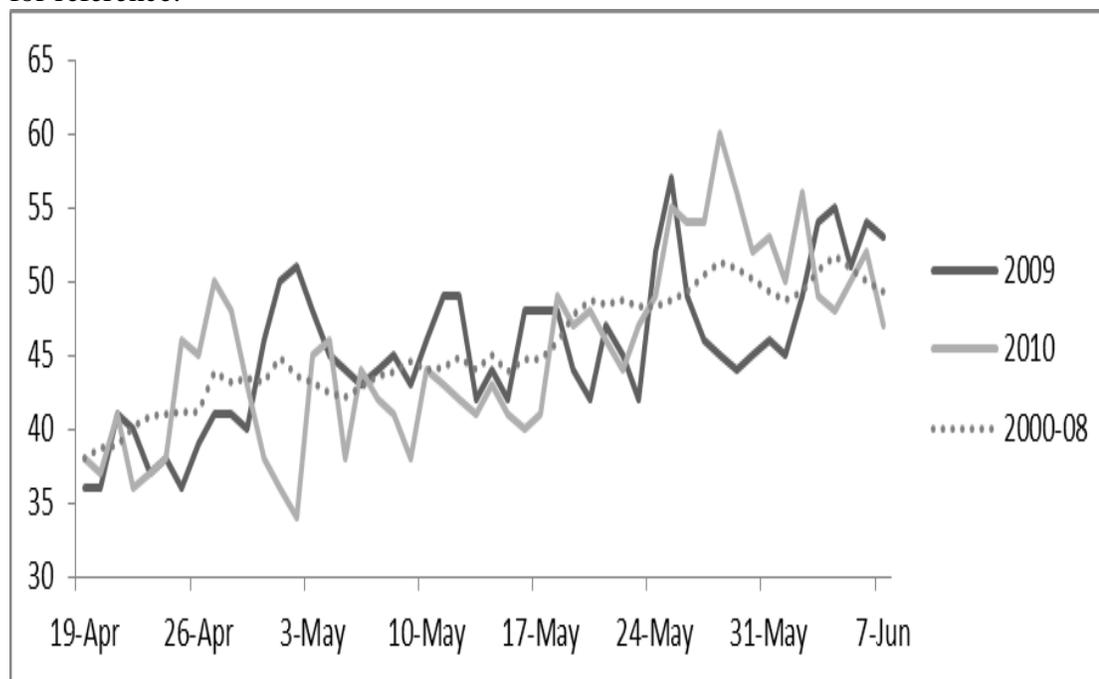
It has long been believed that birds time their migration and breeding activities

to exploit resources when they are most available (Perrins 1970), and the timing of

breeding has been linked to insect abundance in numerous studies (Murphy 1986,

Perrins and McCleery 1989, Decker et al. 2012). The timing of food availability to

provision nestlings may be an important force influencing breeding season chronology

for Rusty Blackbirds nesting on the CRD. Other studies have suggested that breeding

adults are apparently able to predict future environmental conditions later in the

breeding season by indirect or proximate cues and climatic conditions rather than by

food availability at the time of egg laying (Preston and Rotenberry 2006, Decker et al.

2012). For Red-faced Warblers (*Cardellina rubrifrons*) breeding in southern Arizona,

egg-laying was timed so that nestlings were provisioned during the peak of food abundance, and those that did so had the largest clutch sizes (Decker et al. 2012).

Rusty Blackbirds are possibly more specialized than other blackbirds, particularly in relation to their breeding season diet and provisioned food items (Wilson 1978, Orians 1980, Yasukawa et al. 1990, Zimmerling and Ankney 2005, Westneat et al. 2013). It appears that during one year on the CRD, aquatic invertebrate food resources, particularly Anisoptera, were important for successful chick rearing. It is difficult to generalize based on only one year of data, as it is possible that Rusty Blackbirds in my study were highly selective for Anisoptera nymphs because of coincidental overlapping phenology in 2010. However, it's unlikely that Anisoptera would be avoided completely in other years or other systems. Other Rusty Blackbird populations may choose invertebrate prey that are most susceptible to predation at times that correlate to peak chick hatching, and further research with both temporal and spatial replication is necessary to truly understand Rusty Blackbird foraging behavior. Based on pre-breeding season temperatures (Figure 3.6) and significantly different CID dates between years, I speculate that birds in my study area are using proximate cues, such as local weather and vegetation conditions, to purposely time breeding chronology to best coincide with peak Anisoptera availability, after they arrive on the breeding grounds. It is unlikely that Rusty Blackbirds in winter can predict what conditions will be like thousands of miles away in Alaska, particularly as migration chronology is generally triggered by day length changes (review in Coppack and Pulido 2004). Photoperiod ultimately has the largest influence over migration

patterns, thus birds will generally arrive to breeding grounds at approximately the same time annually but must adjust their breeding chronology according to local conditions and food availability. In 2010 Rusty Blackbirds were seen in my study area two weeks prior to mean clutch initiation when the majority of all fresh water in the area remained frozen (Loomis, personal observation), yet laying appeared to commence such that peak chick hatch occurred when Anisoptera were most available to provision. Future studies are necessary to determine if Anisoptera are also as vitally important throughout the Rusty Blackbird breeding range or if invertebrate prey are provisioned more opportunistically elsewhere.

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CHAPTER 4 – GENERAL CONCLUSION

This study suggests that at least during some years, nest survival for Rusty Blackbirds can be quite high (78% across entire nesting period in both years), as the nest survival rates in 2009 and 2010 (Chapter 2) were significantly higher than that reported from other areas in Alaska (56% elsewhere in Alaska; Matsuoka et al. 2010b). Multiple factors likely contributed to high nest success, including reduced predation pressure relative to other nesting populations and a readily available food supply to provision chicks. Provisioning observations revealed that odonates, particularly Anisoptera nymphs, were an important food resource for nestlings and represented the primary provisioned food item at all nests observed. The provisioning observations and results from this and other reproductive studies indicate that Rusty Blackbirds may be a highly specialized blackbird; a trait likely contributing to its range-wide demise. In addition to factors already causing rapid population declines, climate change has the potential to have negative impacts on this species by disrupting the timing of invertebrate food resource availability.

In general passerine nest success rates are rarely as high as what I have observed here for Rusty Blackbirds (Martin 1995) and it appears that on this part of the Delta, both potential avian and terrestrial nest predators (e.g., Northwestern Crow, *Corvus caurinus;* Black-billed Magpie, *Pica hudsonia*; Steller's Jay, *Cyanocitta stelleri*; Red Squirrel, *Tamiasciurus hudsonicus*) occur at relatively low densities, as while all losses were likely attributed to predation (100% of nests lost), that was

relatively few nests overall (4 of 37 monitored; 10.8%). This is in contrast to nest predation rates for passerines at other latitudes which can be quite high (30.7% to 48.5%; Martin 1995). Corvid and red squirrel densities are generally lower in wetlands than upland habitat, thus nesting in wetlands may be an adaptive response to lower predation pressure than would be experienced in uplands (Desanto and Willson 2001). Decreased predation risk for ground-nesting shorebirds has been confirmed in relation to latitude (higher latitudes associated with decreased predation risk; McKinnon et al. 2010), and during early season surveys designed to locate Rusty Blackbird territories, none of the common avian nest predators were encountered in either season. Thus, I believe that slightly lower predation rates in my study area likely contributed to higher nest success in relation to other locations in Alaska, and other passerines at lower latitudes.

This study also indicates that Anisoptera nymphs, at least within my study area, are an important food resource and can provide the bulk of all nutrients to developing nestlings. I observed a temporal relationship between the number of Anisoptera nymphs available to provisioning blackbirds and the total number of nests that hatched weekly (Chapter 3). It appears that the timing of nesting for Rusty Blackbirds on the CRD during the 2010 nesting season coincided with peak availability of the invertebrate group that was almost exclusively observed being provisioned to chicks that year. These soft-bodied food items are theoretically easier to digest than hard bodied terrestrial invertebrates (Morton 1973) and are among the highest caloric content invertebrate that occurs on the CRD or in many shallow water

systems of North America (Orians 1980). Although Rusty Blackbirds appeared to exhibit selectivity in choosing Anisoptera nymphs in the CRD, the provisioning results were based on a single season of observations. Thus, these results may have been coincidentally correlated, so additional work is needed to determine if this pattern is consistent among years and other study sites. Future studies should focus on how the phenology and densities of Anisoptera can influence habitat selection, reproductive success, and reproductive parameters such as clutch size and nestling growth rates.

Incidental sighting of Rusty Blackbirds documented by the USFS Wildlife crews for two seasons (2006 and 2007) rarely recorded sightings outside of my study area (Cordova Ranger District and D. M. Loomis unpublished data). Sitka spruce trees similar in size selected for nesting in my study area occur throughout the West delta. Food availability may be the reason Rusty Blackbirds appear to be using the Delta disproportionately to nest tree availability. Studies comparing Uplifted Marsh (UM) ponds invertebrate communities and abundances on the West Copper River Delta (area that contains my study site) with Outwash Plain (OP) ponds suggest that UM ponds appear to have lower odonate abundances than OP ponds (Van Duzor 2010). I found that one of the least common Anisoptera encountered by Van Duzor (2010) in UM ponds he studied was the most numerous in samples from my study site (Chapter 3). Not only is it possible that the portion of the UM that contains my study site is unique in Anisoptera composition and abundance, but timing of availability to breeding birds due to invertebrate phenology may be an important driver of nest site selection by Rusty Blackbirds. My study area is adjacent to a major channel of the Copper River

Delta (CRD), which winds down through the Alaskan interior. Cold air is funneled down the Copper in winter and spring, resulting in a strong temperature influence on the eastern portion of the West CRD (Boggs 2000). As a result leaf-out and pond thawing is consistently later than on more westerly portions of the West CRD (Boggs 2000). This delayed timing should cause later emergence times of aquatic invertebrates, which could better overlap the chick provisioning phase of Rusty Blackbirds migrating up from the Southeast U.S. each spring. These birds may be selecting this nesting habitat in order to time nesting chronology such that invertebrate food resources are most available to provision chicks.

Much more work is needed to determine if Anisoptera are critical for survival throughout the annual cycle, and/or reproductive success across the Rusty Blackbird's breeding range. These birds are perhaps the most specialized of any North American blackbird (Matsuoka et al. 2010a, Powell et al. 2010) and specialized animals with specific habitat requirements are always most at risk to habitat loss and degradation, with resulting negative impacts on populations. Reduced Anisoptera densities and local extinctions throughout their wintering, breeding, and migration area could explain some of the rangewide population declines. It is estimated that over half of all wetlands in the conterminous U.S. have been lost completely, and many of the remaining wetland areas have been significantly degraded and may not support the high densities of Anisoptera that historically occurred there (Dahl 2011). If Anisoptera are found to be vital to annual survival and nest survival across the species range, then

conservation and/or restoration of existing wetlands to promote these important food resources should be a major priority.

Understanding the relationship between wetland food resources and Rusty Blackbird population dynamics in particularly important as global climate change has the potential to affect this relationship across the species range. In Alaska climate change may affect Rusty Blackbird breeding habitat in two important ways: 1) through direct loss of habitat and/or 2) a disconnect of resource availability associated with changes in life cycle chronology of the predator and invertebrate prey. Alaska has experienced a reduction in the surface area and total number of water bodies across the state, presumably due to the regional warming trend which has created an increased evapotranspiration rate and lowered water tables caused by melting permafrost (Klein et al. 2005, Smith et al. 2005, Riordan et al. 2006). The CRD is dominated by large areas of surface water (chiefly maintained by beaver activity), which helps to maintain a high water table by damming freshwater channels (Cooper 2007). However, the increase in air and water temperature associated with greater evapotranspiration, and natural vegetative succession has the potential to decrease surface water and alter the limnology and aquatic invertebrate community structure. Biomass declines in communities of aquatic invertebrates important to waterbirds as a result of warmer, dryer conditions have been reported in other portions of Alaska (Concoran et al. 2009). Deglaciation across Alaska and Canada is creating new freshwater habitats that are rapidly colonized by invertebrates but these water bodies in recently deglaciated (<50 years) areas are dominated by small-bodied macroinvertebrates (Milner et al.

2009, Milner et al. 2011), and all of my provisioning observations suggest that Rusty

Blackbirds select for large-bodied invertebrates (Chapter 3). Furthermore, because of

their affinity to nesting in close proximity to open water (Chapter 2, Matsuoka et al.

2010a), Rusty Blackbirds would likely avoid deglaciated areas for 50-150 years until

adequate nesting area habitat became available, even if sufficient invertebrate food

resources existed (Milner et al. 2007). Thus, it is uncertain if recently deglaciated

habitat will be a suitable replacement for other surface waters lost from climate

change.

Perhaps the most complicated problem Rusty Blackbirds may face is a

disconnection between their natural life cycle and that of the prey they depend on to

feed their chicks. Climate change is believed to be responsible for causing range shifts

of some species and changing the arrival dates of spring migrants on breeding areas

(Parmesan and Yohe 2003, Deloen et al. 2011). In addition, some migrants may

experience greater warming on their breeding grounds than overwinter areas

(mismatch hypothesis) which triggers a later spring migration than would be necessary

to exploit early breeding season resources that are now available earlier in the spring

(Jones and Cresswell 2010). A long-term data set in England found that between 1960

and 2004, odonates chronologically advanced their phenology by 1.75 days per decade

on average (Hassall et al. 2007). The most alarming change documented in

chronological phenology of odonates is from a study in Japan analyzing data from

1953 to 2005, where the season's first appearance of adult dragonfly has been

significantly delayed (24 days) in the past 50 years (Doi 2008). That research suggests

that increased temperatures provide longer bivoltine periods and an increased growth rate, thus allowing generations to emerge in autumn that previously overwintered to emerge in spring. The result is a greatly reduced population size emerging in spring, which can negatively impact animal species that rely on these invertebrate food resources during the spring/summer breeding season. If other populations of Rusty Blackbirds are as dependent on Anisoptera nymphs to provision nestlings, the later scenario could be devastating to the already drastically reduced global Rusty Blackbird population. Another possibility is that this intelligent species may be able to adapt to changing food availability by altering their breeding chronology, altering prey preferences or shifting breeding areas to locations were invertebrate food resources are more favorable.

This study suggests that Rusty Blackbirds can be highly successful breeders, consistent with results from other studies in Alaska, Canada, and New England that found reproductive success to be quite high relative to other passerines (Martin 1995, Matsuoka et al. 2010a, Powell 2008). Although these studies have provided valuable baseline data about the reproductive ecology of this species, future work is needed to determine if these daily nest survival rates are consistent over time, and across the vast portions of Canadian boreal forests not yet studied. Of particular interest would be long term monitoring of population along the southern border of the range where evidence of range contractions have been reported. If the populations on the southern end of their breeding range are indeed contracting one would expect poor nest success in those areas or limited/changing resources are facilitating the range shift. Powell et

al. (2010a) worked with populations believed to be near the southern range in New England, but reported nest success rates as high as other studies in Alaska and Canada. Logging activities in these areas was found to have a negative effect and significantly reduced nest success, providing further evidence of this species susceptibility to anthropogenic landscape alteration (Powell et al. 2010b).

Future research is needed to identify the food items important to breeding Rusty Blackbirds and their chicks across the species breeding range. In the United States, wetland have been lost or degraded most significantly in the eastern portion of the breeding range and much of those areas have been impacted by acid rain and methylmercury contamination from coal burning industrial activities in Midwestern states (Krajick 2001, Dahl 2011). Concentrations of methylmercury are higher in Rusty Blackbirds breeding in New England than populations breeding in Alaska (Edmonds et al. 2010). Thus, we might expect higher contaminant loads in aquatic invertebrate communities in the northeast compared to Alaska, but this should be investigated. . It is also important to monitor juvenile survival and recruitment throughout the annual cycle between New England and Alaska to determine if a diet consisting of higher mercury concentrations has long term consequences affecting the survivorship of hatch year individuals. More work is also needed to add insight to food requirements in winter as well. Rusty Blackbirds will use agricultural sites adjacent to wetlands (Luscier et al. 2010), but it is not known if they are utilizing the disturbed area out of necessity because of resource deficiencies, or if they are simply foraging opportunistically for easy meals.

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APPENDIX A:

Rusty Blackbird Study Site and Nest Locations for 2009 and 2010 on the western
Copper River Delta, Alaska.