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CHARACTERIZING THE MIGRATORY PHENOLOGY AND ROUTES OF THE LAZULI
BUNTING (*Passerina amoena*) IN NORTHERN UTAH

by

Kim Savides

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

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2022

ABSTRACT

Characterizing the Migratory Phenology and Routes of the Lazuli
Bunting (*Passerina amoena*) in Northern Utah

by

Kim Savides, Master of Science

Utah State University, 2022

Major Professor: Dr. Clark S. Rushing
Department: Wildland Resources

Conservation of plant and animal species requires knowledge of habitat and life history requirements across life stages. This is especially true in migratory species which time their presence with peaks in spatiotemporally abundant resources across distant segments of the full annual cycle. Despite the ubiquity of migration in birds, large gaps remain in our understanding of phenology, routes, and drivers of these movements most species. With advancements and miniaturization of tracking technologies, it is now feasible to address such data gaps by tracking individuals throughout their full annual cycles. Here we investigated the migratory ecology of a breeding population of Lazuli Bunting (*Passerina amoena*) in northern Utah, USA. Lazuli Buntings are a common, moderate distance migrant songbird for which few migratory investigations have been undertaken. We sought to estimate migratory phenology of different demographic groups across an elevational gradient using nearly continuous-time encounter data from radio-frequency identification (RFID)-banded individuals within a customized Bayesian point-process model. Our modelling framework allowed for accounting of daily uncertainty in individual and group-level presence at the breeding site, revealing differences associations in male and female arrival timing between low and high elevations, but little differences between

any groups in departure timing. At low elevations males arrived prior to females, however at high elevations no significant difference was found. These differences indicate selection pressure for protandry at high elevations is low, suggesting protandrous arrival of the species at low elevations may be driven by constraints during the non-breeding or spring migratory period rather than selection-based pressures on early male arrival. We additionally tagged a subset of individuals with archival light-level geolocators to determine locations of migratory stopovers, non-breeding residency, and migratory routes throughout the full annual cycle. Data from the recovered geolocators revealed that all tagged individuals migrated south to western Mexico during the non-breeding season. In four of the five individuals, we found little support for a stopover of adequate length to complete a prebasic molt within the North American Monsoonal region as had been hypothesized for the species. During spring migration, two distinct migratory patterns were observed; a distance-minimizing route mirroring that of fall migration ($n = 3$), and a looping route through California and Nevada ($n = 2$) which was significantly longer in distance with no significant difference time spent migrating. These different spring routes may represent individual-level tradeoffs between time, distance, and resource availability expected en route. Our results revealed distinctive migratory ecologies of the Lazuli Bunting which could have been overlooked in larger scales, highlighting the importance of investigating drivers and variation in migratory at the individual level.

PUBLIC ABSTRACT

Characterizing the Migratory Phenology and Route of the Lazuli

Bunting (*Passerina amoena*) in Northern Utah

Kim Savides

Migratory species time their movements to follow changes in food and environmental resources throughout the year. Despite the ubiquity of migration in birds, little is still known about how birds select routes and time migrations. Recent advancements in miniaturized tracking devices now allow tracking of small birds throughout their annual life cycle, presenting opportunities for migratory ecology research at scales immeasurable in the past. Here we investigated the migratory ecology of a northern Utah, USA breeding population of Lazuli Bunting, a common songbird in western North America for which few migratory studies have been completed. We sought to compare breeding site arrival and departure of male and female buntings across an elevational gradient. We used encounter records of microchip-banded individuals visiting electronic birdfeeders to estimate migratory timings of each sex at high and low elevations. We additionally tagged a subset of birds with light sensing tags from which rough daily locations can be estimated throughout the year to determine where and how the individuals migrated.

We found males to arrive before females at low elevation, while no differences between sexes was found in birds arriving at high elevations. This difference questions traditionally held thoughts on why most male birds typically arrive earlier than females. Our results suggest arrival timing by sex may be driven by differences in constraints on migratory timing rather than evolutionary selection for earlier arrival by males. Our tracking data revealed that tagged individuals migrated south to western Mexico for the non-breeding season. We found little support for a mid-migration stopover long enough to complete an annual molt, as had been

suggested for the species. During spring migration, we observed two distinct migratory patterns: a direct route north made by three individuals, and a looping route through California and Nevada made by two birds. The latter route was significantly longer in distance but not duration. These differences suggest routes may be selected by individuals to balance between length, duration, and food availability of migration routes based on individual conditions each bird experiences. Our results collectively highlight the importance of investigating migratory ecology at the individual level. Such investigations are necessary in understanding how individual birds migrate and are ultimately necessary for effective conservation of birds throughout their annual cycles.

ACKNOWLEDGMENTS

First, I am ever grateful for my advisor Dr. Clark Rushing. Your guidance, patience, and support throughout our time working together is immensely appreciated. Thank you for welcoming me into your family, providing plenty of puppy time, and giving me a start into fly fishing! To my committee members, Frank Howe and Mary Connor, thank you for your thoughts and contributions to this thesis. Thank you to my lab mates Andrew and Aimee for field assistance, camping trips, and lab chats. Aimee, thank you for your help wrangling birds and filling feeders, especially when I quite literally couldn't walk with my broken foot, and providing the best baked goods. To Andrew, thank you for your initial designs and troubleshooting the RFID system, as well as providing the groundwork for my geolocator analysis. To our undergraduate lab assistant, Patrick, thank you for your tireless work keeping the feeders full and conducting surveys, your efforts ensured the highest quality data we could have hoped for. Thank you to Marsha and the rest of the university staff for always answering my questions and making my time here go smoothly, your help is so greatly appreciated. Thank you to Dr. Nathan Cooper for your expertise and guidance in my geolocator analysis.

Thank you to all the wonderful friends and new colleagues I made in Logan for your friendship and support, even though we spent most of our time together across computer screens. Finally, thank you to Alli, for always being there to let me complain about errors in R, recount my latest fish adventure, marvel about odd bird stuff, and for making the cross-country distance feel a little bit more manageable.

This work was supported with funding from Utah State University and Utah State University Agricultural Experiment Station, as well as through donations of seeds from Wasatch Audubon and circuit boards and advice from Dr. Eli Bridge (Oklahoma University).

Kim Savides

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CHAPTER 1

INTRODUCTION

BACKGROUND

Variation in temperature, rainfall, and nutrients across the globe creates a multitude of niches that life has evolved to occupy. These resources are not homogeneous in time or space. Migration, the predictable seasonal movement of individuals, is thought to have evolved as organisms moved to seek these spatiotemporally available resources throughout the full-annual cycle (Cox 1968, Boyle and Conway 2007). On small scales, arctic copepods move tens of meters daily in the water column (Daase et al. 2016), while Arctic Terns (*Sterna paradisaea*) travel upwards of 80,000 km between arctic breeding and Antarctic winter grounds (Egevang et al. 2010). As technology advances, we are tracking the migrations of many additional species at scales immeasurable in the past.

Migration is perhaps most conspicuous and most well-studied in birds. Birds display a wide range of migratory strategies, from altitudinal and regional migrations to migrations that span continents and hemispheres. Flight enables birds to travel great distances and access widely distributed resources, allowing individuals to time their presence with peaks in resource availability and avoid resource scarcity in less productive times of the year. However, tracking resources over space and time has costs. Migration requiring significant fat stores to fuel long sustained flights. Many species utilize stopover sites to replenish depleted fat stores en route. Migrants must additionally contend with adverse weather conditions, unknown food availability, and predator activity during each leg of their journey.

World-wide, migratory birds are experiencing steep declines (Gaston and Fuller 2008, Inger et al. 2015, Stanton et al. 2018, Rosenberg et al. 2019). The ubiquity of these declines across habitats and avian taxa suggests multiple and interacting threats, including climate change

and habitat loss (Rosenberg et al. 2019). But rates of decline are not uniform across populations within individual species (Both et al. 2006). Identifying limiting factors directly causing population declines is especially challenging in migratory species as our knowledge of connectivity between breeding and non-breeding grounds and our ability to delineate biologically relevant populations have been limited (Rushing et al. 2016).

The timing, or phenology, of migration and resource pulses on which birds depend are intricately linked. There is evidence that migration phenology of some species is becoming increasingly mismatched with resource phenology due to climate change (Both and Visser 2001). Spring arrival dates for many migratory birds across the globe have advanced (Lehikoinen et al. 2019). In some cases, these shifts have kept pace with changes in spring leaf-out and insect emergence, while others have led to phenological mismatches (Miller-Rushing et al. 2010, Renner and Zohner 2018). Such mismatches have been linked to population declines in some bird populations, while others experiencing mismatches have yet to exhibit declines (Both et al. 2006, Miller-Rushing et al. 2010, Reed et al. 2013). Thus, increased efforts to understand phenology, demography, and migratory connectivity of interacting species are needed to test hypotheses relating to phenological mismatches and climate driven phenological changes.

Phenological Assignments

Despite a widespread interest in phenology of bird migration over the past 250 years, much uncertainty remains as to how phenology should be measured and characterized (Inouye et al. 2019). Migration phenology is often thought of as a discrete event (i.e., a species arrives to a location; Gordo and Sanz 2005, Inouye et al. 2019) and reported using easily discernible summary statistics including first, mean, and to a lesser extent, last observation dates (Roy and Sparks 2000, Tryjanowski et al. 2005, Lindén 2011, Goodenough et al. 2015, Inouye et al. 2019). Naturalists and bird clubs have recorded first and last seasonal detections of birds dating back

over a century. However, these historical records are often limited to just first detections and provide little information about the timespan of arrival, passage, or departure of species.

Though these measures are easily gleaned from field observations, means and first/last detections present interpretation challenges. Mean dates are often not or only weakly correlated with changes in first/last observation dates (Inouye et al. 2019). First/last observations are additionally sensitive to rare events and can be biased by sampling effort, detectability, and population size (Miller-Rushing et al. 2008, van Strien et al. 2008, Moussus et al. 2010, Inouye et al. 2019, Koleček et al. 2020). Variation in effort or sampling protocols can also make comparisons across time and space problematic, for example by giving the appearance of phenological shifts over time even if the true phenological pattern remains unchanged or vice versa. This is especially true for populations with small or changing sizes (e.g., species of concern), cryptic species, and inconspicuous demographic classes such as females and young (Miller-Rushing et al. 2008, Pearse et al. 2017).

To fully understand a distribution of phenological events, complete observations spanning the full timeline of the event are needed. Such datasets are uncommon and long-term data meeting these criteria are rare (Knudsen et al. 2007, 2011). Factors including inconsistent sampling, low resolution sampling, seasonally truncating data collection, data gaps, and unrecorded effort hamper analysis (Lehikoinen et al. 2004, Knudsen et al. 2007, 2011). Advancements in statistical modeling techniques and increases in data availability (i.e. bird observatories, citizen science observations) have begun to address the limitations of simple summary statistics. Modeling full phenological distributions allows estimation of central tendencies, but also measures of duration, shape, and skewness of phenological events not discernible using first arrival dates and means (Lindén et al. 2017, Miles et al. 2017). Customized modeling frameworks can additionally handle variation in detection probability, observation error, and sampling effort through smoothing or incorporating random effects in the model.

Gaps in Phenological Investigations

Investigations of migratory phenology have been largely focused on broad scale changes in passage dates at the flyway and species-level (Haest et al. 2019, Brisson-Curadeau et al. 2019). Few studies have addressed factors contributing to fall departure from the breeding grounds or quantified population-level differences to phenology. This is due in part to fall migration timing being notoriously challenging to monitor at the individual level. Following breeding, local breeders become less vocal, territories breakdown, adults tend increasingly mobile young, and molt (typically) begins before departure. These impacts to detectability likely obscure true departure dates observed via resighting. The overlap of the autumn equinox with fall migration has also hampered fall phenology studies that use light-level geolocators (Stutchbury et al. 2011). Studies that have successfully documented true departure date from the breeding grounds using automated radio telemetry have noted correlations of departure date with breeding success and weather (Mitchell et al. 2012). However, integration of radio tracking with intensive demographic monitoring remains rare.

Bird banding and ringing at observatories have provided rich, long-term datasets of passage timing and are well suited to observe phenological changes over time (Lehikoinen et al. 2004, Sparks et al. 2005, Knudsen et al. 2007, Miles et al. 2017, Covino et al. 2020). These data represent passage dates of individuals from many distinct populations, each experiencing their own set of en route factors influencing migration timing (i.e., weather systems, stop-overs, route distances; Goodenough et al. 2015, Brisson-Curadeau et al. 2019). Analyzing passage timing within a flyway may provide a benchmark for comparison, however these data are unable to resolve differing phenological shifts between and within individual populations.

Our understanding of bird migration is also largely based on European and eastern North American birds. Bird species of western North American have significantly different life history strategies than their eastern counterparts. Specifically, many western species have molt-

migrations, suspending or delaying their prebasic molt until mid- or post-migration (Carlisle et al. 2009, Pyle et al. 2009, 2018). Eastern passerines typically complete their prebasic molt on or near the breeding grounds before migrating. The topography of western North America also exposes migrants to local clines in climate conditions that would span hundreds or thousands of kilometers in the east. Differences in life history strategies and environmental conditions experienced by eastern and western passerines have potential to influence departure and arrival timings.

To better measure phenology and how it varies, data need to be associated with individual populations, individual IDs need to be known and maintained from arrival to departure, and biases in effort and detectability need to be mitigated. Additionally, arrival and departure phenologies need to be linked to the routes and destinations throughout the full annual cycle to further investigate variation and change through time.

Tracking Avian Movements

Advances and developments of miniaturized tracking technology continue to yield many findings relating to bird migration (López-López 2016, McKinnon and Love 2018). Individually marking birds with numbered metal bands and colored plastic bands have been and continues to be the hallmark of bird tracking. Learning about migration from banding data depends, however, on the low probability of subsequent recapture of marked individuals somewhere along the migratory route, providing sparse information about migratory connectivity between breeding and nonbreeding areas. Global Positioning System (GPS) and satellite tracking have enabled precise location data acquisition on larger species, including raptors, seabirds, and gamebirds. These tracking tags can provide location data with several-meter accuracies at intervals ranging from a few fixes over the tag's lifespan to continuous fixes depending on the battery size and charging ability of the tag. Despite the miniaturization of GPS technology over the past two decades, the

smallest GPS tags are still too large for most small passerines and additionally require return and recapture of tagged individuals to retrieve the stored data (Hallworth and Marra 2015).

Radio tracking has a long history in wildlife studies, including in birds. Radio transmitting tags have short ranges of communication (several hundred meters to several kilometers) and limited battery lives. Use of radio tags is gaining application with development of radio telemetry networks such as the Motus Wildlife Tracking System (Taylor et al. 2017). Unified networks like Motus create multiple opportunities for tagged individuals to be identified by other project receivers. Radio network spanning full ranges of species increase opportunities for tagged individual to be passively “recaptured” during migration and provide greater opportunity to establish population connectivity and investigate migratory phenology. Despite these advantages, radio tag lifespan is mostly limited to several months for small passerines and provide only small windows into avian migration (McKinnon and Love 2018).

Another passive tracking technology is RFID (radio-frequency identification), more commonly used in fisheries sciences as PIT (passive integrated transponder) tags. RFID tags are small, battery-less, encoded tags encapsulated in glass tubes that can be integrated into traditional leg bands or more uncommonly injected subcutaneously. When a tag comes within the read range of an RFID-enabled antenna, the antenna energizes the tag which then emits its unique ID number and is subsequently received by the antenna. The passive nature and small size of RFID tags reduces costs of individually marking and recapturing even the smallest birds, while maintaining a tag lifespan complimentary to the bird. The main drawback of RFID tags is the limited tag read range of a few centimeters, requiring tagged individuals to return to predictable locations to be passively recaptured. Such locations include perches, bird feeders, burrows, nests, or forced travel points like fencing used in penguin colonies. Though limited in scale, RFID tags enable effective and continuous passive monitoring of many individuals.

Light-level geolocation is another tracking option for passerines. These small tags have been placed on increasingly small passerines and record ambient light levels throughout the life of the tag (McKinnon and Love 2018). Times of sunset, sunrise, and solar noon can be deciphered from the geolocators to determine accurate (Hallworth et al. 2013) but imprecise (Lisovski et al. 2018) geographic positions over large portions of the full annual cycle. Geolocators are less weight-limited than GPS tags but share the need for return and recapture to download archived data. Additionally, during the vernal and autumnal equinoxes, geolocators are unable to reliably estimate latitude, limiting interpretations in some species during those periods. Geolocators have gained popularity in migratory studies, including studies of repeatability in migratory route (Stanley et al. 2012), nonbreeding ground identification, variation in migratory duration and stopover use (Cooper et al. 2017), molt migration (Contina et al. 2013, Jahn et al. 2013, Pillar et al. 2016), and migratory connectivity (Tonra et al. 2019).

SPECIES ACCOUNT

The Lazuli Bunting (*Passerina amoena*) is a small, moderate-distance migratory songbird in the Cardinalidae family found in brushy habitats throughout the western United States. Males have brilliant blue and orange plumage, while females are a drabber warm brown with blue hues in older individuals. In the breeding season, this bird ranges from southern California, north to southern British Columbia, and east through the Rocky Mountains, occupying elevations from sea level to above 3000m. Lazuli Buntings winter along the Pacific coast of Mexico and southern Baja (Greene et al. 2020).

In spring, arriving males are often detected before females (protandry), as early as March in the southern portions of its range and as late as mid-June further north (Greene et al. 2020). Lazuli Buntings are socially monogamous, forming pair bonds and sharing in some parental duties (Greene et al. 2020). Females typically build nests in the shrub layer out of grass and other

woven organic matter and lay three to four eggs. Nests are commonly parasitized by Brown-headed Cowbirds (*Molothrus ater*), often resulting in full clutch loss (Greene 1999, Greene et al. 2020). Young are tended to by both parents and fed predominantly insects, contrasting with the mainly seed and fruit diet of the adults (Greene et al. 2020). After fledging, young are variably attended by adults for one to three weeks. Some females may begin a second brood after a successfully fledged first brood. Breeding individuals are thought to depart the breeding grounds before hatch-years, with males appearing, from field observation, to depart slightly before females (Young 1991, Greene et al. 2020).

Song development, hybridization, and cowbird parasitism have been well studied in this species (Greene et al. 2020). However, despite their abundance, wide distribution, and propensity to visit bird feeders, much less is known about their population dynamics, demography, and migratory connectivity. Additionally, little information about wintering ecology or behavior in Lazuli Buntings has been published. Lazuli Buntings are one of several bird species thought to be true molt migrating birds in western North America (Leu and Thompson 2002, Pyle et al. 2009). These buntings begin their prebasic molt on or near the breeding grounds, molting most body feathers, before suspending the molt to migrate to one of two suggested molting areas: the North American Monsoonal area of southern Arizona/New Mexico and northwestern Mexico, and the southern Baja Peninsula (Young 1991, Chambers et al. 2011). Here, buntings are thought to complete their flight feather molt before continuing their fall migration to western Mexico. Though widely cited as a molt migrant with known molting grounds, only two studies have contributed to coarsely defining this critical region for the Lazuli Bunting (Young 1991, Pyle et al. 2009). None thus far have utilized tracking or isotope assignment in this species.

The Lazuli Bunting is a rather representative western North American passerine species. It is far ranging, occupies many habitats, migrates a moderate distance, and has average breeding propensity among its western counterparts. Lazuli Buntings exhibit molt migration, like several

western bird species. This suspended molt isolated from the breeding grounds provides a unique opportunity to study fall migration timing where energetically costly flight feather molt is not a direct factor on departure date. Additionally, Lazuli Buntings can be found, caught, and monitored with relative ease, making them an easily-reproducible study system throughout their range.

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CHAPTER 2

MODELLING MIGRATORY PHENOLOGIES ACROSS AN ELEVATIONAL GRADIENT
CHALLENGES SELECTION-BASED HYPOTHESES FOR A
PROTANDROUS MIGRATION STRATEGY

ABSTRACT

Birds must time their migrations to track spatiotemporally distant resources across their full annual cycles. Understanding drivers of migratory phenology is important for predicting avian population dynamics, especially under climate change. However, accurate estimates of arrival and departure dates are often limited by low detectability of individuals at the start and end of the breeding season due to cryptic behaviors, lower vocalization rates, and shifting territory boundaries. We used digital encounter data of radio-frequency identification (RFID)-banded individuals to quantify migratory phenology of a moderate-distance molt-migrant, the Lazuli Bunting (*Passerina amoena*), across an elevational gradient in Cache County, Utah, USA. The nearly continuous-time monitoring of tagged individuals at RFID-enabled bird feeders, analyzed using a hierarchical Bayesian point-process model, allowed us to accurately estimate group-level arrival and departure phenology while accounting for uncertainty in individual-level presence at the breeding site. We found that buntings breeding at low elevations showed predicted protandrous arrival of males prior females. At high elevations, however, no significant differences were found between males and female arrivals. We found little difference in fall departure date between elevation, sex, or year. These results are consistent with constraint-based hypotheses explaining protandry, possibly related to sex-specific constraints operating during the non-breeding period, and inconsistent with fitness-based hypotheses. We additionally emphasize the need for quantifying uncertainty in phenological estimates and the importance of addressing potential differences across demographic groups.

INTRODUCTION

All organisms must time key biological events, including reproduction, molt, and migration, with peaks in suitable environmental conditions and resources that vary in both space and time (Alerstam et al. 2003, Bauer and Hoye 2014). The alignment, or misalignment, of life history events with resource peaks can have profound effects on individual fitness (survival and reproductive success) and the dynamics of populations (Smith and Moore 2005, Both et al. 2010, Forrest and Miller-Rushing 2010, Reed et al. 2013, Alves et al. 2019, Visser and Gienapp 2019). Shifts in the phenology, both in consumers and the resources they use throughout the annual cycle, are becoming increasingly well-documented (Root et al. 2003, Parmesan 2007, Thackeray et al. 2016), including advancements in spring green-up (Cleland et al. 2007, Piao et al. 2019), insect emergence (Roy and Sparks 2000, Gordo and Sanz 2005), egg laying (Källander et al. 2017, Alves et al. 2019), and migratory passage (Dunn and Møller 2014, Horton et al. 2020, Covino et al. 2020). Such changes are likely to accelerate in the future as climate change causes increasingly profound shifts in temperature and precipitation regimes (Callaghan et al. 2010, Urban 2015).

One area of phenology research that has received considerable attention is the close linkages between the timing of migration and breeding in migratory birds. For these species, migration phenology during both spring and fall is controlled by complex combinations of weather, food availability, and day length cues (Dawson 2008, Tøttrup et al. 2010, Studds and Marra 2011, Klinner and Schmaljohann 2020, Burnside et al. 2021). The timing of migration, in turn, strongly influences resource availability for breeding, fledging young, and preparing for migration (Visser et al. 2004). Early arrival in spring, for example, may expose individuals to adverse weather, limited food availability, and long waiting times before suitable mates are available, while late arrivals may cause a loss of mating opportunities (Møller 1994, Morbey and Ydenberg 2001). In fall, early departure may limit extra mating opportunities while late

departures may expose migrants to adverse weather conditions and decreased resources for migratory preparation (Mills 2005, Newton 2007).

Migratory birds must balance the costs and benefits of migration timing across multiple, distant periods of the annual cycle, a balancing act that is increasingly challenging in the face of changing climates. Both long-term banding data and observational datasets have documented substantial intra- and interspecific variation in the degree to which migratory birds have advanced spring migration timing in response to climate change (Butler 2003, Végvári et al. 2010, Gill et al. 2014, Lehikoinen et al. 2019, Covino et al. 2020, Vitale and Schlesinger 2011, Hurlbert and Liang 2012, Harris et al. 2013), though the causes of this variation remain poorly understood. Even less is known about why and how species are adjusting the phenology of fall migration in response to climate change.

Given the importance of documenting shifts in migration phenology and their impacts on individuals and populations, the ability to accurately measure phenology is central to many questions related to the ecology and evolution of migratory strategies, as well as conservation of migratory birds (Forrest and Miller-Rushing 2010, Gill et al. 2019). Migration phenology has often been described as a discrete event reported using simple summary statistics, including first, mean, and to a lesser extent, last observation dates (Roy and Sparks 2000, Tryjanowski and Sparks 2001, Forister and Shapiro 2003, Tryjanowski et al. 2005, Gordo and Sanz 2005, Inouye et al. 2019, Fric et al. 2020). However, these approximations represent only single point estimates from the full distribution of phenological events that occur across any given population. First and last observation dates, furthermore, are sensitive to rare events, including uncharacteristically early arrivals, and can be confounded by changes in sampling effort, detectability, and population size (Miller-Rushing et al. 2008, van Strien et al. 2008, Moussus et al. 2010, Bertin 2015, Inouye et al. 2019, Koleček et al. 2020).

Advances in modeling and data availability have begun to address the limitations of simple summary statistics by allowing researchers to characterize the full distribution of individual arrival and departures (Miles et al. 2017, Inouye et al. 2019, Edwards and Crone 2020). Estimating the full distribution of migration phenology, in turn, allows for richer inferences about population-level metrics, including central tendencies, duration, shape, and skewness (Knudsen et al. 2007) than are possible using first, last, or mean dates (Lindén et al. 2017, Miles et al. 2017). Advances in statistical modeling can additionally handle issues that arise due to imperfect observations, including variation in detection probability and varying sampling effort that can impose biases on estimations of phenological events (Lehikoinen et al. 2004, Sparks et al. 2005, Knudsen et al. 2007, 2011). Quantifying detection errors and the subsequent uncertainty in individual arrival or departure dates is crucial for accurately characterizing phenology, especially for individuals with low detection probability. Female songbirds, for example, often exhibit cryptic behavior and plumage in spring, making detection of newly arrived individuals challenging (Coppack and Pulido 2009). Both males and females are also difficult to detect prior to fall departure due to territory breakdown, the lack of vocalizations, and cryptic behaviors during molt. These challenges have limited progress on understanding fall migration phenology and female migration phenology more generally (Coppack and Pulido 2009, Gallinat et al. 2015).

Coupled with advances in analytical tools, the rapid miniaturization of tracking technology continues to provide new opportunities for studying the phenology of bird migration (McKinnon and Love 2018). For example, the recent integration of passive radio-frequency identification (RFID) tags, commonly used in fisheries sciences as PIT (passive integrated transponder) tags, within bird leg bands has expanded fine scale tracking of individual passerines (Bonter and Bridge 2011). To date, studies using these bands have generally focused on social and nesting behavioral studies (Bonter et al. 2013, Firth et al. 2018, Bailey et al. 2018, Farine and Sheldon 2019), though this technology has many other possible uses in demography and

phenology investigations. In this study, we used RFID-enabled bird feeders to monitor the daily arrival and departure phenology of a stopover molt-migrant songbird, the Lazuli Bunting (*Passerina amoena*), across two breeding seasons. Data from the feeders provided nearly continuous-time, automated encounter histories, which we used to quantify migratory phenology of male and female buntings breeding along an elevational gradient in northern Utah, USA. We present a novel hierarchical point-process model that uses daily detection data to model individual occupancy states (present on the breeding grounds or absent) while accounting for imperfect detection, which in this case is due to individuals being present but not using the feeders. Daily arrival and departure probabilities for different demographic groups are modeled using parametric distributions, allowing us to characterize phenological timings that have traditionally been difficult to study, including fall departures and female arrivals.

We parameterized our model to test hypotheses about the role of sex and elevation in driving arrival and departure phenology in migratory birds. With regard to arrival phenology, protandry (males arrive, on average, prior to females) has been widely documented in migratory songbirds, though the ecological and evolutionary causes of protandry remain poorly understood (Morbey and Ydenberg 2001). In general, hypotheses about the causes of protandry fall into two primary categories (adapted from Morbey and Ydenberg 2001): hypotheses that assume protandry is selected for due to fitness benefits to early arriving males and/or later arriving females (hereafter “selection”-based hypotheses) and hypotheses that assume protandry results from constraints imposed by selective forces operating at other times during the annual cycle (hereafter constraint-based hypotheses). The elevational gradient at our study site provided a unique opportunity to differentiate between selection-based and constraint-based hypotheses. In particular, buntings have been observed staging locally at lower elevations while waiting for breeding conditions to improve at higher elevations (see discussion). This staging period provides an opportunity for high-elevation birds to time breeding site arrival free from constraints that

might be imposed during the non-breeding season or migration. We therefore predicted that, if there is selection for protandry, male arrival would precede female arrival at both low and high elevations. In contrast, if protandry is the result of constraints, we predicted protandry at low elevations but not at high elevations.

Although sex-related differences in fall departure phenology are less well documented than during spring arrival, we hypothesized that arrival to the prebasic molting grounds in the Sonoran region during the monsoonal rains would be a major driver of breeding-ground departure in Lazuli Buntings (Greene et al. 2020). Based on this hypothesis, we predicted that departure phenology would be similar between sexes and elevations, as all individuals experience similar pressures to make a timely arrival at the molting grounds.

MATERIALS AND METHODS

Study Site and Species

We monitored breeding Lazuli Buntings distributed across an elevational gradient within the Bear River Range of Cache County, UT, USA (41.8° N, -111.7° W). We collected data from April - September, during 2019 and 2020 on two study plots established at low (1450 m) and high (1930 m) elevations, located 24.5 km apart within the same canyon (Figure 2-1). Both study sites provide suitable habitat for Lazuli Buntings but vary in their vegetative composition, with the low elevation site being dominated by non-native grasses and shrubs, while native grasses, sagebrush, and quaking aspen characterize the high elevation site. Males occupy and defend territories throughout the breeding season. Adults typically breed between late May and late June, while some individuals may produce a second clutch into July (Greene et al. 2020).

Lazuli Buntings serve as a good model for studying migratory phenology. This species is a sexually dimorphic, moderate-distance migratory songbird that breeds throughout the western United States and migrates to west-coastal Mexico for the non-breeding season. Though they are

highly omnivorous, Lazuli Buntings readily visit bird feeders when stocked with white millet, making them an excellent candidate species for use of RFID resighting. Lazuli Buntings are also thought to be stopover molt-migrants, completing the prebasic molt at an intermediate molting ground in the North American monsoonal region of northern Mexico and southern Arizona and New Mexico before arriving on the non-breeding grounds (Greene et al. 2020).

Field Methods

At each site we established six RFID-enabled bird feeders spaced 75 m apart in a 2 x 3 grid. Each feeder assembly was mounted on a stationary pole and consisted of a feeder body, two antennas serving as perches, an electronics box housing a battery and circuit board, and a solar panel for remote power (Figure 2-1). All feeders were maintained with white proso millet from before spring arrival (mid-April) through fall departure (mid-September).

We used a combined RFID reader and data-logger similar to that described by Bridge et al. (2019). Each printed circuit board contained an RFID module (UB22270, Atmel Corporation, San Jose, CA, USA), a microprocessor (PIC16F688, Microchip Inc., Chandler, AZ, USA), a memory module (24LC512, Microchip Inc.), a real-time clock (DS1307, Maxim Integrated Products, Sunnyvale, CA, USA), and an SD card slot for data storage. The circuit board's microprocessor emits a carrier wave signal emitted via two loop antennas mounted as perches on the feeder. When passive RFID tags are within range (~3-5 cm), the carrier wave energizes copper coils within the tag, inducing emittance of a unique 10-ascii character code. This code is then received and transmitted by the antenna to the RFID module, where it is interpreted and stored to the onboard SD card with the unique ID and time stamp.

Loop antennas were custom built from coiled wire to produce a target inductance of 1.350 mH, the optimal inductance for RFID detection using this system. Each antenna coil was then wrapped in electrical tape to protect it from moisture and UV exposure. To ensure antennas

and RFID components remained operational, we tested each feeder with a designated RFID tag two to three times per week throughout the season.

We captured and monitored Lazuli Buntings at both study sites from mid-April through late-September in 2019 and 2020. Buntings were captured using a combination of passive and target mist nets and feeder traps. Upon capture each bird was aged and sexed based on criteria from Pyle (1997) and fitted with a federal metal band and a colored 2.6mm diameter plastic band (RFID band) containing a passive integrated transponder (PIT) tag (Eccel Technology, Leicestershire, U.K.). For each bird, we recorded standard morphological measurements, mass, fat, breeding characteristics, and molt status. Once banded, each RFID-marked bird was passively recorded each time it used any feeder within our network, producing a nearly continuous-time encounter record throughout the breeding season.

Analysis

We used the package *feedr* (LaZerte 2020) in R (4.0.3; R Core Team 2019) to organize, clean, and isolate individual feeder visits from the raw RFID data. Single tag reads or reads of the same tag within 30s of each other were considered a single visit. This threshold was selected based on field observations of feeding individuals being displaced temporarily by others without leaving the immediate feeder location (ie. perching on top, or adjacent to the feeder). We then used the *feedr* output to create an encounter history for each individual that consisted of the daily number of observed visits by individual across all feeders within the study sites.

We selected four demographic groups for which to model migratory phenology: males and females at high and low elevations. To isolate locally breeding birds and ensure that migrant or transient individuals did not influence our phenology estimates, we only included individuals in the departure analysis if they were of known sex, were initially marked prior to July 15, and were recorded using a feeder ≥ 10 days during the core breeding period, which we defined as June

15 – July 15. For the arrival model, individuals were included in the analysis if they were marked the prior season and were detected ≥ 10 days between May 15 and July 15. We modelled arrival and departure separately because we did not have sufficient data to estimate survival probabilities between seasons.

Observation Model

We modeled the daily number of visits recorded for each individual, denoted $y_{i,t}$, using a Poisson point process model:

$$y_{i,t} \sim \text{Poisson}(\lambda_{i,t} z_{i,t})$$

where $\lambda_{i,t}$ is the expected number of visits for individual i on day t and $z_{i,t}$ is the true status (present or absent) of individual i on day t . We incorporated daily and individual-level random effects to account for temporal variation and individual heterogeneity in visitation rates:

$$\log(\lambda_{i,t}) = \mu_\lambda + \gamma_t + \epsilon_i$$

$$\gamma_t \sim \text{normal}(0, \sigma_{day})$$

$$\epsilon_i \sim \text{normal}(0, \sigma_{ind})$$

This formulation assumes that the probability of detection given a bird lands on a feeder is 1. In this system, this assumption is likely met, as perching to feed requires a bird to stand on the antenna (distance from PIT tag to the antenna is $< 3\text{cm}$) and the readers scanned for tags every half second.

State Process Models

Each individual i has a true status (present or absent) on each day t that is only partially observable, as individuals can be present at the study site but not using a feeder. To account for this form of imperfect detection, we modeled the latent state variable z as a Bernoulli trial. We modeled arrival as:

$$z_{i,t} \sim \text{Bernoulli} \left([1 - z_{i,t-1}] \alpha_{g[i],t-1} + z_{i,t-1} \right)$$

where $\alpha_{g[i],t-1}$ is the daily probability that an individual in group g arrives between days t and $t - 1$. This formulation ensures that once an individual arrives ($z_{i,t} = 1$), it must remain present for the remainder of the study period. We modeled departure similarly:

$$z_{i,t} \sim \text{Bernoulli} \left([1 - \delta_{g[i],t-1}] z_{i,t-1} \right)$$

where $\delta_{g[i],t-1}$ is the daily probability that an individual in group g departs between days t and $t - 1$. In this formulation, once an individual departs ($z_{i,t} = 0$), it cannot be detected at the feeders for the remainder of the season.

We modeled daily arrival and departure probabilities using survivorship retention curves. Following Pledger et al. (2009), we used a Weibull distribution to model the cumulative daily arrival and departure probabilities for each group:

$$\alpha / \delta_{g,t} = 1 - e \left(- \left[\frac{t+1}{\gamma_g} \right]^{\kappa_g} + \left[\frac{t}{\gamma_g} \right]^{\kappa_g} \right)$$

where γ_g is the scale parameter and κ_g is the size parameter of the Weibull distribution for each demographic group. These parameters can be further used to quantify relevant summary statistics for each group, including daily arrival/departure probability densities and the mean, median, and variance of arrival/departure dates, based on the properties of the Weibull distribution. We modeled group-level variation in phenology by treating the *log* of the Weibull parameters ($\log(\gamma_g)$, $\log(\kappa_g)$) as a normally-distributed random effect with means μ_γ / μ_κ and standard deviations $\mu_\gamma' / \mu_\kappa'$.

We estimated posterior distributions for each parameter using Markov chain Monte Carlo (MCMC) methods implemented in R using NIMBLE (NIMBLE Development Team 2020). We used zero-centered normal priors with standard deviation = 1.75 for all mean parameters (μ_γ , μ_κ , and μ_λ) and half-normal priors with standard deviation = 1.75 for all standard deviation parameters (σ_γ , σ_κ , σ_{day} , and σ_{ind}). In our arrival model, we selected a more diffuse *normal*(0, 5)

prior for μ_y , because initial inspection of the data indicated that timing of first detections differed significantly across the elevational gradient, indicating a potentially wider spread in arrival phenology than departure. For each model, we ran three MCMC chains for 30,000 iterations, discarding the first 5,000 samples as burn-in and thinning by four. For the departure model, we initially estimated separate 2019 and 2020 parameters for each group to assess annual variation in phenology. However, no significant differences were observed between years (Appendix A), so we pooled data from both years in our final analysis.

RESULTS

Across the full two-year study period, we marked a total of 430 Lazuli Buntings with RFID bands. Of these individuals, 286 were estimated to be migrants or non-local breeders based on our filtering criteria, which left 144 unique individuals (56 for arrival and 152 for departure) in our analyses. Over the study period, our feeders recorded 255,553 individual feeder visits made by these 144 individuals (40,563 in the arrival model and 209,990 in the departure model). First detections of breeding Lazuli Buntings at the study feeders spanned from April 29 to June 10 at low elevations ($n = 31$), and May 22 to June 27 at high elevations ($n = 25$), with low elevation breeders first detected approximately two weeks prior to those breeding at high elevation. Last detections at the study feeders spanned from June 30 to August 31 at low elevations ($n = 74$), and June 27 to September 4 at high elevations ($n = 78$).

At low elevation, we found evidence of protandry in arrival dates of males and females. Based on the estimated daily arrival probabilities, 95% percent of male arrivals at low elevation occurred between May 5 and May 13, with a mean arrival date of May 8 ($n = 15$, Table 2-1, Figure 2-2), seven days prior to the estimated arrival of low elevation females ($n = 16$; mean female arrival = May 15; 95% between May 10 and May 21). At high elevations, we found no evidence of protandry, with the estimated arrival distribution of breeding males and females

overlapping significantly (Figure 2-2). Ninety-five percent of high elevation female arrivals were estimated to have occurred between May 21 and May 28, with a mean arrival date of May 26 ($n = 6$). Ninety-five percent of male arrivals were estimated to have occurred between May 23 and June 3, with a mean of May 28 ($n = 19$). In the case of high elevation female arrival, the small sample size, combined with little variation between individuals in first feeder detections (all 6 were detected within four days of one another), resulted in a very narrow arrival curve and caution is warranted in interpreting results from this group.

Estimated daily departure probabilities broadly overlapped between all demographic groups (Figure 2-3, Table 1-1). The majority (95%) of estimated low elevation male departures occurred between August 10 and August 14 (mean = August 12, $n = 39$) and that of low elevation females spanned August 1 to August 11 (mean = August 6, $n = 36$). Similarly, 95% of estimated high elevation male departures spanned August 2 and August 9 (mean = August 6, $n = 54$) and that of high elevation females occurred between August 8 and August 18 (mean = August 13, $n = 23$).

At the individual level, model-estimated arrival and departure dates did not differ significantly from the first and last detections at feeders, suggesting that buntings were likely to use feeders soon after arrival and up until departure. The mean estimated departure dates were one day later in low and high elevation females and two days later in low and high elevation males than the mean observed feeder departure date (i.e., the last day observed). The estimated mean arrival dates were one day earlier than the mean feeder arrival dates of all groups except high elevation females, where the model estimated the same mean arrival date as the feeder.

DISCUSSION

We developed a flexible modeling framework for assessing differences in phenological dynamics between related, but distinct, population segments of a migratory bird using RFID

encounters at bird feeders. By leveraging continuous-time encounter data, this framework allowed us to estimate individual migratory phenology with high resolution, including arrival phenology of females and departure phenology of all groups, two instances in which estimation using traditional survey methods is challenging. The parametric parameterization of the arrival and departure models, combined with hierarchical structure that leverages data from different demographic groups, allowed for straightforward comparisons of different phenologies while simultaneously quantifying uncertainty at both the individual and group-levels. To our knowledge, quantifying the full, daily distribution of migratory phenology has not been previously investigated at this resolution in migratory birds, or at any scale for a passerine considered to be a stopover molt-migrant.

Within our breeding population of Lazuli Buntings, we found evidence of protandry at low, but not at high elevations. The small geographic scale of this elevational gradient provides a unique evaluation of the causes of protandry. At low elevations, the degree of protandry was consistent with previous research on arrival phenology of migratory passerines, which has generally found that male arrival precedes female arrival by several days to two weeks (Bauböck et al. 2012, Hedlund et al. 2015). Many hypotheses have been formulated to explain differences in arrival between the sexes, with each hypothesis receiving some empirical support (reviewed by Coppack and Pulido 2009).

The majority of empirical studies of protandry in birds have focused on selection-based hypotheses, including the “rank-advantage” (Ketterson and Nolan 1976, Myers 1981) and “mate-opportunity” (Wiklund and Fagerström 1977, Bulmer 1983, Iwasa et al. 1983, Parker and Courtney 1983) hypotheses. Under these hypotheses, early arrival by males increases fitness via more and better choices of high-quality breeding territories (rank-advantage hypothesis), whereas later relative arrival by females provides a larger pool of mates to choose from and provides males with more potential mating opportunities (mate-choice hypothesis; Morbey and Ydenberg

2001, Kokko et al. 2006, Møller et al. 2009). Like most migratory passerines for which there is support for selection-based hypotheses, Lazuli Buntings are socially monogamous and territorial, suggesting that protandry may confer fitness benefits for early arriving males. However, the pronounced lack of protandry we observed at high elevations, relative to that observed at low elevations within the same local population and year, raises questions about the generality of selection-based hypotheses in explaining protandry.

Constraint-based hypotheses suggest protandry ultimately results not from selective forces that increase breeding-season fitness, but rather from a limit, or constraint, on an individual's possible arrival time. Such constraints may result from internal factors, including body-size-related temperature tolerances ("susceptibility" hypothesis; Ketterson and Nolan 1983, Francis and Cooke 1986), sex-specific variation in the ability to refuel on migration, or from external factors such as non-breeding habitat quality or range segregation between age or sex classes (Ketterson and Nolan 1976, Norris et al. 2005). If protandry resulted from differential susceptibilities, such as cold tolerance between males and females, we would again expect males, which have slightly larger body sizes than females, to arrive earlier than females at high elevations, as they did at low elevations. Instead, our results are most consistent with constraint-based hypotheses that assume protandry is the result of sex-specific constraints operating during the non-breeding or migratory periods.

At low elevations, buntings at our study site arrived well after snow melt and initiated breeding soon after arrival. High elevation breeders, in contrast, appeared to arrive locally at lower elevations before their breeding sites were clear of snow, and anecdotal observations from our data and fieldwork suggest these birds staged at low elevations while waiting for breeding sites to become suitable at higher elevations. During the spring arrival period, large numbers of buntings were banded at our low elevation feeders, but RFID encounters indicated that the majority of these birds "departed" the low elevation site at about the same time that arrival began

at high elevations. Our feeders also recorded the presence of one confirmed, high-elevation breeding male at our low elevation site, starting on May 20 and over several more days prior to its departure from the low elevation site and arrival at the high elevation site on the same day, May 25. Thus, even if protandry is evident in local arrivals at low elevation staging areas, differences in staging duration between males and females may dilute protandry upon arrival at the final breeding site. If protandry is favored by selection, males could move upslope as conditions improve during spring and females could continue to stage until males had established territories at high elevations. However, neither of such strategies were observed in our study system.

If protandry provides little fitness benefits, the degree of protandry we observed at low elevations may be explained by constraints outside of the breeding season. Migratory constraints may include differential migrations or differential habitat qualities between sexes, where one sex may occupy closer or higher-quality nonbreeding habitats, or one sex may have faster or more efficient spring migratory progression. In either case, differences in constraints between sexes would facilitate earlier breeding arrival on the regional scale. Further research focusing on tracking migration differences between sexes could provide additional insight into causes of arrival constraints in this species. Additional seasons of data collection under varying climate and snow-melt conditions could also provide further insights into this system.

We found little evidence for differences in departure dates between years, sex, or elevational groups, with our model estimating broadly overlapping group-level departure probabilities. Although a number of factors, including reproductive effort (double brooding and reneating), brood rearing, weather, and climate, may influence individual departure decisions, we propose that the similarity between groups in this study is the result of constraints on the timing of annual prebasic molt (e.g., molt constraint hypothesis, Nilsson and Svensson 1996). Lazuli Buntings are thought to be stopover molt-migrants (Greene et al. 2020), suspending their prebasic molt on the breeding grounds and then moving to the North America monsoonal regions of

southern Arizona and New Mexico and northern Sonora, or the southern tip of Baja California, where flight feathers are molted prior to completing their migration their non-breeding grounds. Molt-migration as a life history trait allows birds to take advantage of temporally abundant resources in the monsoonal regions, which are hypothesized to be of higher quality than those available to them during the arid late summer on the breeding grounds (Pageau et al. 2020). As molt-migrants, all individual buntings at our sites likely experience similar pressures to arrive on the molting grounds during the brief flush of resources that occurs during the monsoons, and thus individuals from a given breeding site should depart at roughly the same time in the fall. If this is the case, we hypothesize that departure phenologies of obligate molt-migrants with specific, species-level molting locations are primarily constrained by waiting costs; that is, molt-migrants may time their departure to balance the costs of arriving too early to the molting grounds (prior to the monsoons) with the costs of staying on the increasingly senescing breeding grounds.

Group-level departure phenologies were similar between demographic groups in our system, but within groups there was substantial variation among individuals. Fall departure patterns, although less studied than spring, have been found to be more variable and more weakly correlated with age and sex than those in spring (Swanson et al. 1999, Morris and Glasgow 2001, McKinnon et al. 2016), likely because fall migration is considered less time-constrained than spring migration (Mills 2005, Haest et al. 2019). Correlations between fall departure phenology and climate factors (i.e., temperature, wind, storms, etc.) have previously been documented (Haest et al. 2019). However, the close proximity of our study sites exposed individuals to similar climate and weather patterns, even between elevational sites. Parental investments late in the breeding season have been found to delay breeding ground departures in a number of migratory passerines, including Wood Thrushes (*Hylocichla mustelina*; Stutchbury et al. 2011), Savannah Sparrows (*Passerculus sandwichensis*; Mitchell et al. 2012), female Horned Larks (*Eremophila alpestris*; de Zwaan et al. 2019), and female Barn Swallows (*Hirundo rustica*; Saino et al. 2017).

We were unable to measure individual-level productivity of birds included in this study, but as a facultative double brooding species, we suspect that the observed variation in individual departure probabilities may reflect heterogeneity in reproductive effort and success.

In addition to reproductive effort, age is likely to have important consequences for both arrival and departure timing. The influence of age on arrival timing has been relatively well documented, with older individuals generally arriving to the breeding grounds prior to younger ones (Francis and Cooke 1986, Morris and Glasgow 2001, Stewart et al. 2002). However, because we only included individuals originally banded as second-year (SY) and after second-year (ASY) in our arrival analysis, all returning individuals were ASYs and thus age is less likely to be an important driver of individual-level arrival variation in our data. The influence of age on fall departure has been less well-studied, and variation between SY and ASY individuals may have contributed to the observed variation in departure phenology, especially if age covaries with reproductive effort and success. Larger sample sizes, especially when combined with reproductive monitoring, are needed to address these questions, and our modeling framework provides a flexible means for incorporating these and additional covariates if data is available.

The continuous-time data collected in our study system allowed for very high-resolution estimates of migratory phenology. Unlike data from field observation or passive bird capture efforts, the RFID feeders recorded encounters without data gaps or changes in detection bias over the season. Thus, we believe our estimates of arrival and departure dates are closer in value to the true phenological dates of the population than those that would have been estimated using traditional direct resighting and passive capture methods. Our estimated arrival and departure dates were similar to the first and last dates of birds recorded using the feeders, with means of estimated arrival being 0 to 1 day prior to first feeder use date and estimated departure being 1 to 2 days after the last feeder use date. Though the difference between estimated and feeder-recorded arrival and departure did not differ greatly, the slightly larger difference in estimated vs.

observed departure dates is noteworthy. Detection of individuals post-breeding is often significantly lower than during the breeding season, likely being reduced by decreased territorial defense, tending to mobile young, and behavioral changes due to molting or pre-migratory fattening. Our model may reflect some of these changes in encounter probability by estimating slightly later departure dates than last feeder use. Given the high detection probability of our feeders, we suspect that the difference between observed and modeled phenology of individuals, especially in departure, would be much greater when using resighting methods versus our RFID detections, underscoring the importance of explicitly accounting for uncertainty in phenology studies.

Our model makes a number of assumptions that are critical to interpreting our results. In addition to conventional assumptions of capture-mark-recapture models (distributional assumptions are valid descriptions of the data generating processes, no tag loss, encounters of individuals are independent), our model also assumes that individuals only leave the site due to migratory departure, and not due to emigration or death. Our filtering criteria - only including individuals with 10 or more days of detections during peak breeding season - was used to remove transient individuals. However, we cannot be sure this filtering eliminated all non-breeders, mortalities, or individuals that permanently emigrated during the breeding season. Some of the earliest observed departures, for example, may have been due to mortality or within-season emigration resulting from early nest failure, mate loss, or within-season altitudinal migrations. With additional years of data, the modeling framework presented here could be expanded to simultaneously model arrival and departure phenology and differentiate between migration departure and permanent loss due to emigration or death. If data are available, the model could also be extended to include site-level covariates such as daily weather conditions, and individual-level covariates including reproductive status or body condition.

To date, research on avian migration phenology has been disproportionately based on migratory passage data from bird observatories (Francis and Cooke 1986, Chandler and Mulvihill 1990, Stewart et al. 2002, Covino et al. 2020, Rousseau et al. 2020). These data sample individuals mid-migration, from multiple populations--each of which may be subject to unique factors contributing to their migration timing--where the relationship between passage date and breeding arrival is often unknown (Jonzén et al. 2006, Knudsen et al. 2007, Haest et al. 2019). Without population assignments for individual birds, conclusions from observatory data are limited to broad species- or flyway-level trends which, although useful, likely overlook and dilute differences in migratory phenology at the population and individual levels. Though the findings from these studies have provided important insights into phenological processes and long-term benchmarks by which to investigate phenological changes over time, they lack the individual-level data necessary to directly test hypotheses about phenological drivers. Intensive studies have made steps towards identifying the influence of breeding season carryover effects (Stutchbury et al. 2011, Mitchell et al. 2012, Saino et al. 2017) and timing of flight feather molt (Stutchbury et al. 2011, Borowske et al. 2017) on migration timing. However more research is needed to further characterize these effects and explicitly differentiate between arrival to local stopover or staging sites and breeding-sites.

As we demonstrate here, individual-level studies may be particularly fruitful in montane systems where large differences in plant and insect phenologies exist within a single population experiencing the same regional weather and climate patterns. We also urge researchers to consider, and where possible to quantify, uncertainty in arrival and departure phenology, at both the individual and population-levels. Proper accounting of uncertainty, especially for individuals or groups that are difficult to detect, is critical to accurately characterizing processes such as phenological mismatches, and to predicting responses of populations to future climate change. Thus, it is imperative we improve our understanding of variation in phenological responses and

integrate our understandings in the context of species life history traits and landscape heterogeneity, to recognize and pinpoint needs for conservation throughout the full annual cycle.

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TABLES AND FIGURES

Table 2-1. Estimated distribution parameters and derived arrival and departure dates by sex and elevational group of Lazuli Bunting (*Passerina amoena*). Estimated Weibull shape (k) and scale (g) are median values with associated 95% credible intervals in parentheses. Estimated phenological dates are calculated as days since 21 April.

			Phenology Dates					Weibull Parameters			
			n	Mean	Median	SD	95% CI	k		g	
Arrival	Low	Male	15	17.84	17.70	1.98	(14.35, 22.02)	2.75	(1.73, 3.94)	20.00	(16.15, 24.74)
		Female	16	24.63	24.52	2.67	(19.76, 30.17)	2.51	(1.65, 3.47)	27.68	(22.22, 33.92)
	High	Male	19	37.97	37.97	2.67	(32.74, 43.20)	3.74	(2.643, 4.94)	42.05	(36.57, 47.62)
		Female	6	35.36	35.51	1.09	(32.79, 36.93)	27.05	(6.90, 55.98)	36.26	(34.52, 38.11)
	Population		56					5.11	(1.20, 13.02)	31.01	(18.86, 48.46)
Departure	Low	Male	39	113.70	113.75	1.17	(111.26, 115.82)	20.24	(14.83, 26.19)	116.81	(114.81, 118.79)
		Female	36	107.61	107.70	2.43	(102.61, 112.13)	9.27	(6.88, 11.80)	113.56	(109.08, 117.86)
	High	Male	54	107.39	107.46	1.70	(103.89, 110.52)	10.78	(8.36, 13.46)	112.59	(109.55, 115.60)
		Female	23	114.53	114.61	2.69	(109.03, 119.54)	10.89	(7.59, 14.43)	120.07	(115.176, 125.06)
	Population		152					11.26	(2.69, 20.83)	8.31	(3.15, 22.18)

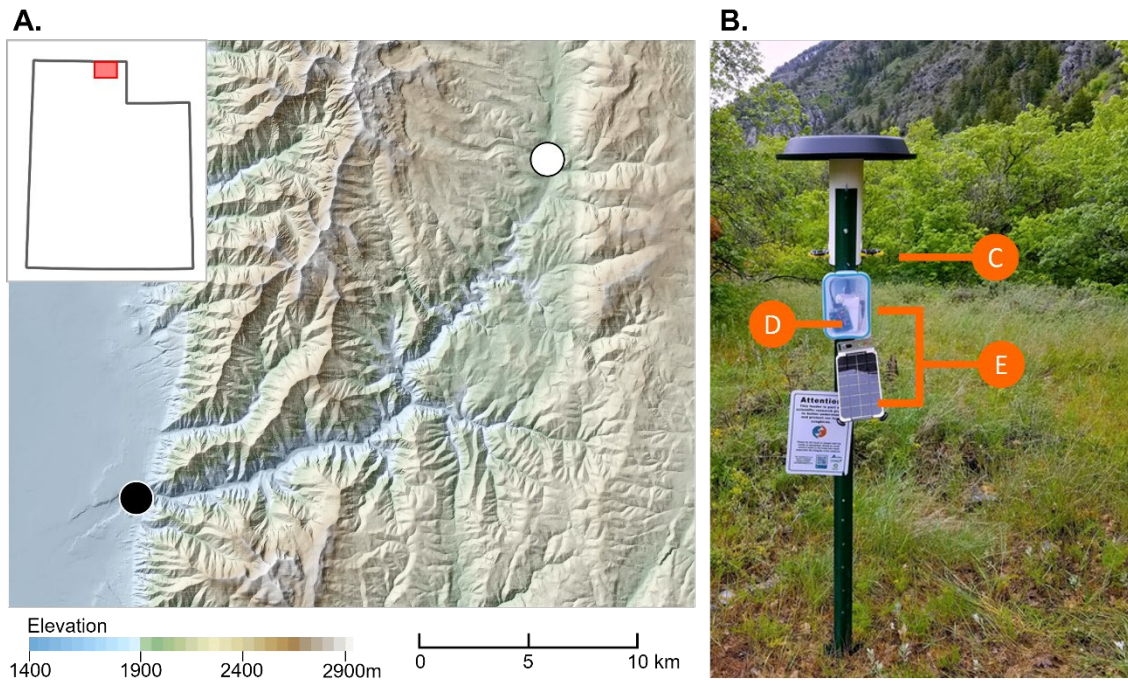


Figure 2-1. (A) Map of low and high elevational capture sites of Lazuli Buntings (*Passerina amoena*) and (B) design of study bird feeders. Low elevation (black, 1450m) and high (white, 1930m) elevation capture sites in northern Utah, USA were separated by a distance of 24.5km, and an elevation difference of 480m. The RFID feeders consisted of a PVC feeder tube mounted on a stationary pole with antennas (C) located on the feeder perch, an RFID interpreting circuit board (D), and a solar panel and battery pack (E).

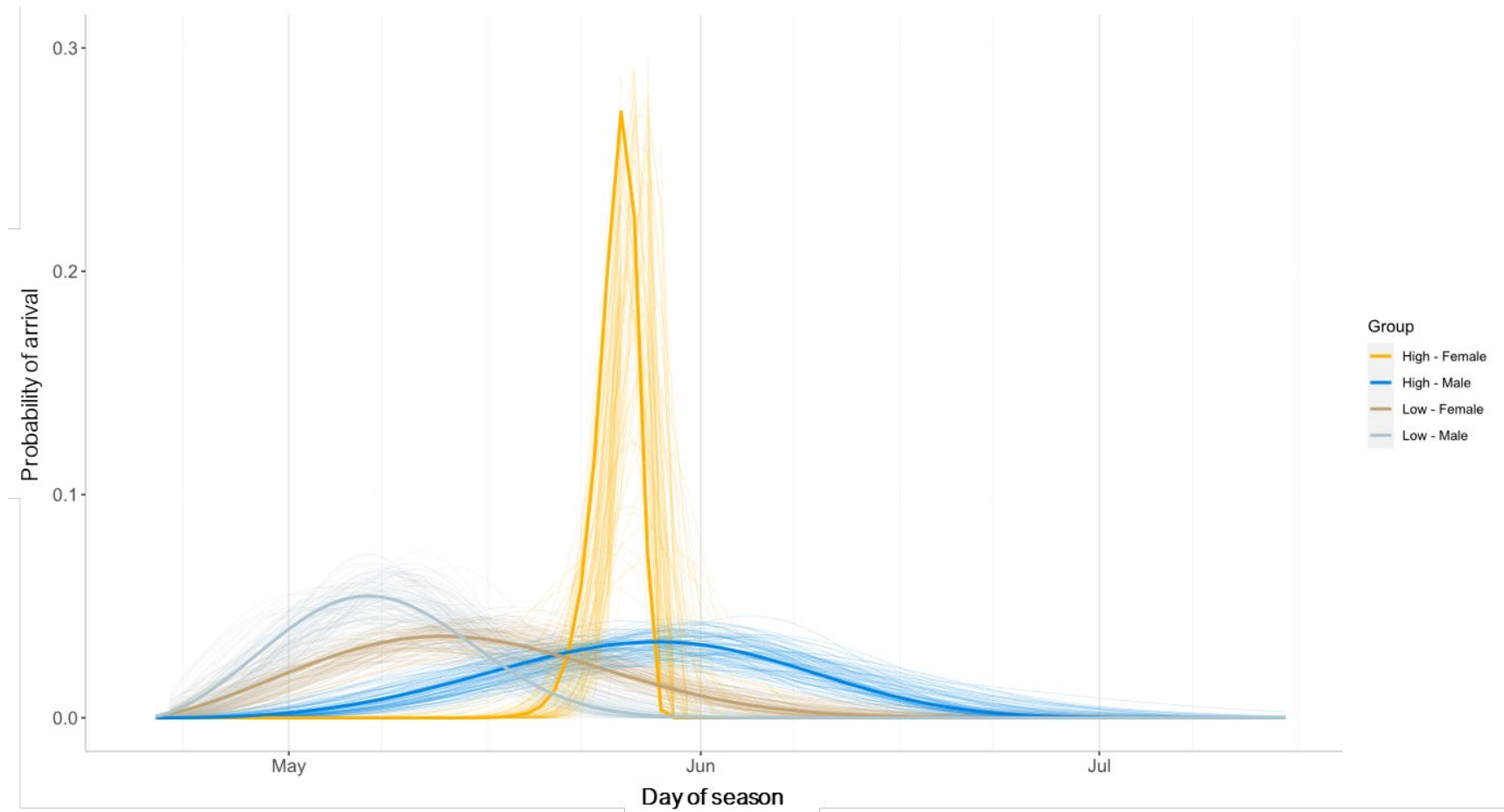


Figure 2-2. Estimated daily arrival probabilities of male and female Lazuli Buntings (*Passerina amoena*) breeding at low and high elevations in northern UT, USA in 2020. Thin lines represent 100 random samples from the posterior, while the thicker lines represent the mean of all samples.

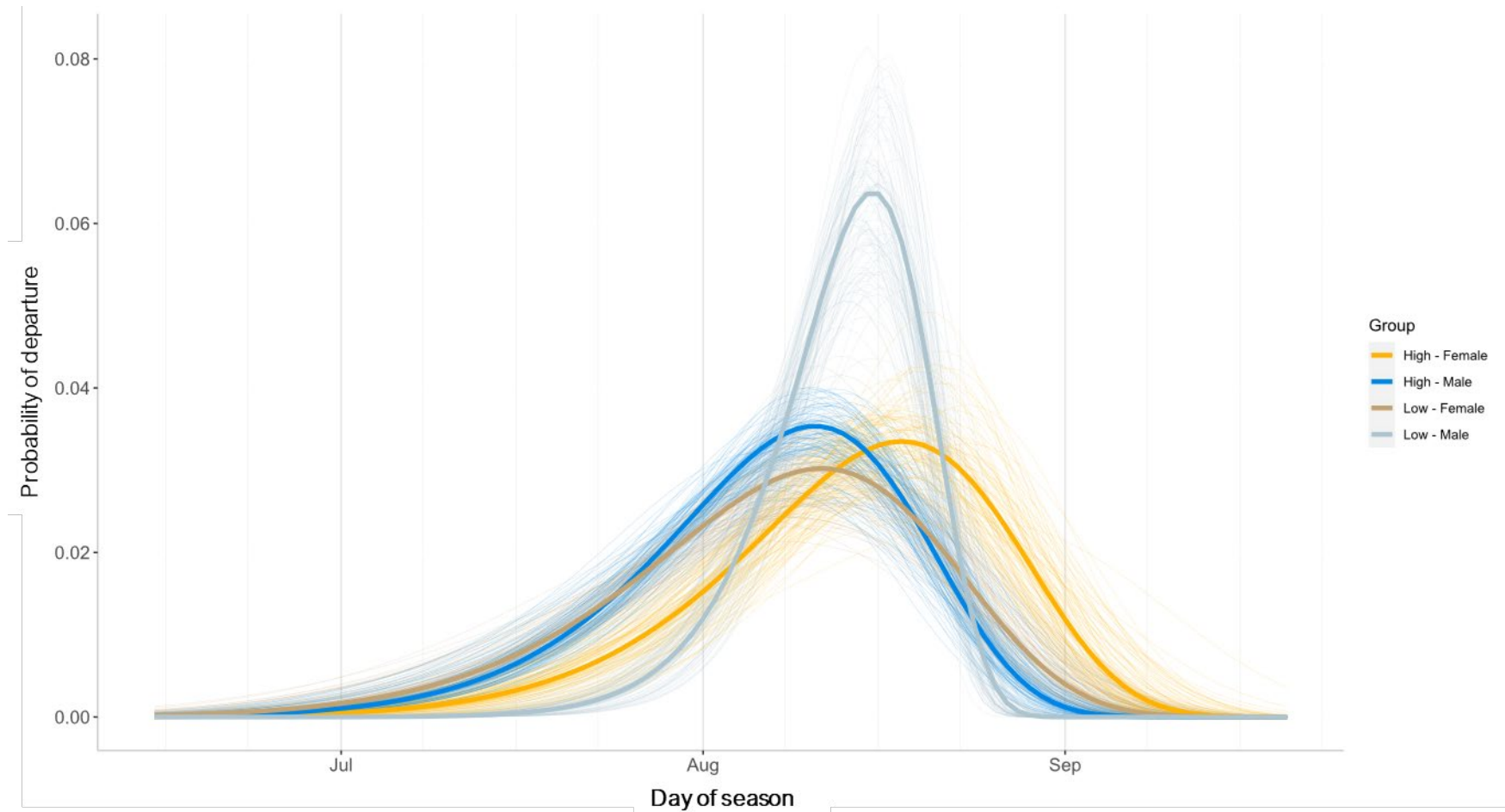


Figure 2-3. Estimated daily departure probabilities of male and female Lazuli Buntings (*Passerina amoena*) breeding at low and high elevations in northern UT, USA during 2019 and 2020. Thin lines represent 100 random samples from the posterior, while the thicker lines represent the mean of all samples.

CHAPTER 3

GEOLOCATORS REVEAL DIVERSITY IN MOLT AND MIGRATION STRATEGIES
WITHIN A SINGLE POPULATION OF LAZULI BUNTING**ABSTRACT**

The Lazuli Bunting (*Passerina amoena*), like many western North American passerines, is thought to be a stopover molt-migrant that uses seasonally-abundant resources in the North American monsoonal region to complete its annual prebasic molt. However, low molting site fidelity and low proportions of molting of individuals recaptured within the monsoonal region point to uncertainty in whether stopover molt-migration is an obligate or facultative strategy in the species. During the 2019 breeding season, we deployed archival light-level geolocators on adult male Lazuli Buntings in northern Utah, USA to identify potential molting and non-breeding areas used by this population. Out of five recovered geolocators, only one individual showed evidence of a sustained stopover of adequate length to complete a prebasic molt during fall migration. The remaining individuals were not stationary during the molting period and may have undergone some molt while migrating or on the non-breeding grounds. All five birds wintered in western Mexico, with four birds wintering along the Sonora-Sinaloa border and one in Durango. On spring migration, three birds took direct routes towards the breeding grounds, while two birds followed a distinct clockwise, looped pathway through California and Nevada. Despite differences in spring migration distance, no significant differences in non-breeding departure or breeding ground arrival were observed between individuals. The difference in spring routes may represent individual-level tradeoffs between time, distance, and resource availability en route. Our results highlight the importance of further investigating the migratory connectivity of suspected molt-migrating species, not only in the traditional breeding to non-breeding sense, but

also in connectivity of populations to molting areas and along migratory routes to best identify areas of possible conservation priority.

INTRODUCTION

Billions of birds migrate annually between spatially distinct geographic areas used to complete the phases of their full annual cycles--including breeding, molt, and non-breeding (Hahn et al. 2009, Dokter et al. 2018). Each of these phases is energetically costly and must be timed to coincide with peaks in resource abundance that vary spatially and temporally. As a result, changes in performance or timing during one phase can carry over to influence performance during subsequent phases, creating trade-offs in the time or energy invested in each phase. Together, these tradeoffs define when and where breeding, molt, and migration take place. Migratory birds have evolved a wide range of movement and life history strategies to accomplish these tasks. Unfortunately, documenting the full range of these strategies within and between species has historically been challenging due to logistical and technological constraints, which have limited our understandings of avian migration and in turn have limited effective conservation planning for these species (Small-Lorenz et al. 2013, Marra et al. 2015, Hewson et al. 2016).

In the last decade, rapid advances in animal tracking have provided opportunities to fill knowledge gaps related to avian movement and ecology, revealing novel insights into the complexity of annual cycles. The miniaturization of tracking technologies, including light-level geolocators, radio, and GPS tags, has allowed researchers to follow increasingly smaller bird species throughout their full annual cycles (Bridge et al. 2013, McKinnon et al. 2013a, McKinnon and Love 2018). These tags have helped identify species-specific wintering locations (Cooper et al. 2017, Tonra et al. 2019), estimate stopover periods (Stutchbury et al. 2011, Callo et al. 2013, Van Loon et al. 2017), identify geographic regions of high mortality risk (Rushing et al. 2021),

characterize migratory routes (Åkesson et al. 2012, Gill et al. 2014, Klvaňa et al. 2018, van Bemmelen et al. 2019), and link life history events throughout the full annual cycle (Tøttrup et al. 2012, Stanley et al. 2012, Delancey et al. 2020). Data from miniaturized tracking devices have also revealed unexpected complexities throughout the annual cycle of migratory birds. For example, many species have been found to engage in loop migrations, using spatially distinct routes during spring and fall migrations (Willemoes et al. 2014, Bradley et al. 2014, DeLuca et al. 2015, Briedis et al. 2018). Although researchers often assume species have only two stationary periods during the annual cycle (breeding and non-breeding), some species, including Bobolinks (*Dolichonyx oryzivorus*; Renfrew et al. 2013), Red-backed Shrikes (*Lanius collurio*; Tøttrup et al. 2012), and Red-eyed Vireos (*Vireo olivaceus*; Callo et al. 2013), appear to have prolonged stopover events of two or more months prior to arriving at a final destination, and still others appear to make long distance movements within the “stationary” breeding (Rohwer et al. 2009, Baldassarre et al. 2019, Cooper and Marra 2020) and non-breeding seasons (Stach et al. 2012, Fraser et al. 2012, Jahn et al. 2013b, Heckscher et al. 2015). Variation in migratory strategies has also been observed between years and individuals (Stanley et al. 2012). Despite these many novel insights, much remains unknown about interacting phases of the annual cycle in the majority of bird species.

One group of birds whose annual cycle remains particularly understudied are those inhabiting arid western North America. In this region, spatial and temporal variability in food and water availability resulting from topographic heterogeneity are thought to have contributed to the formation of complex seasonal movement patterns (Leu and Thompson 2002), including altitudinal migration (Wiegardt et al. 2017b; 2017a, Hedley 2019) and molt-migration (Leu and Thompson 2002, Pyle et al. 2018). Molt-migration, broadly defined as the overlap of feather molt with migratory movements (Tonra and Reudink 2018), has recently been suggested as a widespread fall migration strategy in western birds (Pyle et al. 2018). For these species, molt may

be suspended until arrival on the wintering grounds (Pérez and Hobson 2006), may take place continually throughout migration (Stutchbury and Rohwer 1990), or may be undertaken at a distinct stopover location between the breeding and non-breeding grounds, with the latter of being suggested for many western North American passerines (Jahn et al. 2013a, Siegel et al. 2016, Pillar et al. 2016). This molting strategy contrasts with those of eastern passerines which generally molt on the breeding grounds and migrate directly to their non-breeding areas (Pyle 1997). In western North America, it is thought that increasingly arid conditions in late summer may “push” individuals away from breeding areas due to declining food and water resources in favor of molting in the North American monsoonal region (NAM; Comrie and Glenn 1998), where late summer rains produce a flush of productivity needed to grow high quality feathers (Rohwer and Manning 1990, Young 1991, Rohwer et al. 2005, Pageau et al. 2020).

Research on the migration ecology of western molt-migrations has only been undertaken in a handful of species. Much of our initial understanding of which species molt-migrate and to where stem from observations and museum collections of molting birds in the NAM during late summer and early fall (Hutto 1985, Young 1991, Butler et al. 2002, Rohwer et al. 2007, Chambers et al. 2011). To date, few direct tracking studies focused on molt-migration have been conducted, leaving hypotheses about stopover molting behavior and locations largely untested for most suspected molt-migrating species. From the limited number of direct tracking studies on western molt-migrants, most have found evidence of stopovers within the monsoonal region that are long enough for molt to occur (Contina et al. 2013, Jahn et al. 2013a, Siegel et al. 2016, Pillar et al. 2016). Annual variation in capture rates and molting status of museum specimens suggest however, that molt-migration may be facultative at the individual or species level (Pyle et al. 2009, 2018). Describing the patterns of and propensity for molt-migrations in western North American birds therefore remains a high priority for understanding evolutionary, ecological, and

demographic consequences of avian molt and how it interacts with other stages of the annual cycle.

In this study, we used archival light-level geolocators to track the annual migration of Lazuli Buntings (*Passerina amoena*) breeding in northern Utah. Although this species is a widely distributed breeder across the western United States, research on its molt and migration patterns remains limited. Some have hypothesized that Lazuli Buntings are obligate stopover molt-migrants (Greene et al. 2020, but see Young 1991), completing their definitive prebasic (or pre-supplementary molt in the case of hatch-year individuals) within the NAM or Baja Peninsula prior to arrival on the final non-breeding grounds. This hypothesis, which is primarily based on banding data and specimens collected within the NAM, has yet to be tested with direct tracking data. Here we describe the details of the fall and spring migratory routes and phenology exhibited during a single season of tracking individuals from the same age class, sex, and breeding population to determine whether their migrations are consistent with the hypothesized stopover molt-migration of the species. We discuss possible factors that may contribute to heterogeneity in route, timing, and distance within a single population of breeding birds.

MATERIALS AND METHODS

Study Site and Species

This study was conducted at two sites across an elevational gradient within the Bear River Range of Cache County, UT, USA (41.8° N, -111.7° W) where Lazuli Buntings are a common breeding bird. Habitats varied in composition across the 480m elevational gradient from non-native grasses and shrubs at low elevations (1450 m) to grasses, sagebrush, and quaking aspen characterizing the high elevation site (1930 m). Individual birds at these study sites had *ad libitum* access to bird feeders throughout the season as part of a migratory phenology study using RFID (radio-frequency identification) leg bands (see Chapter 2).

Geolocator Deployment and Recovery

In 2019 we captured Lazuli Buntings at both study sites using mist nets set around either audio lures and decoys, or baited bird feeders. Upon capture each individual was fitted with a federal metal band and a 2.6mm diameter plastic band (RFID band) containing a passive integrated transponder (PIT) tag (Eccel Technology, Leicestershire, U.K.). Each captured individual was aged and sexed according to Pyle (1997), and we recorded standard morphological measurements, mass, fat, and breeding characteristics. A subset of captured males ($n = 25$) were fitted with archival light-level geolocators (Migrate Technology, Coton, Cambridge, UK) using an adjustable leg-loop harness, where the tag and harness did not exceed 4% of the bird's mass. Harnesses were constructed of polypropylene stretch cord (1mm Stretch Magic®, Pepperell, MA) and were custom sized to each bird using crimp beads. Once banded, RFID-marked birds were passively recorded each time they used a feeder within our study network, producing a nearly continuous-time encounter record. These automated resightings provided additional knowledge used in defining location calibration dates as well as possible comparisons to arrival and departure timings estimated using geolocators.

Returning individuals with geolocators were recaptured the following breeding season (2020) using manually triggered wire feeder traps or mist nets. Upon recapture, we removed geolocators for data retrieval. Due to limitations of interpreting light-level data and tag battery life, data gaps surrounding both vernal and autumnal equinoxes, as well as gaps or inconsistencies in data from dates towards the completion of the spring migratory period (end of battery life) were expected.

Geolocation Analysis

Prior to analyzing the light-level data, we processed and log-transformed light values in R 4.1.0 (R Core Team 2019) using the *TwGeos* package (Lisovski et al. 2016). We then used the

Solar/Satellite Geolocation for Animal Tracking (*SGAT*) package (Sumner et al. 2009, Wotherspoon et al. 2013) to determine times of sunrises and sunsets (twilight events). We used a light threshold value of 0.8 within *SGAT*'s `processLight` function, where sunrise and sunset events were defined as light levels rising above or falling below this user-defined threshold value. To identify outlier and clean twilight event data, we ran the `twilightEdit` function using the following criteria: (1) the daily twilight event times had a time difference of 45 min or greater from twilight times ± 2 days of a suspected outlier, and (2) the daily twilight event times of those surrounding days (± 2 days) occurred within 25 min of one another (Lisovski et al. 2016). To calibrate each tag, we estimated two sun zenith angles representing breeding and wintering periods for each individual (McKinnon et al. 2013b), where RFID encounter data was used to define known breeding site occupancy dates, while stationary winter periods were estimated from December 1 through March 31 to exclude any post molt-migration or pre-spring migration movements. Sun zenith angles for the breeding season were adjusted in cases where estimated geographic position differed from known site occupancy from RFID encounters. This is likely due to the reduced number of potential calibration days from late season geolocator deployments. In these cases, zenith angles were manually adjusted to reflect the individual's known location.

We estimated geographic positions from twilight events in a Bayesian framework within the *SGAT* package, where we used a movement model to define probable flight speeds (gamma distribution, mean = 1, SD = 0.08) and a land mask to limit the probability of stationary locations to land. We used a custom land mask restricted to the geographic range of the Lazuli Bunting, while including the Gulf of California. This was done to reduce extraneous locations estimated during the equinox to the known range of the species and to reduce bias in wintering locations and movement between the Baja Peninsula and coastal mainland Mexico. For each individual, we generated a posterior distribution, from three successive MCMC runs consisting of one, three, and one chain respectively of 3,000 samples with thinning by 20. Location summaries from the

previous run were used to initialize each successive model run. The final location estimates were used to infer geographic position and estimate stationary periods of each individual throughout the life of the tag.

We estimated migratory routes and timing using the MigSchedule function within the *LLmig* package (<https://github.com/MTHallworth/LLmig.git>). The MigSchedule function uses a change point analysis based on mean latitudinal and longitudinal estimates to determine stationary locations with uncertainties. The posterior location estimates and accompanying uncertainty were used to determine geographic locations during stationary periods that lasted >3 day. Because latitude estimates around the equinoxes can be unreliable, we excluded latitudinal movements occurring within 7 days on either side of each the vernal and autumnal equinox. To generate the most probable migration route, we used a three-day moving window average of median locations weighted by location uncertainty. We calculated the great-circle distance between breeding and nonbreeding locations to represent the minimum migratory distance for each individual. We additionally measured a conservative migration distance for each bird by summing the great-circle distances between the breeding location, either the east or west most intermediate point during migration, and the nonbreeding location. All values are reported as mean \pm 1 SD.

RESULTS

Bird Recaptures

During the 2020 recapture season, our RFID feeder network recorded the presence of six birds tagged with geolocators in 2019, one of which was recorded on only a single day and was presumed to have bred outside the study area. We recaptured the remaining five birds and recovered geolocators from each (20% recovery rate), among which we experienced no tag failure and no tag loss. Return rate of birds marked with RFID bands only as observed through

feeder encounters, was 40.2% (n=80). Mass of geolocator-tagged birds upon recovery averaged 16.3 ± 0.46 g (n=4), as compared to an average of 14.8 ± 0.86 g for recaptured birds marked with RFID bands only (n=24). Mass of geolocator-tagged birds did not differ significantly between mass at initial capture and recapture the following year (T score = 0.362, alpha = 0.728, df = 6.92). The geolocators recorded data for an average of 302 (range 283 - 322) days (Table 3-1), over which the majority of the spring migratory route was recorded for each individual.

Fall Migration

All five individuals migrated from the breeding grounds to non-breeding areas in northwestern Mexico (Figure 3-1), travelling an average great-circle distance of 1,846 km (1,625 – 2,177; Table 3-2). Four birds wintered in the same geographic area bordering the Mexican states of Sonora and Sinaloa. The remaining individual wintered further southeast in the state of Durango. Pairwise distances between estimated wintering locations centroids ranged from 55 to 670 km (mean = 332 ± 231 km).

Although migratory paths and timings differed between individuals, each bird took a fairly direct southerly route towards the non-breeding region. During fall migration, none of the five individuals proceeded nonstop to the non-breeding grounds, but instead made multi-day stopovers along their migration route. Stopover location and duration varied by individual, however we were largely unable to define precise stopover locations or durations during fall migration due to increasingly imprecise latitudinal estimates around the autumnal equinox, which coincided with passage through the NAM (Figure 3-2). Prior to the equinox, stopovers ranging from 3 to 5 days were taken by two individuals in eastern Utah and the greater Grand Canyon region respectively. A single bird remained stationary for an extended period (43 days) in central Arizona. The remaining two individuals made no significant stopover prior to the equinox period (Figure 3-2, Appendix B). After the autumnal equinox (September 23), each bird completed a

rather direct migration southward from the NAM and arrived at their final non-breeding location around the first to second week of October. Migration routes taken were greater than the direct great-circle distances (Table 3-2), ranging from +39 km to + 433km. Location estimates for each individual by migration season can be found in Appendix B.

Spring Migration

The birds remained on the non-breeding grounds for an average of 181 days (150 – 207) before initiating spring departure (Table 3-1). The timing of spring migration departure showed substantial variation among the five individuals, ranging from March 15 to April 29, 2020. Three individuals from the northern non-breeding location took a direct route north during spring migration, during which several short- to moderate-length stopovers (3 to 22 days) were made (Figure 3-3). The remaining two individuals migrated north and west across Arizona and into southern California before turning north and east through Nevada, towards northern Utah, completing a looped migratory route. These two individuals (BT181 and BT192) made less distinct and shorter regional stopovers ranging from 2 to 9 days. Spring migration route distances were greater than the great-circle distance between breeding and non-breeding locations and were longer than those in fall migration in all but one individual (Table 3-2). The migratory distance of BT181 and BT192 were significantly longer than both their respective fall migrations and the spring migration routes travelled by the other three individuals.

DISCUSSION

Our results present the first direct tracking dataset of migrating Lazuli Buntings, a species thought to be a stopover molt-migrant dependent on the North American monsoonal region. We found substantial variation in migratory phenology and routes within our northern Utah breeding population, though all individuals spent the non-breeding season in western Mexico. Overall, our results support the importance of the NAM as a stopover location for migrating birds. However,

contrary to our expectations, we found little support that Lazuli Buntings from our study population used this region as a single stopover molting location, which has previously been suggested as a widespread phenomenon in Lazuli Buntings and other western migratory passerines. We also found two contrasting spring migratory strategies--one direct north-south route mirroring that of fall migration and a significantly longer and westerly looped route veering through California and Nevada. Though our results were drawn from a single year of tracking, they highlight the underlying complexity of migratory strategies exhibited within Lazuli Buntings from a single breeding population and underscore the need for more range-wide investigations into the propensity and connectivity of suspected stopover molt-migrations in western North America.

Our tracking data suggests that male Lazuli Buntings in our study population did not use a single location between the breeding and non-breeding grounds to complete their definitive prebasic molt. Rather, individuals likely spent shorter periods in several locations in the northern NAM and adjacent areas where some, but not all, of their definitive prebasic molt was likely completed. Using museum specimens, Young (1991) estimated the definitive prebasic molt in Lazuli Buntings to span 57 days. In four individuals we found little support for a single stopover of this length, even after accounting for 30 to 40 days of data being excluded during the fall equinox period. None of these individuals remained stationary for periods prior to or after the censored equinox period that would have allowed a stopover of necessarily length to complete a prebasic molt. A single individual (BT192) however did appear to spend around 43 days in central Arizona, including the whole equinox period, during which it likely completed all or most of its prebasic molt at this stopover. Our ability to detect this individual's prolonged stopover strategy despite censoring the equinox period, adds further support to the probable lack of a continuous stopover molt in the other four individuals. Our results suggest that northern Utah

breeding Lazuli Buntings are not obligate stopover molt-migrants. Instead, we suggest that stopover molt-migration may be a more facultative process in this population.

Of the western molt-migrants that have been directly tracked, almost all individuals were observed to have used the NAM for extended periods of time. Using geolocators, Western Kingbirds (*Tyrannus verticalis*) were estimated to have stopped over in northwest Mexico for 62 to 85 days (n = 14, Jahn et al. 2013a), Bullock's Orioles (*Icterus bullockii*) for 73 to 80 days (n = 2, Pillar et al. 2016), and a single Black-headed Grosbeak tracked with a GPS tag was observed to have spent at least 56 days in northwest Mexico (Siegel et al. 2016). The largely obligatory stopovers and consistent molting location in these previous studies contrast with our results as the Lazuli Buntings did not spend stopover time within northwestern Mexico like the other species prior to arrival on the non-breeding grounds. Interestingly, tracking data from the closely-related western Painted Buntings (*Passerina ciris*) also found evidence of intra-specific variation in fall stopover behavior, with 13 individuals stopping in the NAM for at least several weeks while two others from the same population did not (Contina et al. 2013).

Previous research on the prebasic molt in Lazuli Buntings found support for molt-migration to the NAM (Young 1991, Pyle et al. 2009). Most museum specimens exhibiting active molt were collected from the United States-Mexico border region and southern Baja California. However, only a small proportion of the total specimens from those regions were found to be in molt (Young 1991), suggesting molting may be happening in other regions between the US-MX border and the core non-breeding grounds of the species. Young (1991) did highlight a lack of specimens collected from northwestern Mexico, the region in which our tracked birds wintered. Similar proportions of molting Lazuli Buntings were observed during banding captures in the NAM (Pyle et al. 2009). In Arizona 38% of 151 banding captures were in active molt and a single bunting captured in Sonora was additionally in molt. Pyle et al. (2009) also reported low between-year site fidelity within their NAM capture sites as compared to both breeding and non-

breeding capture sites, ultimately concluding that stopover molt-migration is likely a stochastic or plastic process across molt-migrating species, influenced by individual-level behaviors.

Based on our tracking data and previously published molting observations, Lazuli Buntings clearly undergo molt-migrations, however the location of molt seems to be variable among individuals. One explanation, proposed by Pyle and colleagues (2009) of molt timing and location being an individual-level choices around climate and breeding season dynamics, is a likely possibility. Late season breeding efforts are known to delay fall migrations and put pressure on molt timing in passerines (Stutchbury et al. 2011, Mitchell et al. 2012, Borowske et al. 2017, Imlay et al. 2021). Similarly, individuals which complete breeding efforts early or have access to abundant resources may not be as temporally or energetically constrained (Reed et al. 2003, Fayet et al. 2016). In these manors, positive or negative carryover effects from the breeding season may force molt-migrants to forgo molting during migration, allow for migration to a stopover location to molt, or vice versa depending on an individual's set of conditions.

Migratory distance may also play a role in individual decisions around molt-migration. Long distance migrants are more time and energy constrained in their migrations than short distance migrants (Nilsson et al. 2014, Arlt et al. 2015, Packmor et al. 2020). Given this, longer distance migrants may need reliable access to high quality resources, like the NAM, to quickly grow high quality flight feathers. In contrast, shorter distance migrants may be able to find adequate resources in lower abundances and grow feathers more slowly or may not be as dependent on high quality feather production. Additionally, molt-migration is hypothesized to result from a necessity to depart an area of few resources for an area with higher resources (Rohwer et al. 2005, Barta et al. 2008, Pyle et al. 2009, Pageau et al. 2020). If those resource areas are potentially variable in space and time, as the amount and location of seasonal rains in the NAM are (Comrie and Glenn 1998, Hu and Feng 2002), long distance migrants may have evolved to select stopover locations where resources are more consistently available through

time, while shorter distance migrants may have more flexibility to seek out high quality resource areas with each given season. Our tracked buntings wintered in the northern portion of the species' non-breeding range, overlapping with the southern portion of the NAM. Given the short distance of this migration, these individuals may not have been as energetically constrained as longer distance migrants breeding further north. We additionally cannot eliminate the possibility that the individuals in our study may have molted on the wintering grounds, which is included in the southern extent of the NAM.

The data in our investigation were limited in respect to the precision of our geographic location estimates, especially during the periods around the vernal and autumnal equinoxes. Inferences during the autumnal equinox may have also been obscured due to environmental or life history factors of the species. Lazuli Buntings migrate to the NAM during the autumnal equinox to take advantage of seasonal rains and vegetation growth. During this period, our geolocators likely experienced inconsistent shading events during periods of precipitation, as well as possible changes in lighting regime in association with changes in habitat or behavior during possible molt. Any of these factors could have additionally contributed to variation in daily location estimates, especially with regards to latitude. Our inference on movements during these imprecise periods were further hindered by the lack of longitudinal movements, which remain accurate throughout the equinox periods. However, because longitudinal changes are more reliably estimated, we have high confidence the two distinct migratory routes we observed during spring migration represent true migratory movements.

In spring, three individual Lazuli Buntings took a distance-minimizing route between the non-breeding and breeding grounds, while two individuals took a counter-clockwise route through California and Nevada before arriving in northern Utah to breed. Evidence for clockwise loop migrations, like we observed, have been found in analyses of western North America bird occurrence data (La Sorte et al. 2014b; 2014a, Supp et al. 2015). Loop migration strategies are

thought to arise where environmental conditions, such as prevailing wind patterns or stopover conditions, differ predictably between migration seasons (Klaassen et al. 2010, Tøttrup et al. 2012, Mellone et al. 2013, Kranstauber et al. 2015). La Sorte et al. (2014a) found western passerines take more direct routes in the fall between the breeding and non-breeding grounds, often occupying high elevational sites, which are not necessarily the greenest or most productive sites within the flyway at that time. During spring migration, occurrence data suggest that many birds migrate northward and westward along lower elevations, where these spring routes are significantly greener than the fall migration routes (La Sorte et al. 2014a). Thus, the western loop migration we observed may be a trade-off of migratory length for a route with higher resource abundance in the spring. Similar resource tracking loop migrations have been observed in western hummingbirds tracking flower blooms (Phillips 1975, Supp et al. 2015), as well as from direct tracking data within the European-African flyways (Klaassen et al. 2010, Tøttrup et al. 2012, Mellone et al. 2013).

The differences in spring route we observed between the two groups cannot be explained by differences in age or sex class, breeding population, or differences non-breeding ground departure schedules. Migratory routes are known to have genetic controls and are often repeatable across individuals (Berthold 1996, Pulido 2007, Delmore and Irwin 2014, Delmore et al. 2015), however intra-population differences or variation in routes are not wholly unexpected (Stanley et al. 2012, Jacobsen et al. 2017). Our observation of two distinct spring migratory strategies could be the result of genetic differences within a single population, but more likely represent the balancing of migratory trade-offs throughout the annual cycle at the individual-level. Due to the imprecision of geolocated data, we were unable to test individual-level hypotheses relating habitat quality or wind effects on migration route choice, or trade-offs of molt-migration. It is additionally possible that breeding effort, molt, or non-breeding conditions may lead to carryover effects (Norris et al. 2005, Robinson et al. 2010, Hargitai et al. 2014, Imlay et al. 2021) that

influence migration route selection. For instance, birds departing in good condition may be able to tolerate less resource-filled spring routes, whereas migrants in poorer condition may need to seek routes with higher resource availability, even if these routes are longer in distance. Detailed demographic, tracking, and environmental data are necessary to test such hypotheses.

Though molt-migration is not unique to western North America, this strategy's prevalence among western passerines presents interesting opportunities to study carryover effects and tradeoffs in the ecology and evolution of molt and migration. Despite the lack of support for a complete stopover molt in this population of Lazuli Bunting, our results continue to support the NAM as an important area for western birds during fall migration regardless of its usage as stopover molting habitat. More and repeated tracking of individual Lazuli Buntings and across additional species of suspected molt-migrants are needed to identify specific areas of importance for migrating birds within the NAM and surrounding areas. Our results highlight the importance of looking at migration at the individual level and the need for precise tracking data to explore the connectivity of molt-migration, and connectivity of migratory routes more generally. Knowledge of where and when molt-migrants travel, and how tightly they depend on particular resources is necessary to assess habitat needs and inform conservation of critical habitat across western species. As GPS devices with higher spatial and temporal resolution become sized for smaller passerines, and other tracking initiatives like the Motus network (Taylor et al. 2017) expand in capacity, greater opportunities to investigate hypotheses of molt-migration will be possible.

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TABLES AND FIGURES

Table 3-1. Migratory phenology of Lazuli Buntings (*Passerina amoena*) breeding in northern UT, USA based on RFID feeder encounter data and location data from geolocators between 2019 and 2020. Dates in parenthesis are estimated based on inconsistent location estimates when arrival dates coincide within a few days of tag battery death, or date fell within a period around the equinoxes where little longitudinal movement were accompanied by imprecise latitude estimations. Note that the earlier relative study site arrival of BT195 may be attributed to the substantially lower breeding elevation of this bird than the other individuals, where vegetation green up precedes that of the higher elevation breeding site.

Bird ID	Depart Study Site ^A	Arrive Wintering Location ^B	Depart Wintering Location ^B	Wintering Period Days	Arrive in Breeding Area ^B	Arrive at Study Site ^A	Active Tag Days
BT164	Aug 16	Oct 5	Apr 29	207	May 11	May 26	304
BT179	Aug 16	Oct 7	Apr 13	189	(~May 21)	May 26	290
BT181	Aug 16	Oct 10	Apr 25	198	May 29	Jun 9	322
BT192	Aug 18	Oct 27	(Apr 8)	164	(~May 14)	May 25	310
BT195	Aug 14	Oct 7	(Mar 5)	150	(~May 6)	May 8	284

^{A.} As estimated by first and last detection dates at feeders from RFID encounters

^{B.} As estimated from LLmig package change point analysis

Table 3-2. Differences in great-circle migratory distances by individual and migration leg. Minimum distances represent the great-circle distance between the breeding and non-breeding grounds. Seasonal leg distances represent the summed great-circle distance between the origin, the furthest west or east estimated location and the destination, whichever intermediate point produces the longest summed distance.

Bird ID	Minimum Distance (km)	Fall Distance Sum (km)	Fall Difference	Spring Distance Sum (km)	Spring Difference
BT164	1625	1755	+130	1733	+108
BT179	1744	1783	+39	1813	+69
BT181	2177	2610	+433	2824	+647
BT192	1916	1977	+61	2617	+701
BT195	1769	2061	+292	1952	+183

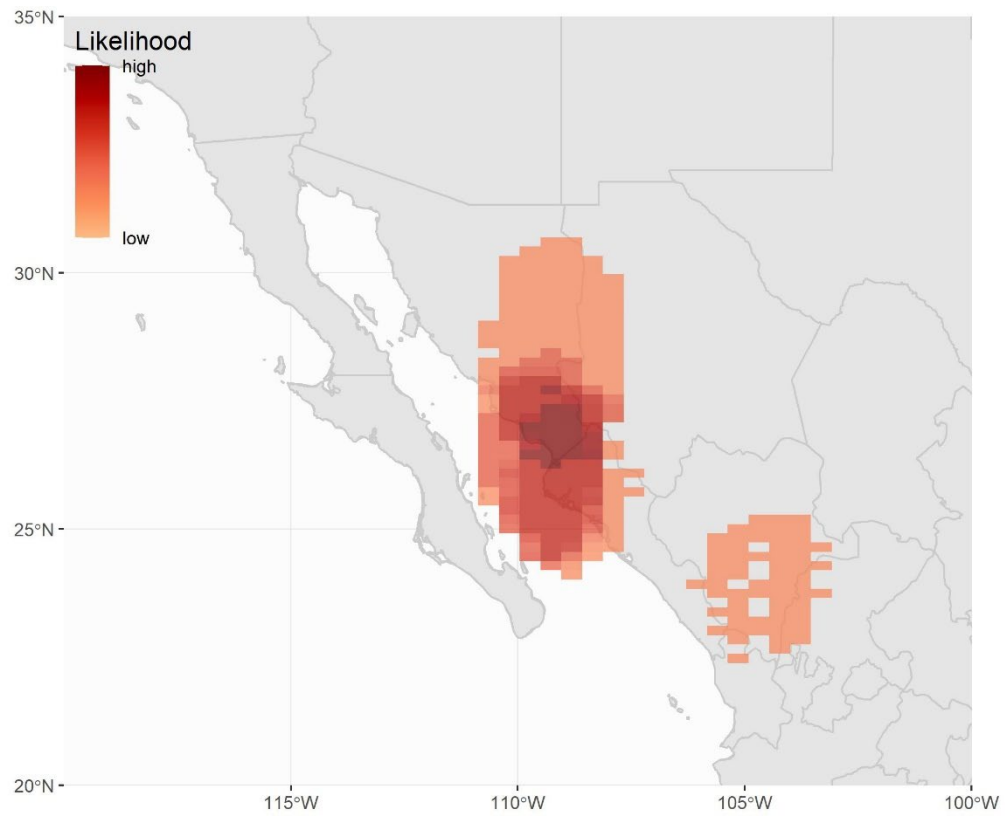


Figure 3-1. Probability of non-breeding residence (December 1, 2019 – February 1, 2020) of Lazuli Buntings tagged with geolocators in northern Utah, USA. Darker red indicates areas of overlapping probability between individuals.

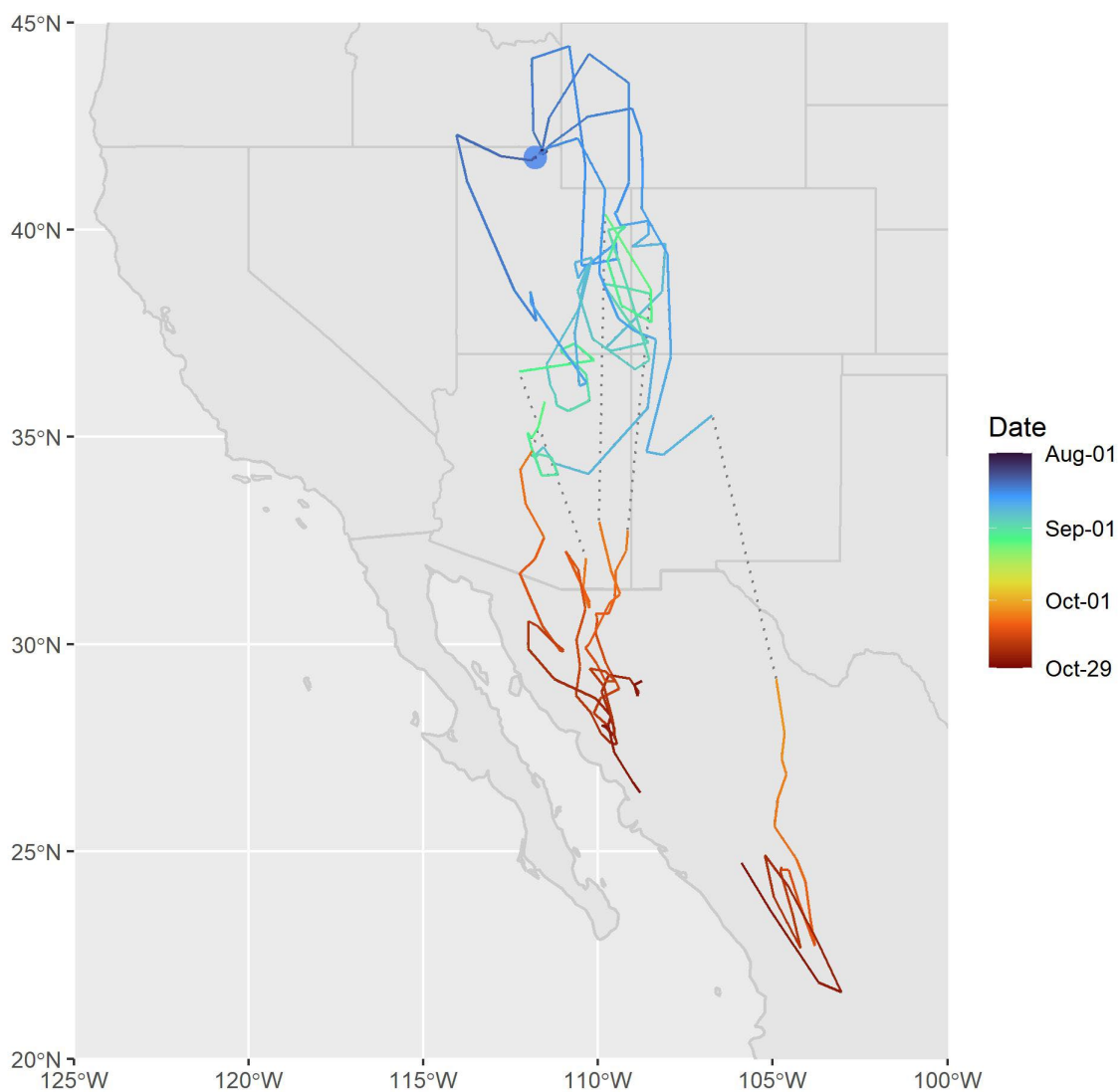


Figure 3-2. Fall migratory pathways of Lazuli Buntings (*Passerina amoena*) estimated from archival light-level geolocators deployed in northern UT, USA in 2019. Migratory paths represent three day moving averages of estimated locations and are colored by date. Dotted line segments represent periods surrounding the autumnal equinox where latitude estimates were unreliable. Three birds made stopovers during fall migration in eastern Utah, the Grand Canyon region, and central Arizona, while two additional individuals made no significant stopovers. Deployment location in northern UT is represented as a blue circle.

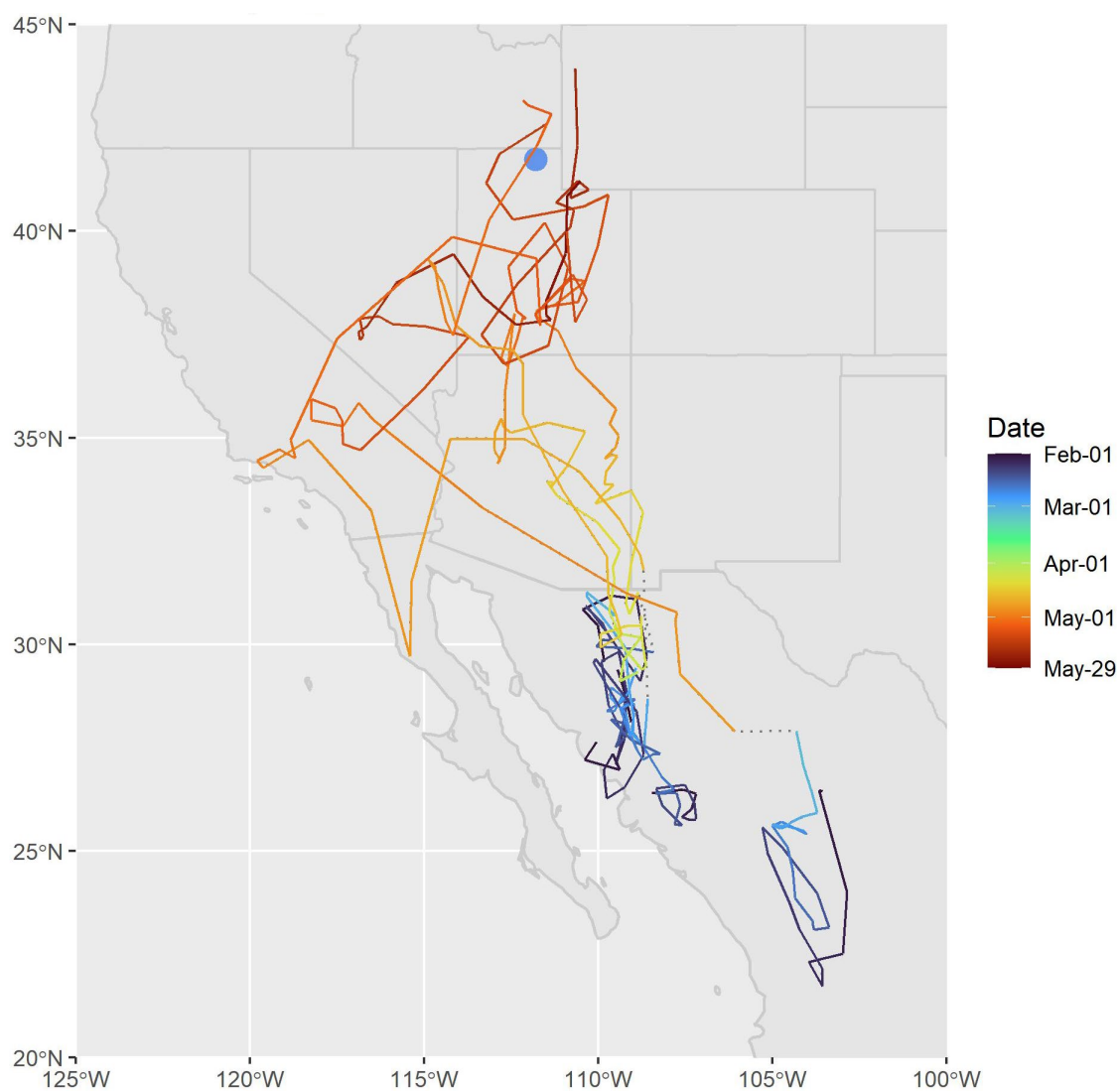


Figure 3-3. Spring migratory pathways of Lazuli Buntings (*Passerina amoena*) estimated from archival light-level geolocators deployed in northern UT, USA in 2020. Migratory paths represent three day moving averages of estimated locations and are colored by date. Dotted line segments represent periods surrounding the vernal equinox where latitude estimates were unreliable. Recapture location in northern UT is represented as a blue circle.

CHAPTER 4

SUMMARY

This study provides insight into the migratory ecology of Lazuli Buntings (*Passerina amoena*) breeding in montane systems in northern Utah, USA. During this investigation we captured, marked, and monitored 430 individual buntings across low and high elevational sites within Cache County to compare migratory phenology across demographic and elevational groups and determine migratory pathways and destinations undertaken by the species.

In Chapter 1 we sought to characterize the migratory phenology of the Lazuli Bunting for males and females at low and high elevations. Precise migratory phenologies within birds are challenging to estimate, especially in the case of cryptic arrivals and departures due to low vocalization rates, fluid territorial boundaries, and transient individuals during arrival and departure windows. To better estimate migratory phenologies and reduce potential observer and detection biases, we captured and marked buntings with radio-frequency identification (RFID) leg bands which were passively monitored by electronic bird feeders throughout the migratory and breeding seasons. Using this nearly continuous-time encounter data, we wrote a custom Bayesian point-process model to estimate migratory phenology by group, while accounting for individual and group-level variability in detections. From these models we found evidence of a protandrous arrival at low elevations but no significant difference in arrival between males and females at high elevations. Additionally, no significant differences in departure date were found between sex or elevation.

The pronounced lack of protandry we observed at high elevations, relative to that observed at low elevations within the same local population and year, raises questions about the generality of selection-based hypotheses in explaining protandry. Evidence of selection-based causes of protandry are common in the published literature, suggesting males receive fitness

benefits from early arrival in the form of more and better options for high-quality habitat and mating opportunities. Though we were unable to address direct fitness consequences of migratory timings, our results indicate early male arrival at high elevations are not being strongly selected for. Protandry may alternatively result from limits, or constraints, on the migratory timing of one or both sexes, such as body-size-related temperature tolerances, sex-specific variation in the ability to refuel on migration, or from external factors such as non-breeding habitat quality or range segregation between age or sex classes. Based on the differences in protandry between sites and field observations of buntings staging at low elevations prior to arrival at high elevations, we suggest protandrous arrival to the larger breeding region at low elevations is controlled by differing constraining factors between males and females, while differences in staging duration between males and females dilutes protandry upon arrival at the final breeding site. These results highlight the utility of full distribution modelling in identifying differences in phenologies across groups and the importance of accounting of uncertainty, especially for individuals or groups that are difficult to detect. Full and accurately characterization of phenological processes is necessary to identify possible phenological mismatches and to predict population responses to future climate change.

In Chapter 2 we used data from archival light-level geolocators to investigate locations of possible stopover molt areas, winter residencies, and migratory routes of Lazuli Buntings. Lazuli Buntings, like many western passerines, are thought to be stopover molt-migrants, dependent on seasonally abundant resources of the North American monsoon region (NAM) to complete their prebasic molt during fall migration. Studies of museum specimens and bird captures in the NAM demonstrated buntings molt in the region, however variation in percentage of molting individuals and recapture rates between years suggested molt-migration in the species may be a more plastic or individual process than previously thought. We attached archival light-level geolocators to a subset of breeding birds in 2019 and recovered five tags from returning individuals in 2020. From

these light-level data we were able to estimate daily position estimates throughout the life of the tag. We found all individuals to have migrated to western Mexico for the non-breeding season. We found support for a molt-length stopover in only one of five individuals. The remaining individuals spent adequate time within the NAM during the typical molting period, however, did not remain stationary at a stopover site. These results support previous hypotheses that stopover molt-migration is likely varied by individual. We additionally observed two distinct spring migratory patterns; a distance-minimizing route mirroring that of fall migration exhibited by three birds, and a looping route through California and Nevada made by two birds which was significantly longer in distance but not time. Loop migrations are thought to commonly arise with predictable changes in environmental factors, such as prevailing winds and food resources, are experiences between migratory seasons. Changes in wind patterns in western North America are not as predictable as in other flyways due to topographic heterogeneity across the region but marked differences in spring green-up exist within the region. Lower elevation areas in the western portion of the flyway green-up quicker than interior areas within the Rocky Mountain region and remain greener throughout the spring migratory season. The different spring migration strategies we observed may represent individual-level tradeoffs between time, distance, and resource availability en route.

Our results in whole highlight the importance of investigating drivers of and variation in migratory ecology at the individual and demographic levels. Knowledge of where and when birds migrate, and how tightly they depend on particular resources throughout the full annual cycle is necessary to assess habitat needs and inform conservation of critical habitat across bird species.

APPENDICES

APPENDIX A. SUPPLEMENTARY TABLES

Table A-1. Weibull distribution parameters and derived arrival and departure dates by sex, elevational group, and sampling year of Lazuli Bunting (*Passerina amoena*) as modeled from full phenological distributions. Modeled Weibull shape (k) and scale (g) are median values with associated 95% credible intervals (in parentheses). Estimated phenological dates are calculated relative as days since 21 April.

		Modelled Phenology Date				Estimated Weibull Parameters			
		Mean	Median	SD	95% CI	k		g	
Low - Male	2019	12.59	112.72	1.85	(108.51, 115.89)	18.41	(11.59, 26.559)	116.02	(112.67, 119.16)
	2020	115.05	115.14	1.49	(111.82, 117.69)	20.39	(13.11, 28.77)	117.22	(114.51, 119.74)
Low - Female	2019	105.71	107.08	6.37	(90.06, 114.66)	7.19	(3.33, 11.65)	113.17	(98.84, 122.54)
	2020	110.43	110.53	2.37	(105.59, 114.90)	10.25	(7.411, 13.52)	114.55	(110.19, 118.94)
High - Male	2019	113.27	113.37	1.60	(109.34, 116.63)	18.51	(11.29, 27.44)	116.73	(113.60, 119.96)
	2020	106.72	106.73	2.34	(101.92, 111.25)	9.50	(7.02, 12.23)	111.00	(106.70, 115.65)
High - Female	2019	108.46	109.13	6.84	(91.89, 119.44)	7.31	(2.94, 12.08)	116.04	(101.58, 127.41)
	2020	116.27	116.39	3.00	(110.28, 121.68)	12.60	(8.26, 17.63)	119.83	(115.55, 124.98)

APPENDIX B. SUPPLEMENTARY FIGURES

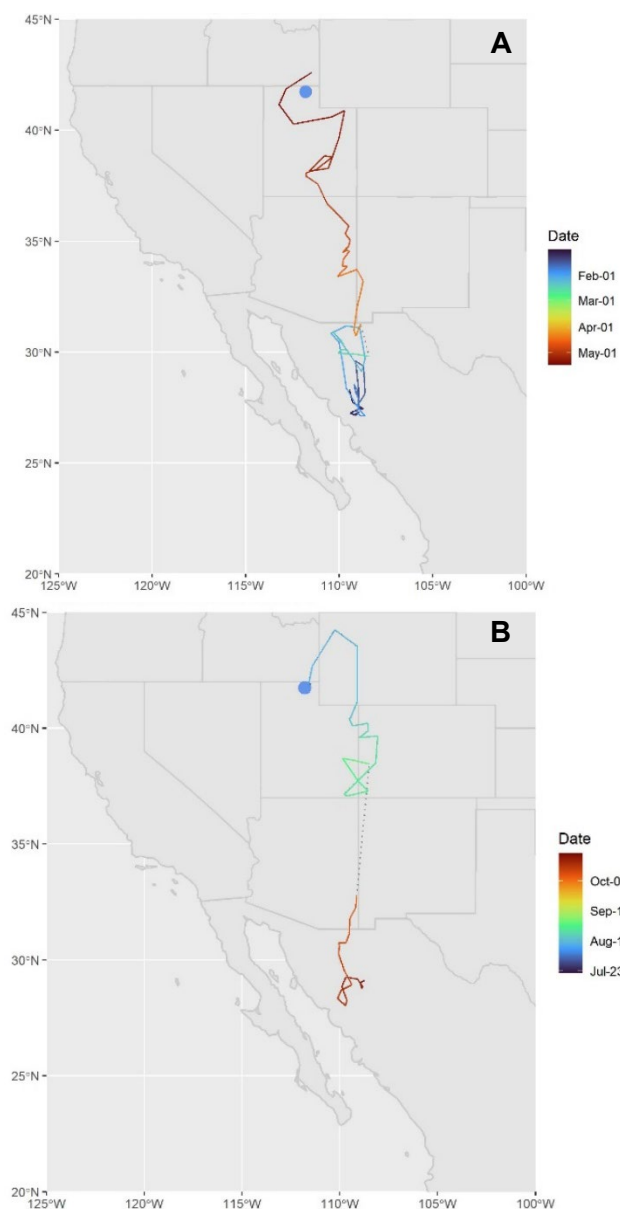


Figure B-1. (A) Fall and (B) spring migratory pathways of individual BT164 estimated from archival light-level geolocators deployed in northern UT, USA in 2019. Migratory paths represent three day moving averages of estimated locations and are colored by date. Dotted line segments represent periods surrounding the vernal equinox where latitude estimates were unreliable. Deployment location in northern UT is represented as a blue circle.

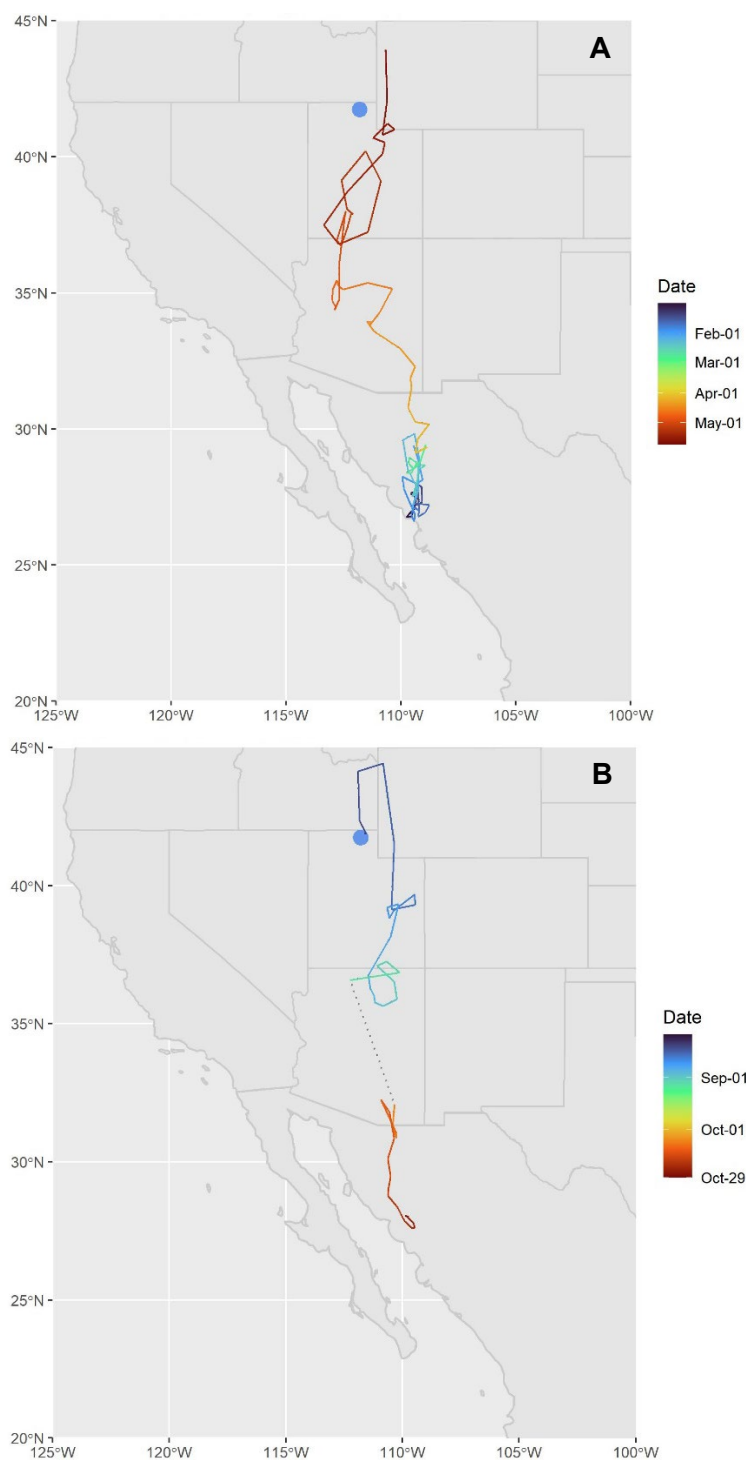


Figure B-2. (A) Fall and (B) spring migratory pathways of individual BT179 estimated from archival light-level geolocators deployed in northern UT, USA in 2019. Migratory paths represent three day moving averages of estimated locations and are colored by date. Dotted line segments represent periods surrounding the vernal equinox where latitude estimates were unreliable. Deployment location in northern UT is represented as a blue circle.

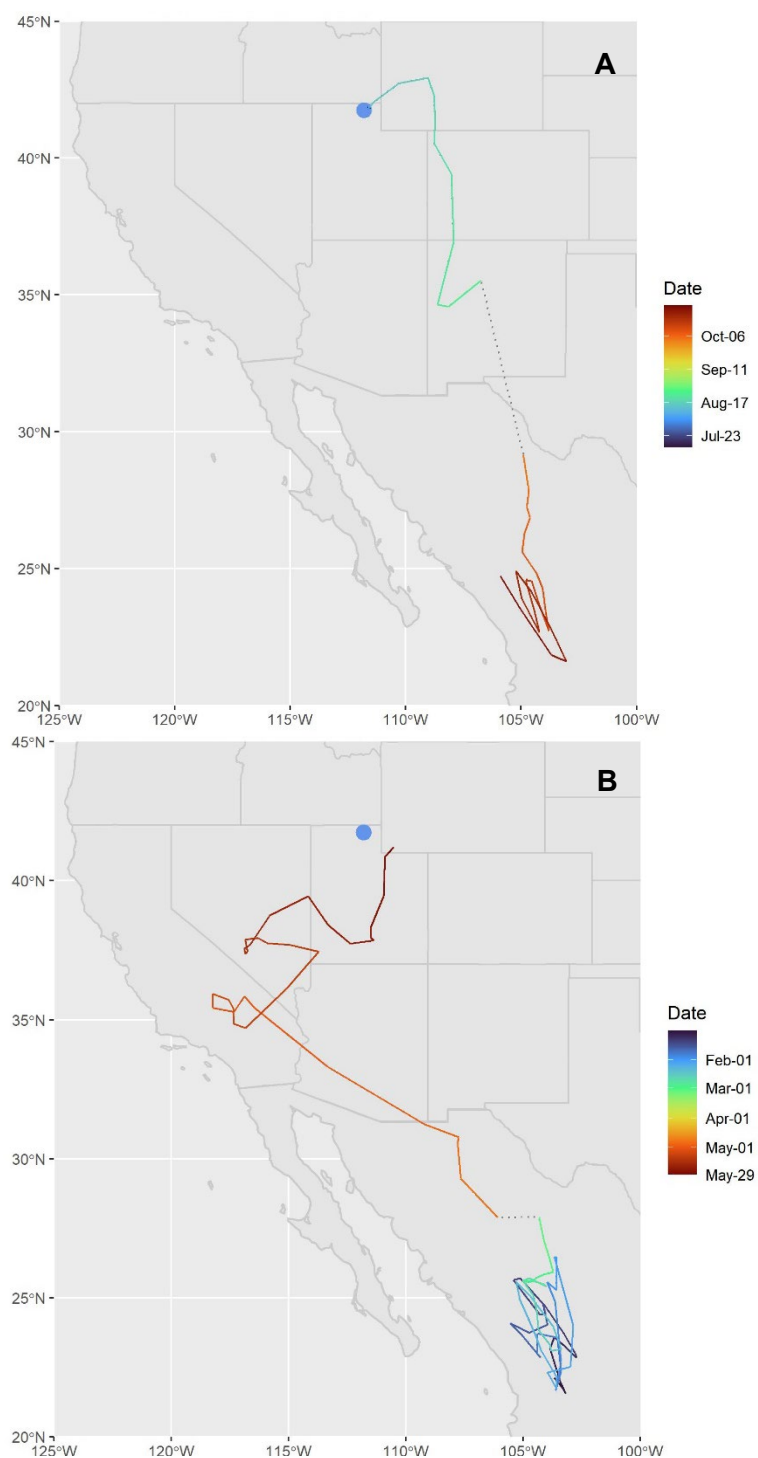


Figure B-3. (A) Fall and (B) spring migratory pathways of individual BT181 estimated from archival light-level geolocators deployed in northern UT, USA in 2020. Migratory paths represent three day moving averages of estimated locations and are colored by date. Dotted line segments represent periods surrounding the vernal equinox where latitude estimates were unreliable. Recapture location in northern UT is represented as a blue circle.

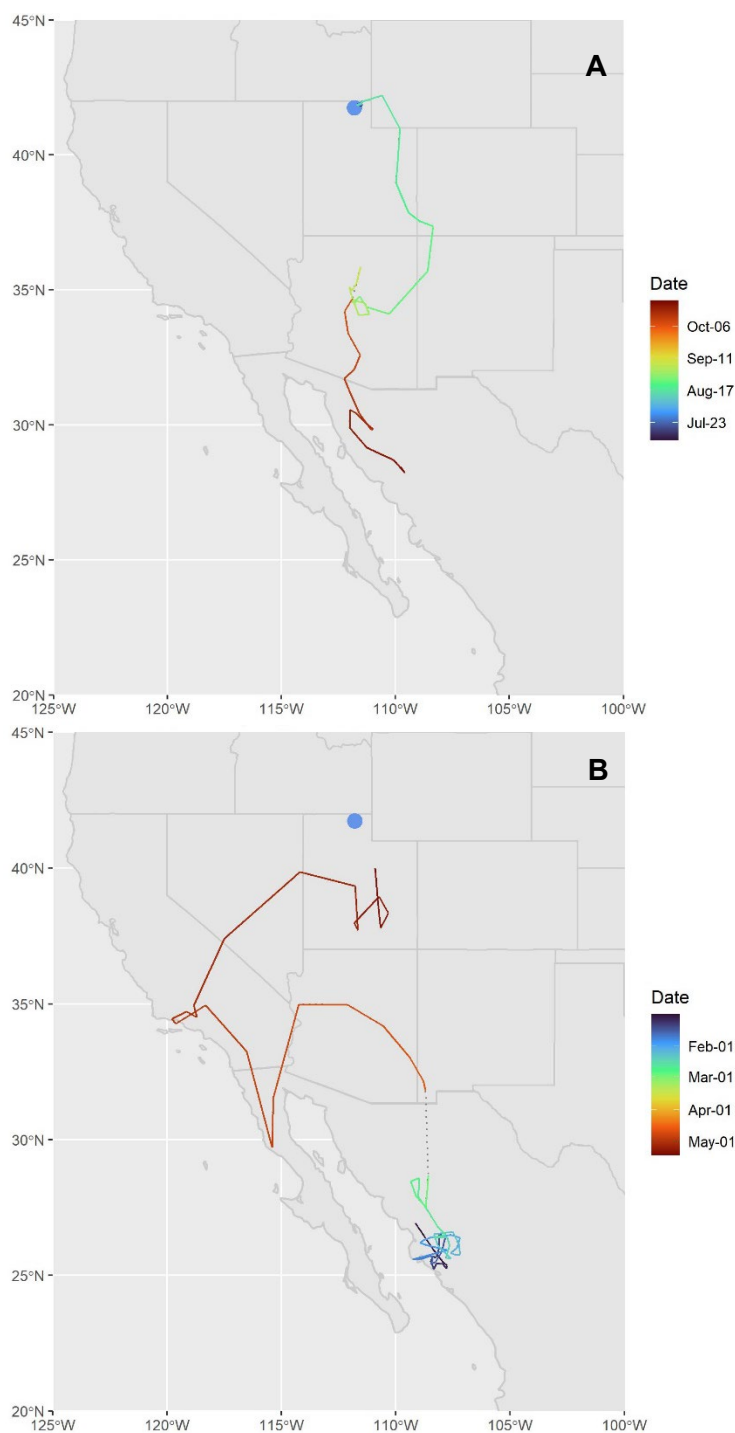


Figure B-4. (A) Fall and (B) spring migratory pathways of individual BT192 estimated from archival light-level geolocators deployed in northern UT, USA in 2020. Migratory paths represent three day moving averages of estimated locations and are colored by date. Dotted line segments represent periods surrounding the vernal equinox where latitude estimates were unreliable. Recapture location in northern UT is represented as a blue circle.

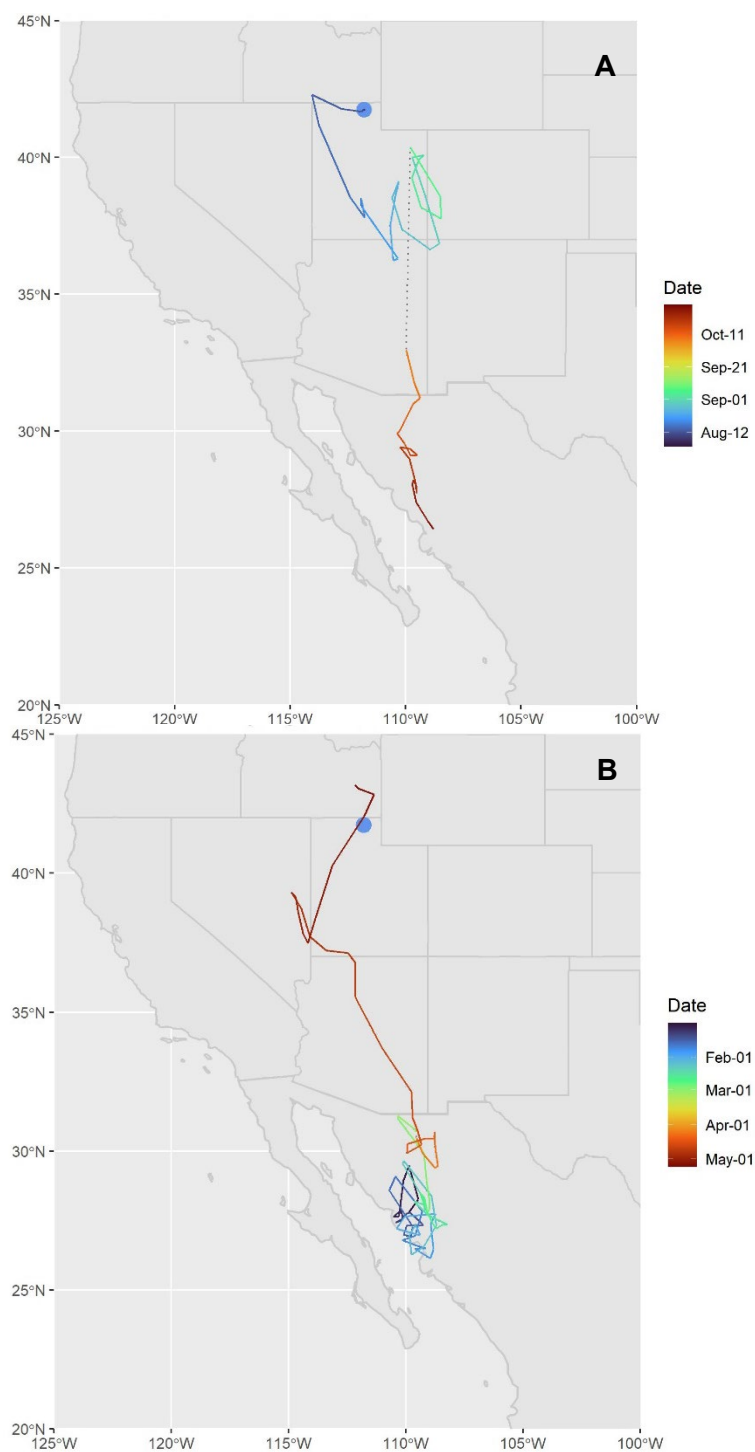


Figure B-5. (A) Fall and (B) spring migratory pathways of individual BT195 estimated from archival light-level geolocators deployed in northern UT, USA in 2020. Migratory paths represent three day moving averages of estimated locations and are colored by date. Dotted line segments represent periods surrounding the vernal equinox where latitude estimates were unreliable. Recapture location in northern UT is represented as a blue circle.