

2021

Impact of the North American Monsoon on Molt Migrant Passerines

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Impact of the North American Monsoon on Molt Migrant Passerines

An Honors Thesis

Presented to

The Faculty of The Department of Biology

Colby College

in partial fulfillment of the requirements for the

Degree of Bachelor of Arts with Honors

by

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22 May 2021

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Abstract

Breeding, molt, and migration place considerable yearly demands on migrating passerines in North America. Due to conflicts in energy allocation, many species have evolved migration strategies that prevent temporal overlap in these processes. However, there is recent evidence that some passerines which breed in western North America migrate to intermediate stopover sites to carry out molt, conflating molt and migration. Factors influencing the evolution of such a strategy are believed to include both aridity on breeding grounds and dependable flushes of late-summer productivity in the southwestern United States and northwestern Mexico. This productivity occurs due to the brisk rainfall of the North American monsoon, and it results in a dramatic increase in many types of food resources. In this study, I use precipitation records and pre-existing surveys of breeding birds in the Great Basin region to investigate the relationship between migration strategy and influence of monsoon precipitation. Specifically, I model abundance changes using various precipitation and population explanatory variables in five molt migrants and five non-molt migrant controls. This study did not provide strong evidence that monsoon rains have distinct effects on passerines of divergent migration strategies. However, I found that molt migrants may be subject to weaker density-dependent effects, possibly due to relaxed constraints on the molting ground.

Introduction

Molt and migration

Neotropical migrant passerines in North America are annually subject to three major energetic demands: breeding, molt, and migration. These songbirds move northward to breed in favorable conditions, return to their wintering grounds in the south, and molt at some point in the yearly cycle (Pageau et al. 2020). Because high-quality feathers require an abundance of certain resources, molt must be situated in a time and place with environmental conditions conducive to acquiring these food resources (Pageau et al. 2020). Successful migration requires a careful coordination of behavioral and morphological traits, including timing of migratory restlessness, navigational mechanisms, and the sequence of feather replacement (Rohwer and Irwin 2011, Pyle 1997).

Generally, these three annual energetic burdens show significant temporal separation in passerines (Rohwer et al. 2005). Most north-temperate birds molt into their basic plumage immediately after the breeding season (Pyle 1997). Generally, this prebasic molt occurs between July and September (Pyle 1997). Annual molt in adult birds may occur on the breeding grounds prior to migrating in the fall, in the wintering range after fall migration, or both (Rohwer et al. 2005). Historically, passerine migration has been viewed under this uniform, simplistic lens in which all birds separate breeding, migration, and molt to prevent conflicts in energy allocation (Pageau et al. 2020).

However, there is more flexibility in this regime than previously thought. Migration and breeding are more temporally fixed than molt, as food availability and climatic conditions tie passerines to their breeding and wintering grounds (Rohwer et al. 2005). In other words, molt scheduling is less constrained (Rohwer et al. 2005). For instance, some populations initiate molt on the summer range, suspend it during fall migration, and finish molting on the wintering grounds (Pyle 1997). Furthermore, researchers have found passerines molting during fall migration both in the form of utilizing intermediate stopover sites to molt and in the form of molting while undertaking migratory flights (Pyle 1997; Voelker 2004; Rohwer et al. 2005).

Molt migration is a type of migration strategy in which birds overlap molt and migration in time (Rohwer et al. 2005). Some North American passerines delay molt until reaching a stopover site during fall migration (Pageau et al. 2020). In particular, these are western species which pause to initiate or complete their prebasic molts in the North American monsoon region before continuing to wintering grounds (Rohwer et al. 2005, Voelker 2004). This strategy separates fall migration into two phases: one to move from the breeding territories to a stopover site and one to move to the wintering range afterwards (Rohwer et al. 2005). In most North American passerine populations known to molt migrate, researchers have found no or minimal overlap between the molt migration area and the breeding or wintering grounds (Voelker 2004).

Although the evolution of this overlap in molt and migration has only recently been under study, a few themes have emerged. One of these better understood theories is the push-pull hypothesis (Rohwer et al. 2005, Pageau et al. 2020). This hypothesis conceptualizes the drivers of molt migration as two joint forces: a “push” from the breeding territories and a “pull” toward

the North American monsoon region (Rohwer et al. 2005). Thus far, there is little research which specifically tests the push-pull hypothesis, but recent work strongly supports the “push” aspect of the theory (Pageau et al. 2020). The “push” in this framework are factors driving passerines to leave their summer range post-breeding; these are ecological, demographic, or climatic conditions that disfavor molting in the breeding territories (Rohwer et al. 2005). While the ecological and demographic conditions may require further study, a 2020 study found strong evidence that aridity on the breeding grounds encouraged the evolution of molt migration (Pageau et al. 2020). Much of the lowland habitats in western North America are exceedingly dry and unproductive in the late summer months following passerine breeding season (Rohwer et al. 2005). In much of the area, most of the precipitation conducive to vegetative growth comes from winter rains and snow (Rohwer et al. 2005). As described in the next section, the hypothesized “pull” is drastically different.

North American monsoon

In late summer, the North American monsoon region of coastal Sinaloa and Baja California Sur in Mexico as well as New Mexico and Arizona in the United States represent a remarkable departure from this overall arid pattern (Rohwer et al. 2009). In this area, tremendous changes occur July through September as monsoon rains supply most of the region’s annual precipitation (Rohwer et al. 2009). This moisture, coming from the eastern Pacific Ocean, Gulf of California, and Gulf of Mexico, facilitates a rapid increase in primary productivity (Adams and Comrie, 1997). Forests quickly green as previously leafless trees experience a flush of

productivity (Rohwer et al. 2009). Food resources grow immensely for insectivorous and granivorous birds alike. This constitutes the climatic pull, a noteworthy factor which can make molting in this stopover site worthwhile (Rohwer et al. 2005).

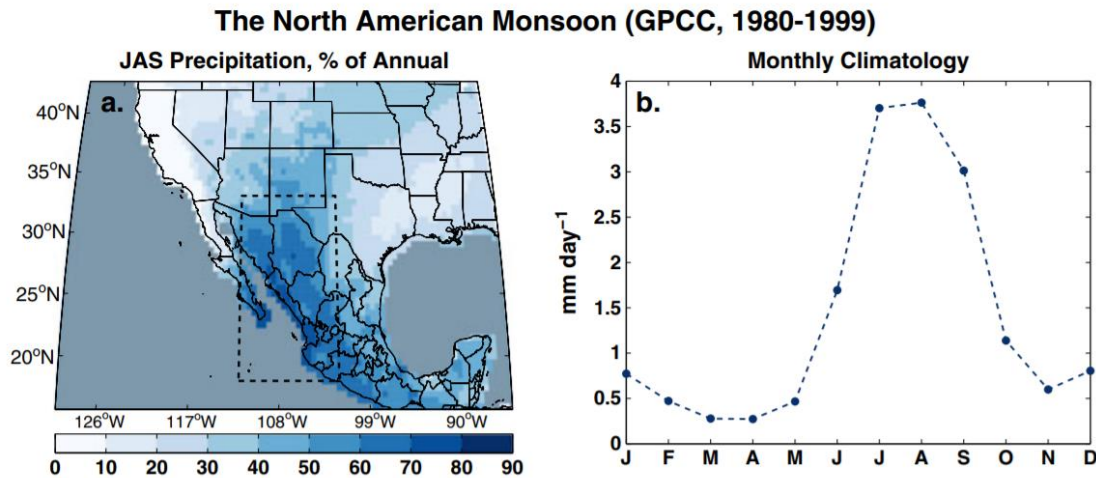


Figure 1: Climatology in the North American monsoon zone. (a) Percent of annual precipitation which falls during the peak period of July, August, and September. A black dashed rectangle outlines the core monsoon region. (b) Monthly precipitation (mm day⁻¹) averaged over the core region (figure from Cook and Seager 2013)

In the monsoon zone, extremely dry conditions before June give way to high amounts of rainfall in July (Adams and Comrie, 1997). The rain usually lasts until mid-September, when dry conditions resume (Adams and Comrie, 1997). The North American monsoon covers a large spatial domain and augments precipitation in much of the western United States and northwest Mexico (Adams and Comrie, 1997). The rainfall is centered on the western foothills of the Sierra Madre Occidental in Mexico, wherein the rainfall intensity shows an extreme peak in July through September (Adams and Comrie, 1997). In this core region, the rainfall during the July through September maximum constitutes over 70% of the area's annual rainfall (Cook and Seager 2013; figure 1). Moving northward, however, the distinctiveness of the July through September peak declines rapidly (Adams and Comrie, 1997). Researchers suggest that New Mexico is generally most affected by the monsoon, but parts of Arizona and Colorado also

receive precipitation (Adams and Comrie, 1997). The rainfall in these parts is much more variable in timing and amount than the precipitation in northwest Mexico where the monsoon is centered (Adams and Comrie, 1997; figure 1).

Among neotropical migrant passerines of North America, many more western-breeding species than eastern-breeding ones carry out part or all of their fall migration before molting (Rohwer et al. 2005). Scientists have suggested that differences in molt and migration scheduling are influenced significantly by the disparity in summer precipitation and primary productivity experienced in the continent's two sides (Rohwer et al. 2005). In the western part of the continent, as described above, precipitation is highly variable. Productivity also varies substantially; deciduous forests are highly seasonal and remain leafless for much of the predominantly dry year (Rohwer et al. 2009). In the eastern counterpart, however, annual precipitation is high (Rohwer et al. 2005). Differences in precipitation levels between seasons and across regions are much smaller (Rohwer et al. 2005). As such, many habitats can sustain high levels of primary productivity into the late summer (Rohwer et al. 2005).

Background on species

Molt migration was first described in waterfowl in the 1960s, and its occurrence in other taxa is a recent discovery (Tonra and Reudink 2018). The phenomenon of passerines stopping over in the North American monsoon zone seems to have been found in the 1990s (Rohwer and Irwin 2011). Since then, a variety of granivorous, insectivorous, and frugivorous birds have been identified as molt migrants to the monsoon region (Chambers et al. 2011). These species include

the Ash-throated Flycatcher, Western Kingbird, Warbling Vireo, Lucy's Warbler, Western Tanager, Chipping Sparrow (western populations), Lark Sparrow, Lark Bunting, Black-headed Grosbeak, Lazuli Bunting, Bullock's Oriole, and Lesser Goldfinch (Chambers et al. 2011). While I have chosen several species of molt migrants and presumed non-molt migrants to analyze, I will here describe the natural history of the Lazuli Bunting (*Passerina amoena*), as it is a well-studied and apparently straightforward example of a molt migrant.

The Lazuli Bunting is a granivorous and insectivorous songbird in the family *Cardinalidae* found in brushy, open, and semi-open habitats including grasslands, overgrown fields, woodlands, chaparral, and thorn forest (Greene et al. 2020, Chambers et al. 2011). Its range is strictly limited to western North America, where it breeds in U.S. states ranging from California to North Dakota and winters around Sinaloa through Michoacán in Mexico (Cornell Lab of Ornithology 2019; figure 2).

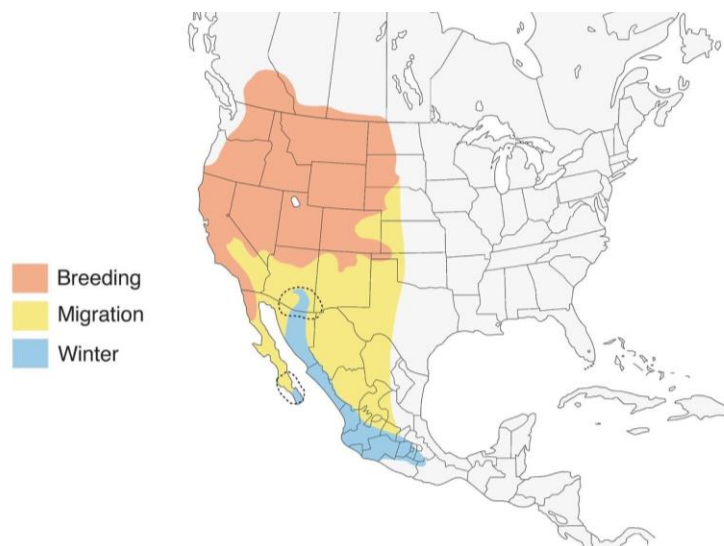


Figure 2: Range map of Lazuli Bunting breeding, migration, and wintering grounds (Cornell Lab of Ornithology 2019)

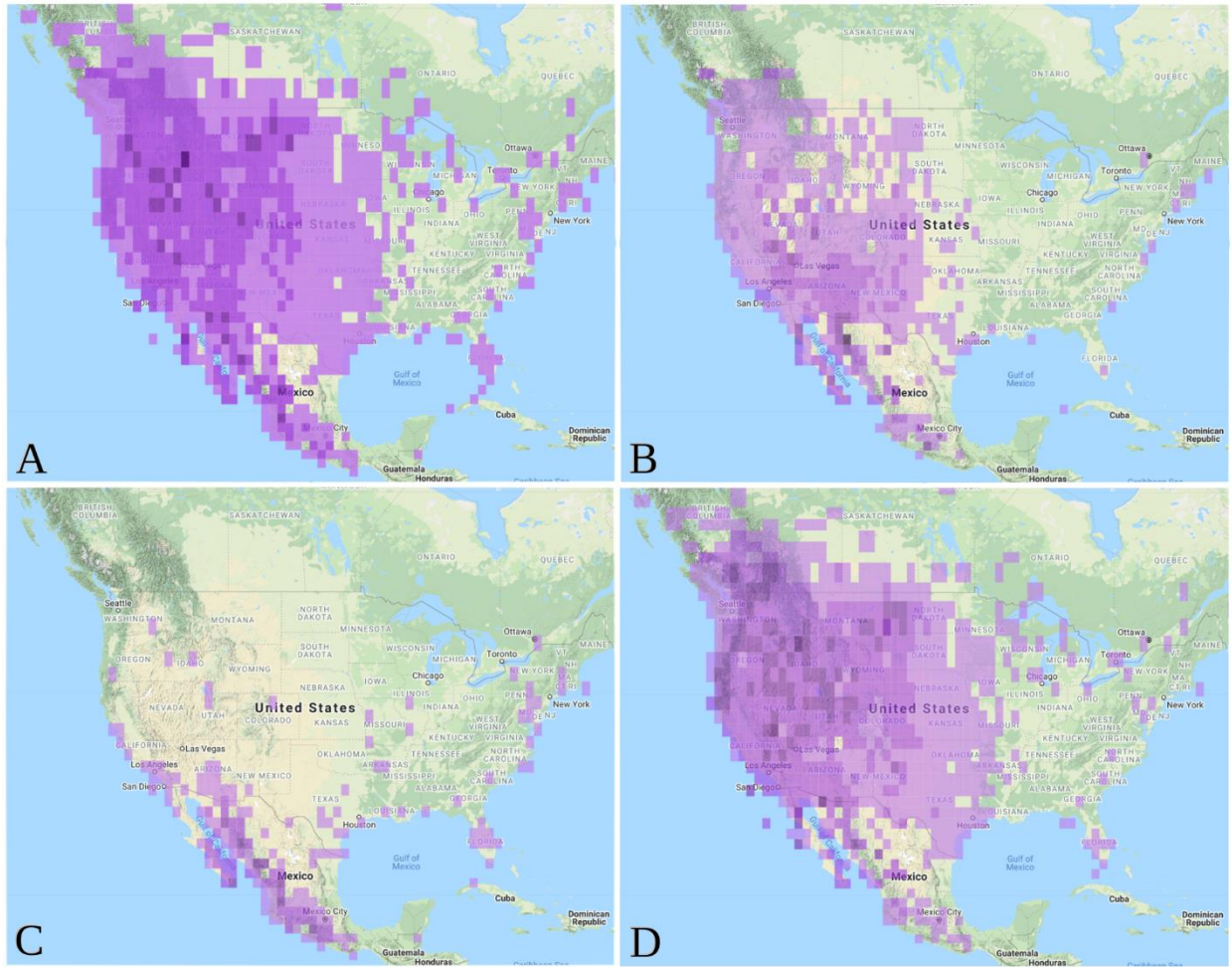


Figure 3: Map of Lazuli Bunting reports throughout all years of eBird data. Darker purple represents higher frequency of observation. (a) Year-round sightings (b) Sightings September through November (c) Sightings December through March (d) Sightings April through July. (Images provided by eBird (www.ebird.org) and created 5-22-21)

Lazuli Buntings arrive on the breeding grounds March through June, with southern breeders arriving earliest (Greene et al. 2020). First broods occur in late April through early June (again, depending on placement in the range) (Greene et al. 2020). Individuals breeding in the southern or middle portions of the range often lay a second brood and continue rearing chicks into late June and July (Greene et al. 2020). Populations of Lazuli Bunting undergo a pre-migratory fattening period beginning in July or August where individuals leave their mated pair

structure and assemble small flocks instead (Greene et al. 2020). Afterwards, they begin migrating southward, with males leaving before females and older birds leaving before hatch-year birds (Greene et al. 2020). Individuals remain in the monsoon stopover sites for about a month, and the population overall can be found there between late August and November (Greene et al. 2020). Then, the birds arrive at their wintering grounds in Mexico in October and November (Greene et al. 2020). The Lazuli Bunting is a case study which exemplifies molt migration phenology while also demonstrating how an individual's characteristics such as maturity and position in the range may affect behavior.

Significance to conservation

It is difficult to study migration as migratory behaviors within populations are difficult to describe and categorize. For instance, a challenge in study design and data collection is that samples of molt migrants at stopover sites may include molt migrating birds as well as those just passing through (Chambers et al. 2011). Very frequently, scientists may only access data on the presence or abundance of a species at various points rather than yearly movements of a particular individual. Furthermore, an individual's movements will not necessarily represent the set of migration strategies of the population. There are still many unanswered questions about migration strategies, their evolution, their influences, and their implications. In a quickly changing environment, research in movement and life history strategy is essential and urgently needed.

Environmental factors impact passerines greatly. For instance, there is evidence that monsoon rain quantities strongly impact the laying date of Mexican Jays (Brown and Li 1996). Environmental changes may change the availability of many resources spatially and temporally; however, many physical and behavioral traits relevant to migration are highly heritable (Rohwer and Irwin 2011). As such, ornithologists are concerned that passerines may not quickly adapt to changes in climate or land use. Therefore, conservation may be well served by understanding the drivers of migration strategy evolution.

For example, many conservation efforts have endeavored to conserve grasslands in Arizona. These efforts are invaluable, as large proportions of grassland-dwelling species are declining, and our new knowledge of molt migrant passerines places new urgency on this cause (Rosenberg et al. 2019, Chambers et al. 2011). Furthermore, it is important to consider molting habitats separately from breeding habitats, as evidenced by a 2011 study showing that several molt migrant species select certain stopover habitats at high rates which are distinct from their breeding habitat choices (Chambers et al. 2011).

To understand the best practices for managing passerine species, it is necessary to investigate factors which drive phenology (Pageau et al. 2020). Research in this field may reveal elements of migration strategy that impact a population's resilience to changes in climate or land use (Pageau et al. 2020). In this study, I aim to investigate the relationship between migration strategy and climate change by looking for differences in the way that the North American monsoon impacts molt migrant and non-molt migrant passerines.

Hypotheses and predictions

I hypothesize that monsoon precipitation patterns impact molt migrants more than they influence non-molt migrants. I predict that higher levels of monsoon precipitation will increase molt migrant populations. Non-molt migrant species may show qualitatively similar relationships with the monsoon, but I predict that these relationships will be weaker if present. Within a coherent region, I predict that change in abundance on breeding grounds between years for molt migrant species will show positive associations with monsoon precipitation amounts. For non-molt migrant birds, I predict that this relationship will be identifiable less often and that the strength of the association will be lower.

To test this hypothesis, I must assume that individual birds will return to the same region every spring (that is, that these populations are philopatric). This means that first-year birds will attempt to breed where they hatched, and older birds will migrate to their past breeding areas. Under this assumption, changes in abundance observed in the region do not reflect differential land use on the breeding ground by birds between years. As I predict that levels of monsoon rainfall impact bird abundances and habitat use, this assumption implies that changes in observed abundances are influenced by breeding success and not choices of breeding region. However, differential land use on the molting grounds remains possible.

To test this hypothesis, I use surveys of breeding birds within a set region to build linear regression models predicting changes in abundance between years based on precipitation variables and bird abundance. I predict that the mean of abundance changes calculated in a

sliding window of time, the amount of precipitation in the later months of the monsoon season, and the year could make a good model for year-to-year abundance change. The sliding window abundance changes account for the fact that abundance change partly follows a larger-scale population trajectory. The monsoon precipitation later in the season may be most significant because birds may be breeding and beginning migration during the early monsoon season; therefore, early precipitation may not affect molt migrants strongly. Finally, the year variable is another way to account for population trends that might not be related to the monsoon precipitation.

Methods

Bird data

The Breeding Bird Survey (BBS) is a joint effort of the United States Geological Survey and the Canadian Wildlife Service created to monitor over 400 bird species breeding in North America (Ziolkowski et al. 2010, USGS). Although BBS data are collected by volunteers, each survey follows a strict protocol. Breeding Bird Survey routes are randomly established following roadsides (Ziolkowski et al. 2010). These surveys occur annually during the peak of the breeding season, which may lie in May or June depending on the location (Ziolkowski et al. 2010). To maintain detection consistency, breeding bird surveys are not conducted on days with high winds or precipitation (Ziolkowski et al. 2010). Half an hour before sunrise on the survey date, participants arrive at their respective routes (Ziolkowski et al. 2010). Each route has 50

designated stops, where a single surveyor conducts three-minute stationary counts of birds heard and seen within a quarter mile (Ziolkowski et al. 2010). Surveyors are not allowed to pish, use playback, or employ other methods of increasing bird responses (Ziolkowski et al. 2010). The surveys typically take around four hours to complete (Ziolkowski et al. 2010). Due to its voluntary nature, the BBS coordinators cannot guarantee that every route will be run every year.

I found short lists of previously studied molt migrants in the primary literature which share a breeding region. Then, I identified suitable controls: passerine species which breed in the study site which are not identified as molt migrants in papers reviewing molt migration in passerines. I downloaded raw data from the Breeding Bird Survey for ten species, matching pairs taxonomically by family. I used four species in the family *Cardinalidae*; the molt migrants were Western Tanager and Lazuli Bunting, and the non-molt migrants were Blue Grosbeak and Black-headed Grosbeak. I used two species in the family *Icteridae*: the molt migrant Bullock's Oriole and the non-molt migrant Yellow-headed Blackbird. I used two *Vireonidae* species which were both in the genus *Vireo*: the molt migrant Warbling Vireo and the non-molt migrant Plumbeous Vireo. Finally, I used two flycatchers in the *Tyrannidae* family: the molt migrant Ash-throated Flycatcher and the non-molt migrant Western Kingbird.

I specified the years 1980 through 2019 and used data collected using the Standard BBS - 101 protocol. For each species, I downloaded the "breeding species summary data" with the "total number of individuals" option. This provides a dataset with columns for country, state, route, year, species code, and species total.

Bird Conservation Regions (BCRs) are ecologically distinct regions with coherent bird communities and habitats (U.S. NABCI). In 1998, the North American Bird Conservation Initiative developed 66 BCRs in North America, and these regions are commonly integrated into the presentation and analysis of bird survey data (U.S. NABCI). In this study, I analyzed the Great Basin bird conservation region (BCR9; figure 4). It is a vast, largely dry area with lowlands dominated by grass and- shrubland (U.S. NABCI). It includes pine forest habitats as well as several substantial wetlands in the form of marshes and lakes (U.S. NABCI). Given these dry conditions, the large spatial region, and the wide variety of habitat types, the Great Basin BCR is representative of the molt migrant breeding range.

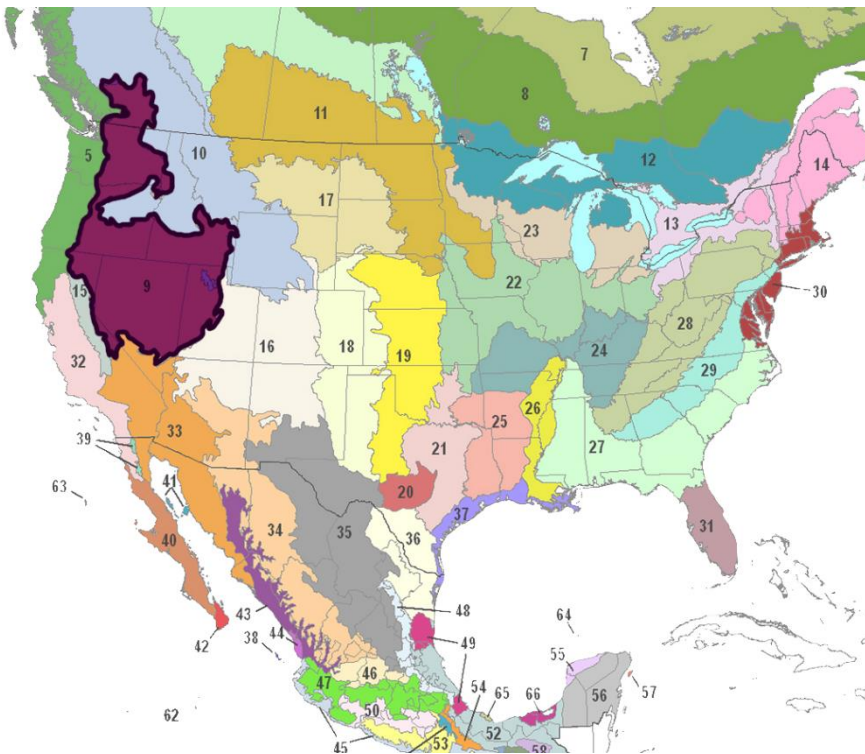


Figure 4: The Great Basin bird conservation region (edited from a map by NABCI)

Zero counts cannot be distinguished from unsurveyed routes in the breeding bird data. To add zero counts, I downloaded a global “routes” dataset matching routes with their respective BCRs (this was needed as route numbers were nonunique). Also, as all surveys are required to

report weather data, I downloaded a “weather” dataset to represent a comprehensive list of routes surveyed in each year. I then removed the records which failed to meet BBS standards. By merging these additional datasets to each other and then to my breeding summary dataset and assigning zero counts to those entries in the weather dataset that do not appear in the breeding summary dataset, I arrived at a full representation of birds detected in each route in each year.

In the resulting dataset, I calculated the average of the species counts per route for each year from 1980 to 2019. I then found the change in mean from year to year and deleted the final row which has no value for this variable (resulting in a dataset from 1980 to 2018). To compare abundance changes with precipitation in the initial year, I assigned these values to the initial year’s entry. Then, I calculated the mean values of these changes in mean abundances within a sliding five-year window using the R package `data.table`. As the three outermost years on each end (the years 1980, 1981, 1982, 2016, 2017, and 2018) cannot receive a value from this sliding window, they are assigned the nearest inner value. These variables are summarized in Table 1. I merged the bird data with the monsoon data by matching the year variables for each row.

Table 1: variables derived from monsoon data and breeding bird survey data.

Variable name	Variable description
wide prcp	sum of precipitation June through October
early prcp	sum of precipitation June through July
late prcp	sum of precipitation September through October
monsoon halfway	number of days from June 1 when sum of precipitation reaches half of the year's total
yearly mean	mean birds per route
yearly change in mean	mean in year $n+1$ minus mean in year n , assigned to the row for year n
sliding changes	mean of changes in mean in a five-year sliding window
year	numeric year value

Monsoon data

Daymet is a data product designed to provide daily weather parameters using interpolation and extrapolation (Daymet). It is supported by the U.S. Department of Energy and by NASA through the Earth Science Data and Information System and the Terrestrial Ecology Program (Daymet). I used a dataset of precipitation on each day of each year from 1980 to 2019 for 2 degree x 2 degree tiles over North America (Figure 5). I included only those tiles that receive large amounts of precipitation from the North American monsoon, and there were 47 such tiles. Using the dplyr package in R, I created the precipitation variables seen in Table 1.

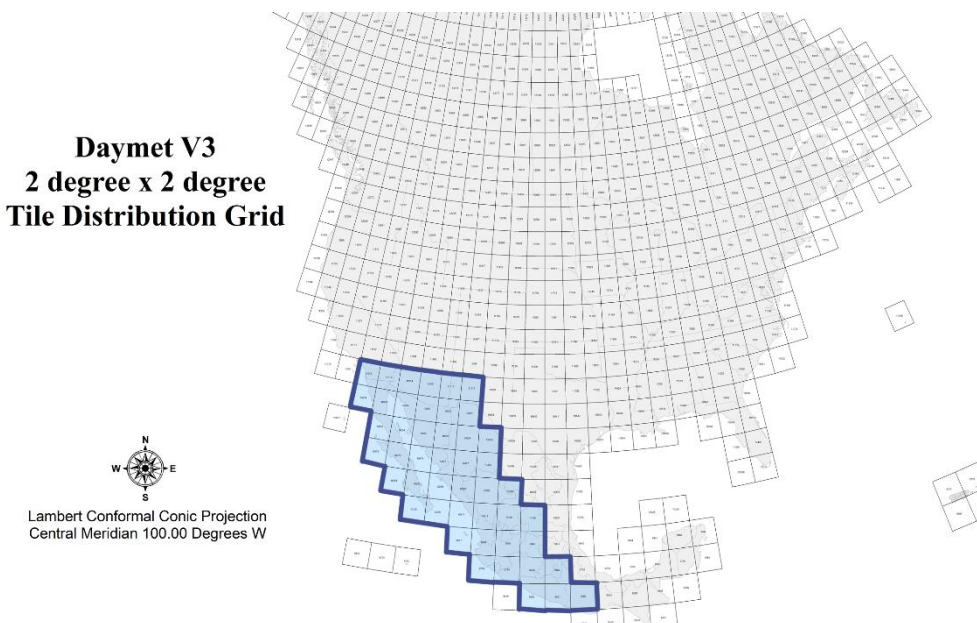


Figure 5: Precipitation tiles used from the 2 degree x 2 degree grid (edited from Daymet)

Analysis

I made several multiple linear regression models for the ten species. First, for each species, I modeled year-to-year abundance change using mean changes on a sliding window, sum of late precipitation, and year. This is the proposed model which tests my prediction about the importance of later season precipitation. Next, I created a model which uses every variable in table 1, and I used an Akaike information criterion (AIC) stepwise algorithm to remove terms from this model and arrive at a model that balances goodness of fit and simplicity.

I noted the general trajectories of abundances over time and found the mean across years of abundance. As this relationship was significant in nearly all cases, I noted the results of simple linear regressions modeling yearly changes in means using yearly means for each species in each BCR. Upon observing trends in these results, I conducted randomization tests for differences in means using the online analysis and visualization resource StatKey (www.lock5stat.com/StatKey/). Otherwise, I used R version 3.5.1 for all analyses.

Results

Predicted model

In the model predicted using a priori conjectures (modeling yearly change using sliding change, late precipitation, and year), I found no significant or near significant terms in the Lazuli Bunting, Blue Grosbeak, Black-headed Grosbeak, Yellow-headed Blackbird, and Western

Kingbird. In most of the other species, I found significant or near-significant slopes associated with the predictor variable sliding changes (Table 2). Late precipitation, however, was never significant in these models.

Table 2: Slopes for sliding window changes, late precipitation, and year in multiple linear regression models explaining year-to-year change in abundance. Species appear in family blocks with orange text for molt migrants and blue text for non-molt migrants. Bold values are significant at a 0.05 level, and underlined values are significant at a 0.10 level.

Species	sliding changes	late precipitation	year
Western Tanager	<u>1.28</u>	-4.51e-5	-0.00428
Lazuli Bunting	0.754	3.85e-5	-6.15e-4
Blue Grosbeak	0.473	-1.00e-4	1.23e-4
Black-headed Grosbeak	0.643	4.42e-6	-1.70e-3
Bullock's Oriole	<u>1.14</u>	-1.55e-5	0.00124
Yellow-headed Blackbird	-0.414	-3.12e-5	-0.0141
Warbling Vireo	1.34	-1.16e-5	3.71e-3
Plumbeous Vireo	0.954	3.71e-6	-1.16e-4
Ash-throated Flycatcher	0.486	-2.73e-5	1.41e-3
Western Kingbird	0.391	6.77e-5	-2.26e-3

AIC models

Of the models suggested by the AIC stepwise algorithm for each species, five of the ten involved precipitation variables (Western Tanager, Warbling Vireo, Plumbeous Vireo, Ash-throated Flycatcher, Western Kingbird). The model suggested for the Bullock's Oriole included only yearly means. Three species (Yellow-headed Blackbird, Black-headed Grosbeak, and Blue Grosbeak) had suggested models which used only yearly means and year. Finally, the Lazuli Bunting model used year, yearly means, and sliding window mean abundance changes as explanatory variables.

In these models, year usually had a small positive slope, and yearly means usually had sizable negative slopes. Sliding changes only appeared in three cases, but it typically had large positive slopes. Total precipitation appeared in two models, both of which were for molt migrants. In these, it had very small positive slopes (Table 3). Early precipitation appeared in equal frequency for molt migrants and non-molt migrants (two cases each). For the molt migrant cases, the slopes were small and negative; for the non-molt migrant cases, the slopes were very small and positive. Late precipitation never appeared in these models. The number of days to the halfway point was in the model for Western Tanager and had a small negative value. The intercepts in these models varied widely and were somewhat evenly split between positive and negative values.

Table 3: Models suggested by AIC stepwise algorithm for each species. Each number is the slope associated with the variable in the model except for those in the intercept column, which are the values of β_0 . Empty cells indicate variables which did not appear in the model for the species. Species appear in family blocks with orange text for molt migrants and blue text for non-molt migrants. Bold values are significant at a 0.05 level, and underlined values are significant at a 0.10 level.

Species	year	yearly means	sliding changes	total prcp	early prcp	late prcp	days to halfway	intercept
Western Tanager Lazuli	0.0819	-0.606		0.000252	<u>-0.000449</u>		-8.17E-02	-156
Bunting	<u>0.0117</u>	-0.397	0.735					<u>-22.4</u>
Blue Grosbeak	-0.00142	-1.00						2.85
Black-headed Grosbeak	0.034	-0.897						-66.1
Bullock's Oriole		-0.658						1.77
Yellow-headed Blackbird	-0.0589	-0.548						<u>123</u>
Warbling Vireo	0.0533	-0.538	1.06	3.46e-5				-0.0105
Plumbeous Vireo	2.00e-3	-0.543	0.822		<u>7.66e-6</u>			-4.00
Ash-throated Flycatcher	0.0234	-1.09			<u>-1.90e-5</u>			-45.8
Western Kingbird		-0.429			9.60e-5			<u>1.83</u>

Population information

The passerine populations studied differ substantially in density. As the metric for abundance used is mean birds per route in a year, I averaged these values across years for each

species. This average varied from 0.029 to 9.5, and its distribution across these ten species was skewed to the right (Figure 6).

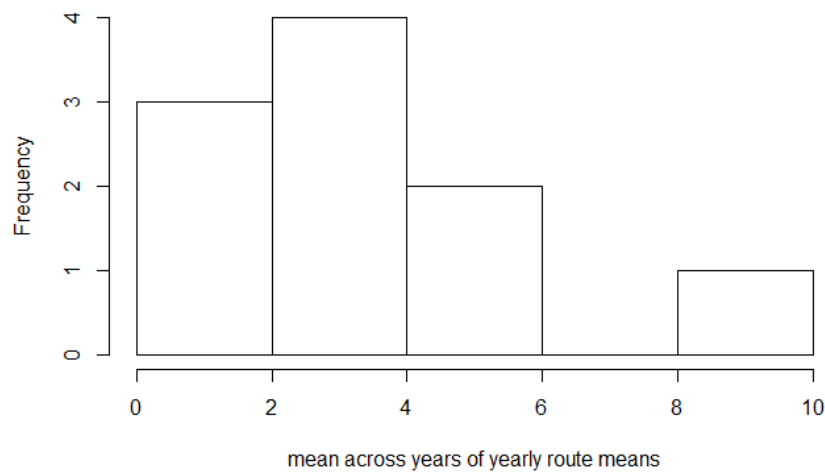


Figure 6: the distribution of abundances among the ten studied species

In addition, populations of the ten studied species trended in different directions. The observed abundances of Western Tanager, Lazuli Bunting, Black-headed Grosbeak, Warbling Vireo, Plumbeous Vireo, and Ash-throated Flycatcher showed some extended periods of increase (Figure 7a). The Bullock's Oriole and Western Kingbird seemed approximately stable, and the Blue Grosbeak and Yellow-headed Blackbird seemed to show extended periods of decline (Figure 7b, 7c). Even while adhering to these large-scale trajectories, many studied species show large fluctuations between years and on the short term.

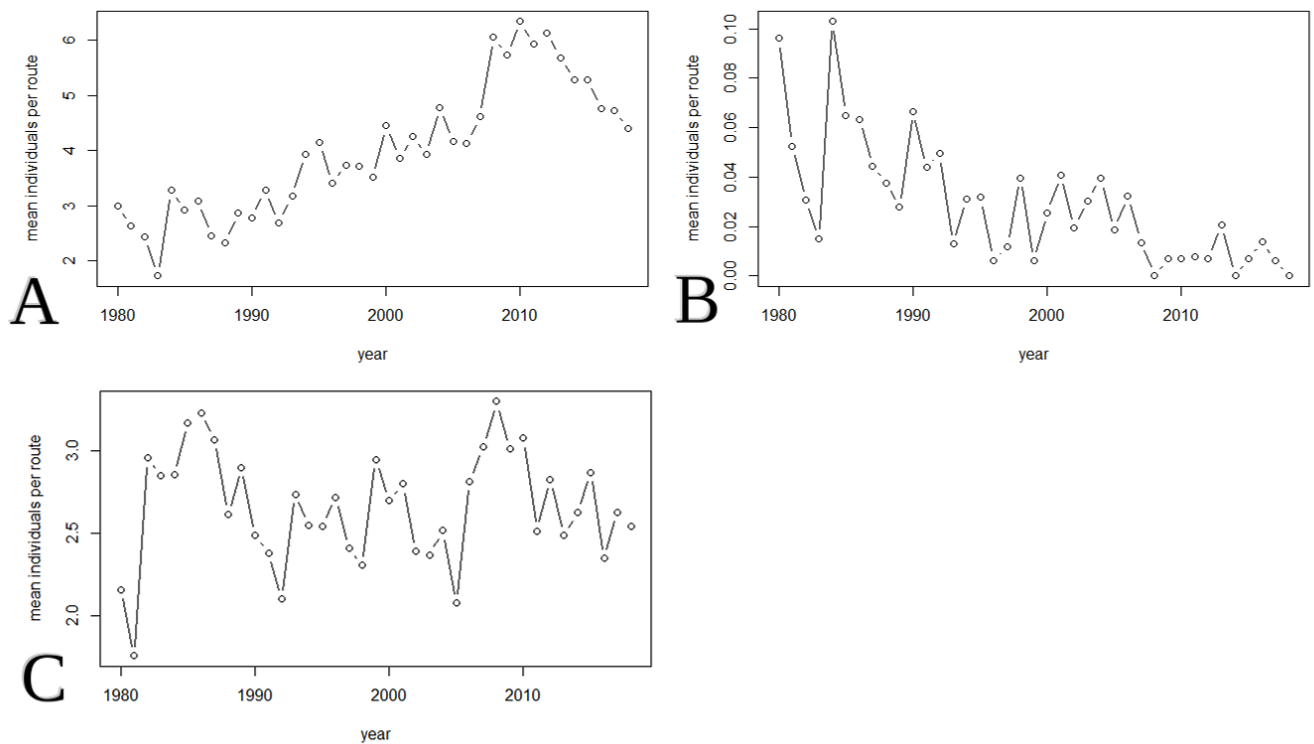


Figure 7: Abundance vs. year for (a) Warbling Vireo (b) Blue Grosbeak (c) Bullock's Oriole

Abundance change vs. abundance

In models predicting change in abundance using abundance in the initial year, both the intercept and slope terms were very frequently significant (Table 4). The least significant intercept term ($p=0.118$) and the least significant slope term ($p=0.145$) still had small p-values. These less significant terms come from the model for Warbling Vireo, a molt migrant.

In these regressions, the correlation coefficients for molt migrants appear higher than those for non-molt migrants, and there seems to be little overlap. The values of r for molt migrants lie between -0.352 and -0.238 with an outlier at -0.580 (Bullock's Oriole). The values

for non-molt migrants are between -0.563 and -0.456. A two-sided randomization test for difference in means between the two categories showed that molt migrant correlation coefficients were significantly greater than non-molt migrant correlation coefficients with an average difference of 0.144 (15,000 samples, $p=0.050$, $p=0.025$ for a one-tailed test). The mean was -0.348 for molt migrants and -0.485 for non-molt migrants.

Similarly, the slopes associated with abundance in molt migrant models are higher than those of non-molt migrants with little overlap. The slopes for molt migrants lie between -0.248 and -0.116 with an outlier at -0.657 (Bullock's Oriole). The slopes for non-molt migrants lie between -0.538 and -0.374. A two-sided randomization test for difference in means between the two categories showed that molt migrant slopes were significantly greater than non-molt migrant slopes with an average difference of 0.205 (15,000 samples, $p=0.050$, $p=0.025$ for a one-tailed test). The mean was -0.277 for molt migrants and -0.439 for non-molt migrants. Note that I conducted both randomization tests two times as I changed this test from one-sided to two-sided. Here, I report the latest result.

Table 4: Intercepts, slopes, and correlation coefficients in simple linear models of abundance changes using current year abundance. Species appear in family blocks with orange text for molt migrants and blue text for non-molt migrants. Bold values are significant at a 0.05 level, and underlined values are significant at a 0.10 level.

Species	intercept	slope	correlation coefficient
Western Tanager	<u>1.072</u>	<u>-0.179</u>	-0.305
Lazuli Bunting	0.705	-0.248	-0.352
Blue Grosbeak	0.013	-0.538	-0.563
Black-headed Grosbeak	0.811	-0.375	-0.456
Bullock's Oriole	1.768	-0.658	-0.580
Yellow-headed Blackbird	4.557	-0.469	-0.491
Warbling Vireo	0.518	-0.116	-0.238
Plumbeous Vireo	0.047	-0.392	-0.453
Ash-throated Flycatcher	<u>0.144</u>	-0.186	-0.264
Western Kingbird	2.562	-0.423	-0.463

Discussion

Population information

The differences in density between species did not noticeably impact the analysis. However, species which persist at naturally lower densities may differ from more abundant species in life history and behavior. Furthermore, the Great Basin bird conservation region lies in the core of the breeding range more so for some species than for others. The characteristics of the birds breeding at the edges of their range may differ from those of birds breeding at the center. For example, later migrants may need to find territories farther away if earlier-arriving individuals position themselves at more optimal sites first. Finally, the monsoon may impact

species with declining population trajectories differently from those with steadily fluctuating or increasing numbers. This study could not address this possibility; however, future research which can investigate these factors would be biologically interesting and relevant to conservation. Additionally, the assumption that the studied populations are philopatric appeared reasonable due to the high heritability of traits related to migration and the prevalence of philopatry among birds, but I found no direct support for this claim.

Models

Within my theorized models, I did not find precipitation late in the monsoon season to be a useful predictor for population change. This does not support my prediction that there would be a positive association between later precipitation and population change in molt migrants. If birds do not use the area in the way that I expected, an explanation could be that molt migrants arrive earlier or travel for shorter periods of time than predicted. In the case that my hypothesis is correct, birds do use the monsoon zone in those times, but the effect was not detectable using this study's methods. It is likely that too many other factors influence abundance changes as detected in the Breeding Bird Survey to truly find the impact of late precipitation.

Another reason the study might not pick up on the relationship between abundance changes and late precipitation is that the passerines studied do use precipitation late in the season, but their population changes are minimally affected within the observed range of late precipitation values. If these populations do occur in the late monsoon season (and figure 3

suggests that this is true for at Lazuli Buntings), it is easy to reason that there are levels of precipitation at which bird populations would respond differently. That is, if birds are in the monsoon zone at those times, then late precipitation would influence change in abundance at some point. Those more distinctive levels of rainfall may just not appear in the range of values naturally observed in this time frame. Other ways that birds could use this precipitation without showing it in the model are that different parts of the population have differing relationships to monsoon rain timing- they migrate at vastly different times to much different latitudes, after all. Stratifying by these sub-populations may reveal clearer relationships.

Among the AIC-suggested models, precipitation had very small effect sizes, usually on the order of 10^{-6} to 10^{-4} (in units of birds per route). Early precipitation seemed to have slightly greater effect sizes for molt migrants than non-molt migrants. Also, early precipitation in molt migrants was associated with smaller or more negative population changes, while it was associated with increases in population for non-molt migrants. These observations come from extremely preliminary results, but these findings do suggest different relationships to monsoon precipitation among passerines of different migration strategies. This study suggests not only that non-molt migrants may be impacted by monsoon precipitation, but that the North American monsoon may influence bird species of different molt strategies in diverging ways. It is not surprising that the monsoon impacts non-molt migrants, as they do spend time moving through the region even if they do not molt there. It is worthwhile to investigate this relationship further in future studies.

In the AIC-suggested models, total precipitation appeared with positive effects on two molt migrant species (Western Tanager, Warbling Vireo). This fits the hypothesis that increased monsoon rains will positively impact molt migrant population change. It may be that this relationship holds true for all molt migrant and non-molt migrant species, but this study did not find evidence of that. Western Tanager was the only species for which the AIC-suggested model included the number of days to halfway; strangely, the days to halfway term has a relatively large negative effect while the early precipitation has a smaller negative effect. While this may seem contradictory, it may reflect some nuance in timing and quantity of precipitation that this study lacks the power to discern.

The intercept terms in these models cannot sensibly be compared across species, as models for different species incorporated different explanatory variables. The precipitation and year variables typically took on large values, which can result in highly variable intercept values. Future studies which have more statistical power may be able to meaningfully compare the same models across species. Otherwise, it may be useful to standardize the values of these inordinately large variables.

Density Dependence

The models which used yearly means to predict year-to-year abundance changes clearly indicate density-dependent effects in essentially all ten of the species studied. The positive intercept values implied that populations would increase at lower abundances, while the negative

slopes indicated that populations would grow more slowly and then begin to decrease as the population sizes increased (Figure 8). This is an indication of density-dependence, as population growth rates are high when resources are plentiful in relation to bird abundance, and populations decline when they are relatively large. The precise value of the intercept is not accurate, as the value is extrapolated from data that do not cover that range. The qualitative interpretation that populations would grow fastest at miniscule densities seems qualitatively wrong for this system, as populations would be expected to enter an extinction vortex at these abundances. However, intercept values do reflect the fact that abundance changes are highest at the lower end of the abundances found in this study.

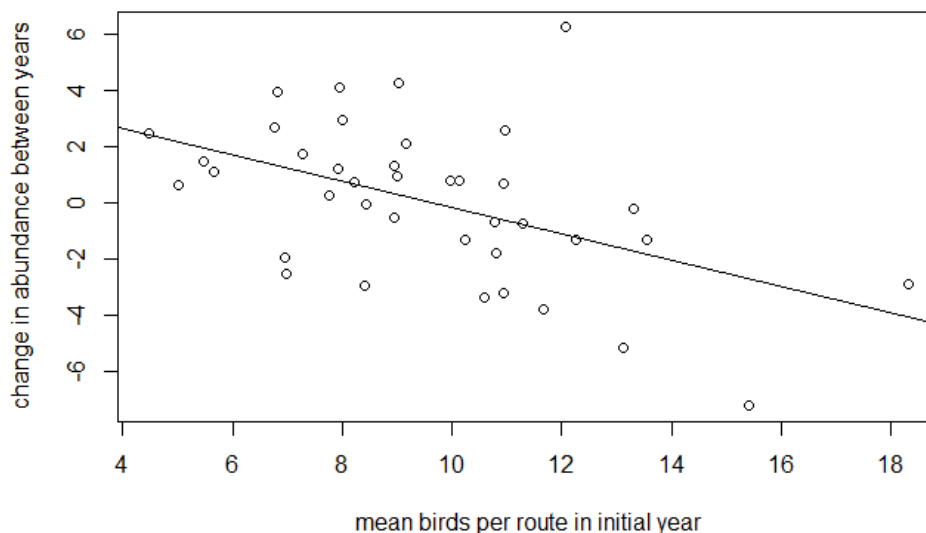


Figure 8: abundance change vs. initial abundance and a best-fit line (predicted change = $4.557 - 0.469 \times \text{abundance}$) for the Yellow-headed Blackbird, a non-molt migrant.

It appears that density-dependent effects for molt migrants have weaker impacts on the population compared to non-molt migrants. The density fluctuations that result from density dependence may appear smaller in molt migrants than in other passerines. A preliminary explanation for this effect is that the abundant resources of the monsoon region may reduce the

constraints that result in density-dependence; thus, populations may be controlled more by factors other than food or territory resources. It is also possible that other forces continually kept molt migrant populations low enough to avoid much intraspecific competition, but this does not seem as likely.

Matching species by family allowed me to control for some confounding variables. However, it is strange that Bullock's Oriole shows even stronger evidence of density dependence than its non-molt migrant match, the Yellow-headed Blackbird. The relationship may be different in different taxonomic groups, and my sample may emphasize those groups for which this pattern holds true. Although the relationship appears strong enough to conclude that molt migrants experience weaker density-dependent effects, further study which stratifies by family may reveal more granular differences. It would be valuable to study the mechanisms for this effect as well, if possible. (Figure 7a shows an example of minimal fluctuation in a molt migrant, figure 7b shows large fluctuations in a non-molt migrant, and 7c shows large fluctuations in the Bullock's Oriole, the outlier molt migrant.)

Nuances and further directions

Strategies for situating molt in migration show complexity beyond our present understanding. Molt migration and non-molt migration are not easily defined and do not perfectly describe many species. There is evidence of different molt strategies arising over relatively small lengths of evolutionary time, and this suggests that molt is rather labile (Tonra

and Reudink 2018). Regional climates are an important driver of evolution of unconventional molt strategies, and the North American monsoon is particularly influential (Rohwer et al. 2009).

There are many potential factors for diverging strategies in molt and migration. For example, among passerines breeding in the western U.S., rates of molting vary greatly and depend on such factors as whether birds are strictly transient through the monsoon zone or whether they breed there (Voelker 2004). Also, age may greatly influence these behaviors. In some species where adults migrate and molt on the wintering grounds, juveniles molt before migrating instead (Rohwer et al. 2005). This variation may be because juvenile plumage quality differs between species (Rohwer et al. 2005).

There are nuances too in how molt migrants use the monsoon zone. There is some evidence that habitat use by Lazuli Buntings varies based on monsoon precipitation. In a 2011 study, the species was found at higher rates in grasslands in very dry years than in very wet years, which could mean that relevant grasses produce more seeds in drier years (Chambers et al. 2011). In the very wet year, these buntings were found in greater abundance in desert scrub instead (Chambers et al. 2011). There is evidence, also, that Lazuli Buntings may broaden their habitat use during wetter monsoon seasons; that is, they may be found in a larger set of habitat types (Chambers et al. 2011). This broader use of habitat during wetter years true for some chiefly insectivorous species as well (Chambers et al. 2011).

Furthermore, there is evidence that Lazuli Buntings stage outside the southern monsoon zone and instead use the Arizona-Mexico border to molt (Voelker 2004). This pattern of

avoiding the southern monsoon zone was also found in Baird's Sparrows and Painted Buntings which molt in the monsoon area (Voelker 2004). This suggests that heavy rainfall in the southern monsoon zone may impact thermoregulation or decrease available food or foraging conditions during molt, meaning that some parts of the monsoon zone may facilitate rapid molt at certain times, but others do not (Voelker 2004). Altogether, these species show that higher precipitation levels do not always benefit birds and reinforce the notion that non-molt migrants use the monsoon zone as well.

The evolution of migration strategy has many influences. Though the push-pull hypothesis is most frequently imagined in the framework of populations that molt in the monsoon region, another form of "pull" in the various types of molt migration is the migration to more productive high elevation habitats (Rohwer et al. 2005). Furthermore, there are many other factors which contribute to the evolution of molt and migration strategy. Breeding season time constraints vary between species, as some birds require longer periods of parental care (Rohwer et al. 2005). Certain life histories necessitate slower rates of flight feather replacement, and flycatching insectivores especially need these gradual molts to maintain aerial maneuverability (Rohwer et al. 2005). The rates and methods of replacement of primary flight feathers are associated with the evolution of body size (Rohwer et al. 2009). Finally, methods of territoriality at various places also influence the favorability of different movement strategies (Pageau et al. 2020).

Understanding how environmental conditions impact avian migration is essential to studying life history, phenology, and morphology. Furthermore, weather, climate, and habitat

availability will change, but birds will likely retain historic genetic instructions that influence their annual movements. As such, it is important to identify how this altered future will impact migratory populations. This knowledge helps to identify and preserve important geographic areas, species, habitats, and conditions.

Migratory behaviors are highly complex, varying across taxa as well as life stage (Pyle 1997, Rohwer et al. 2005). Behavior and morphology related to molt and migration distinguish populations and drive speciation due to the high heritability of these traits and the oft-reduced fitness of hybrids (Battey et al. 2018). Migration strategy connects life history, ecology and conservation, and there is much value in its study. Further research in defining migration types and clarifying the full range of strategies within “molt migration” and “non-molt migration” is vital. This knowledge would empower us to investigate why climatic factors led to evolution of molt migration in some western-breeding species and not others. Finally, as changes in climate and land use pose special risks for migratory populations, understanding relationships between migration strategy, climate patterns, and habitat selection will help us define conservation priorities and direction.

Acknowledgements

I am very grateful to Judy Stone for shaping this project with me and for the guidance. Thank you for believing in me. I would also like to thank Catherine Bevier and Allison Barner for the insightful feedback on this paper. I appreciate my friends Zelia Sequeira and Peter

Fabinski for troubleshooting code with me and making it fun to wrangle data. Very many people played helped me in very many ways during my time in college, and I think of that often.

Finally, I cannot forget that this project relies on the efforts of numerous BBS coordinators, volunteers, and subjects. I am grateful to the people and the birds who make projects like this possible.

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