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Abstract. Climate change is having a dramatic effect on many migratory species. Changes in climate may lead to changes in food availability or other proximate cues that affect migratory behavior. We used 13 years (2000–2012) of data on songbird banding and raptor migration counts and captures during autumn migration in the intermountain West to evaluate whether regional temperature or precipitation or hemispheric climate indices predicted autumn migratory timing and energetic condition. We examined overall trends and evaluated the effects of diet and migratory distance on phenology and conditional responses. For the 13-year study period, no temperature, precipitation, or climate index trends were evident. There was no change in migratory timing for all species combined, but trends were apparent when evaluated by diet and migratory distance. The magnitude of these changes varies by diet and by migratory distance, but not as predicted by previous research of autumn timing in other parts of the globe. Long-distance migrants tended to migrate later in autumn, whereas short-distance migrants exhibited no change in timing. Annual variation in timing was predicted by regional temperature and precipitation and by hemispheric climate indices, and the predicted effects differed by diet and migratory distance. Granivores responded to the broadest set of climate indices, whereas avivores responded to the least. Frugivores responded with the greatest magnitude to annual variation in climate. We did not measure food availability but in most cases the predictive effect of climate on migratory timing of birds was consistent with predicted effects on food. Frugivorous birds migrated earlier in warmer years when fruit quality and quantity were expected to be lower. Energetic condition measurements supported the food hypotheses in some, but not all cases. The different responses of species to annual variation in climate suggest that different species integrate difference cues in their decision to migrate.

Key Words: Accipiter cooperii, A. striatus, Empidonax oberholseri, Idaho, Junco hyemalis, Oporornis tolmiei, Pipilo maculatus, Spizella passerina, timing, *Zonotrichia leucophrys.*

Climate change has influenced biotic communities and those impacts may be amplified in the coming decades. Plant and animal distributions (Parmesan and Yohe 2003, La Sorte and Thompson 2007, Huntley et al. 2008) and phenologies are changing (Cotton 2003, Gordo 2007, Nufio et al. 2010, Anderson et al. 2012). Changes in distributions and phenology may have complex and dramatic impacts on food webs when responses to climatic shifts differ between species in different trophic levels. For example, some butterflies and moths have been shown to migrate earlier as spring warming advances, whereas timing is unchanged for their predator, the Pied Flycatcher (*Ficedula hypoleuca;* Altermatt 2010). A mismatch has been the hypothesized cause of population declines observed in the Pied Flycatcher (Both and Visser 2001, Both et al. 2006).

Annual variation in climate adds additional complexity, making it more difficult to identify responses of organisms in complex food webs to these changes. Prey abundance often varies with daily weather patterns as well as annual fluctuations. Blancher and Robertson (1987) found that flying insect abundance varied with daily temperature and date, while annual differences were explained by the previous year's precipitation. Bell (1985) found that arthropod abundance declined in periods of drought. An increase in a previous year's precipitation and earlier spring warming can advance all phases of plant phenology including fruiting and seeding (Inouye 2008, Lambert et al. 2010). An advancement may cause plants to flower earlier, exposing them to greater frost mortality, which can decrease food for frugivorous and granivorous birds (Inouye 2008). Warmer temperatures may decrease the number of flowering plants, number of seeds per unit area, and the availability of lightweight seeds that some species require, or increase seed production and germination rates (Meunier et al. 2007, Gao et al. 2012). Mismatch of timing has larger potential effects among individual species in habitats where prey fluctuates sharply than in habitats with a more constant prey supply such as forests versus marshes (Both et al. 2009, Zuckerberg et al. 2011).

For migratory species such as birds, the ability to respond to changing resources may depend on annual cycle constraints such as diet, migration distance, and weather. During spring migration, short-distance migrants have shown a greater response to change in climate, possibly because of a greater sensitivity to changing weather patterns (Butler 2003). Earlier spring migration and earlier breeding can lead to greater re-nesting or earlier autumn departures (Cotton 2003, Halupka et al. 2008, Lehikoinen et al. 2010), but advancement of spring migratory timing may be constrained in some species by a lack of physiological or behavioral plasticity (Both and Visser 2001, Dawson 2008).

The majority of avian climate studies have focused on timing of spring migration and the initiation of breeding. The effect of climate change on autumn migration has generally received less attention, with a few notable exceptions (Jenni and Kéry 2003, Van Buskirk et al. 2009, Filippi-Codaccioni et al. 2010, Rosenfield et al. 2011). Autumn migration represents a significant portion of the annual cycle of avian migratory species and plays a large role in their annual survival (Sillett and Holmes 2002). Evolutionary pressure on energetic condition can be strong, but few studies have evaluated how condition is affected by changes in climate or phenology (Swanson et al. 1999). In eastern North America, autumn migration has become earlier among long-distance Neotropical migrants, but is later for short-distance temperate migrants (Van Buskirk et al. 2009, Rosenfield et al. 2011). In Europe, autumn migration has also advanced among long-distance migrants, while no change or later departures were measured in short-distance migrants or bird species with a variable number of broods (Jenni and Kéry 2003, Filippi-Codaccioni et al. 2010).

We used 13 years of data (2000–2012) from two migratory monitoring stations to evaluate the correlation of climate change on the autumn migration of songbirds and raptor species that prey on songbirds in the western United States. We hypothesized that annual variation in climate would explain annual variation in timing and energetic condition as we expect weather to impact food responses directly; this is believed to be the ultimate driver of migratory behavior (Newton 2008). We hypothesized that changes over time in migration phenology would depend on migration distance, diet, or both. Specifically, we predicted that long-distance Neotropical migrants would migrate earlier or have no change, whereas short-distance temperate migrants would migrate later (Jenni and Kéry 2003, Van Buskirk et al. 2009, Rosenfield et al. 2011). Also, we predicted that climate effects on phenology would differ

dependent upon diet as weather should influence food availability differently. Alternatively, migratory birds could show more plasticity in body condition than in phenology.

METHODS

Study Sites and Species

The study was conducted in southwest Idaho along the Boise Foothills, which comprise north–south trending peaks and hills in the Boise Mountains. The foothills form the southernmost extent of the central Idaho mountains. Specifically, our two study sites were Lucky Peak (1,845 m), located 12 km east of Boise, Ada County, Idaho (43° 36′ N, 116° 03′ W), and Boise Peak (1,992 m), located 14 km northeast of Boise, Boise County, Idaho (43° 42′ N, 116° 05′ W). We obtained songbird counts and measures at Lucky Peak, raptor counts at Lucky Peak, and raptor measures at both

Lucky Peak and Boise Peak. The study area is part of the intermountain corridor migratory flyway (Goodrich and Smith 2008) and is located at the boundary between the mostly forested mountains to the north and the shrub steppe to the south (Carlisle et al. 2004).

We started with an initial list of abundant birds, including 25 species of songbirds and two species of primary bird-eating raptors. We selected the top 17 species of songbirds and top two species of raptors based on capture volumes that did not show trends in total volume or the ratio of juveniles to adults during the duration of our study (Table 11.1). Estimates of phenology trends may be biased if the sampling of cohorts with different migratory timing changes over time (R. A. Miller, pers. obs.). We chose to focus on the most abundant species to maximize compatibility with our generalized data collection approach, to minimize the influence of outliers, and to enable the broadest general conclusions possible (minimum

TABLE 11.1

Seventeen songbird species and two raptor species, in taxonomic order, used for analysis of diet, migratory distance, and climate on passage date, and energetic condition (mean ± SE) of migratory landbirds in the Boise Foothills, Idaho, 2000–2012.

Species	Diet[a]	Distance	Mean passage	Mean condition
Sharp-shinned Hawk (*Accipiter striatus*)	Birds	Short	266.2 ± 0.10	2.04 ± 0.00
Cooper's Hawk (*Accipiter cooperii*)	Birds	Short	262.6 ± 0.10	2.67 ± 0.01
Hammond's Flycatcher (*Empidonax hammondii*)	Insects	Long	237.2 ± 0.55	3.37 ± 0.01
Dusky Flycatcher (*Empidonax oberholseri*)	Insects	Long	222.9 ± 0.24	3.94 ± 0.01
Warbling Vireo (*Vireo gilvus*)	Insects	Long	227.2 ± 0.37	4.24 ± 0.01
Mountain Chickadee (*Poecile gambeli*)	Insects	Short	243.8 ± 0.98	3.75 ± 0.01
Red-breasted Nuthatch (*Sitta canadensis*)	Insects	Short	250.6 ± 0.66	3.58 ± 0.01
Ruby-crowned Kinglet (*Regulus calendula*)	Insects	Short	266.1 ± 0.15	3.34 ± 0.00
Hermit Thrush (*Catharus guttatus*)	Insects	Short	259.6 ± 0.87	3.54 ± 0.02
American Robin (*Turdus migratorius*)	Fruit	Short	259.9 ± 0.98	3.60 ± 0.02
Townsend's Warbler (*Setophaga townsendi*)	Insects	Long	243.7 ± 0.48	3.69 ± 0.01
Wilson's Warbler (*Cardellina pusilla*)	Insects	Long	241.2 ± 0.43	4.51 ± 0.01
Spotted Towhee (*Pipilo maculatus*)	Seeds	Short	237.4 ± 0.41	6.56 ± 0.01
Chipping Sparrow (*Spizella passerina*)	Seeds	Short	230.4 ± 0.48	3.68 ± 0.01
White-crowned Sparrow (*Zonotrichia leucophrys gambelii*)	Seeds	Short	261.3 ± 0.11	5.79 ± 0.01
Oregon Junco (*Junco hyemalis, oreganus* group)	Seeds	Short	271.7 ± 0.20	4.15 ± 0.01
Western Tanager (*Piranga ludoviciana*)	Fruit	Long	237.7 ± 0.23	4.00 ± 0.01
Black-headed Grosbeak (*Pheucticus melanocephalus*)	Fruit	Long	225.1 ± 0.56	4.85 ± 0.02
Pine Siskin (*Spinus pinus*)	Seeds	Short	228.4 ± 0.57	3.40 ± 0.03

[a] Diet guild information sourced from Sedgwick 1993, 1994, Chilton et al. 1995, Greenlaw 1996, Dawson 1997, Middleton 1998, Wright et al. 1998, Ammon and Gilbert 1999, Ghalambor and Martin 1999, Hudon 1999, Mccakkum et al. 1999, Sallabanks and James 1999, Bildstein and Meyer 2000, Gardali and Ballard 2000, Nolan et al. 2002, Curtis et al. 2006, Swanson et al. 2008, Ortega and Hill 2010, and Dellinger et al. 2012.

capture rates > 30 birds per year per species). We acknowledge that climate is likely influencing rare species as well, but a more focused study approach would be warranted for those situations. We categorized the migratory distance for each species as long distance if their winter range was clearly separated from their breeding range and the bulk of their winter range was south of the US–Mexican border; otherwise, we classified them as short-distance migrants (Table 11.1). We classified the diet for each species as avivore, insectivore, granivore, or frugivore based upon their primary diet during breeding and early autumn migration stages. Nearly all nonraptorial species of birds consume insects to some degree, but we assigned species to other diets if plant materials made up a significant portion of their diet during breeding or autumn migration. For example, Western Tanagers (*Piranga ludoviciana*) eat insects but we classified the species as a frugivore because the diet is primarily fruits during autumn. In contrast, the Ruby-crowned Kinglet (*Regulus calendula*) was classified as an insectivore because its diet is almost entirely insects and insect products (Hudon 1999, Swanson et al. 2008).

Songbird and Raptor Survey Methods

We captured songbirds at Lucky Peak using 12 m × 2.5 m × 36 mm mesh mist nets in mountain shrubland habitat (Carlisle et al. 2004). The standard operation consisted of 10 nets operated daily for 5 hours beginning at sunrise from 16 July to 15 October, except in the case of high winds or continuous precipitation. We trapped migrating raptors at both sites using a variety of traps (dho-gaza, bow net, and mist net) and avian lures (Bloom et al. 2007). Captured birds were identified to species, age, and sex (Pyle 1997, 2008). We recorded date of capture, wing chord length, mass, and other morphological characteristics of each bird. For the purpose of this analysis, birds were not counted on their second or subsequent captures within or among years (Miller et al. 2011). We used Julian date to represent each bird's passage date. We divided mass by wing chord length cubed to calculate a size-corrected mass as an index to energetic condition (Swanson et al. 1999, DeLong and Gessaman 2001). We multiplied this value by 100,000 to avoid influences of rounding and to make the calculated measurements easier to report (Winker et al. 1992). Within a given

species, we considered birds with a higher size-corrected mass to be in better energetic condition relative to birds with lower size-corrected mass.

We conducted raptor migration counts at Lucky Peak using standardized methods (Hoffman and Smith 2003). Migrating raptors were counted daily from 25 August through 31 October by a minimum of two trained observers. Counts were curtailed only during periods of prolonged precipitation. Counts began at 12:00 MST during August and 10:00 MST for the remainder of the season and continued throughout the day until raptor flights ceased, usually between 17:00 and 19:00 MST. Best efforts were made to ensure that only migrating raptors were counted (Kaltenecker et al. 2012).

Climate Data

We obtained monthly temperature and precipitation data during the study period from the Global Historical Climatology Network (GHCN) Daily, version 2 (US Department of Commerce 2012). The data are provided as monthly means for temperature and monthly totals for precipitation, and they have been subjected to a suite of quality assurance. We chose climate data from stations spread across the Northern Rockies Bird Conservation Region (BCR, US NABCI Committee 2000, Figure 11.1). We restricted our area of consideration to portions of the Northern Rockies BCR north of our monitoring station and west of the continental divide to best represent the breeding areas of the birds migrating through southwestern Idaho. We further restricted the data to that gathered from weather stations greater than 50 km apart and with complete data sets over our 13-year study period, resulting in the use of data from 17 weather stations (Figure 11.1). We averaged the data from the 17 stations to produce a monthly index for temperature and precipitation across the region. Our intent was to generate broad weather averages across the region where our sampled birds breed, and we made no attempt to further correct for latitudinal or elevation effects.

We obtained monthly data for two atmospheric pressure indices from the National Center for Atmospheric Research. The North Pacific index (NPI) is an area-weighted sea level pressure measurement from the North Pacific intended to measure variations in atmospheric circulation
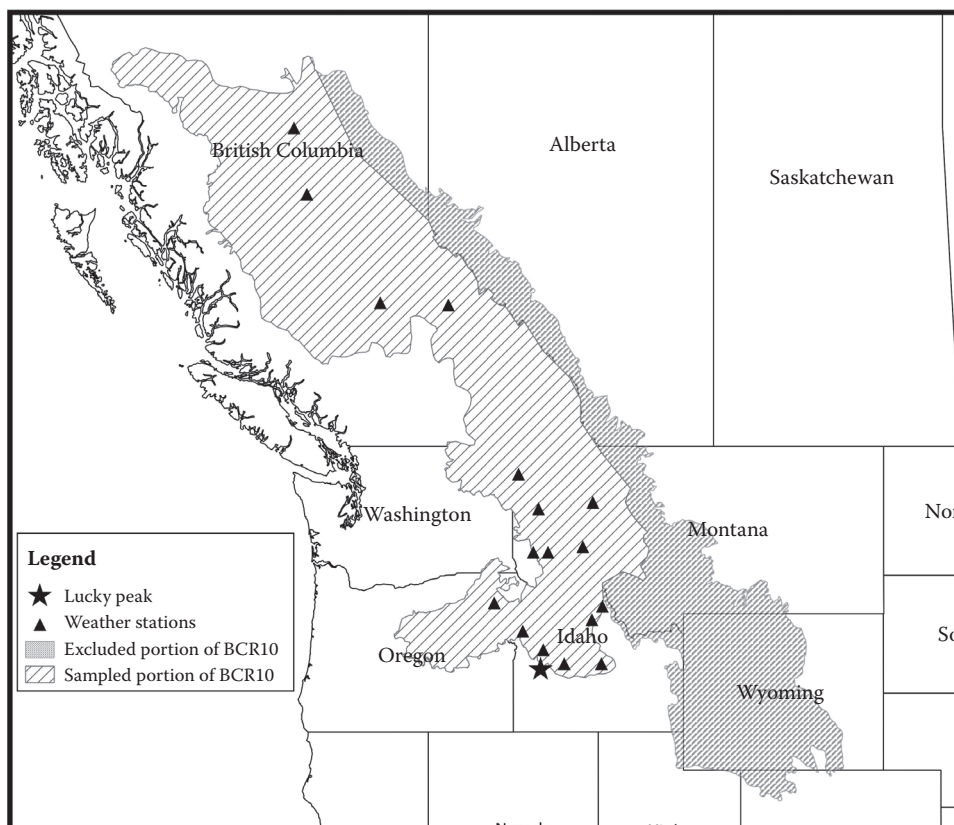
Figure 11.1. Map of Bird Conservation Region 10 in the northern Rocky Mountains, separated by the continental divide with eastern portion excluded from consideration. The map includes locations of 17 weather stations in the western portion of the BCR that had consistently reliable data over the period of this study and the location of our "Lucky Peak" monitoring station. The "Boise Peak" monitoring station was situated 11 km NNW of Lucky Peak (not pictured).

(Trenberth and Hurrell 1994, Hurrell and National Center for Atmospheric Research Staff 2013). The multivariate El Niño/southern oscillation index (MEI) is a standardized combination of six common El Niño measures focusing on the broader Pacific region (Wolter and Timlin 1993, National Center for Atmospheric Research Staff 2013). We included the hemispheric-scale indices to represent more general and larger scale climate influences not captured by regional temperature and precipitation indices and because they have been shown to be influential on the timing of avian migration (Nott et al. 2002, Van Buskirk et al. 2009). Higher values for each index are expected to be correlated with warmer temperatures, drier winters, and extreme weather events in the northern–western United States.

For each climate/weather index we created a 3-month index (July–September), a 6-month index (April–September), a 9-month index (January–September), and a 12-month index (previous October–September). The indices align well with peak periods of avian migration in Idaho and with standardized "water-year" measurements reported for precipitation. We created the indices for temperature, NPI, and MEI by averaging the monthly values across 3, 6, 9, and 12 months. We created the index for precipitation by summing across 3, 6, 9, and 12 months. Climate indices and year were scaled and centered to assist in model convergence. Centering was performed by subtracting the mean of the index over the length of the study period from each value. Scaling was performed by dividing each value by the standard deviation of the index.

Statistical Analyses

We checked for trends in each climate index at each time scale using linear models with year

as the predictor and the climate index as the response. We used an alpha level of 0.05 to measure significance of these trends. For analyses of migratory timing and energetic condition we followed the same analytical procedure. We used generalized linear mixed modeling and maximum likelihood with a Gaussian distribution for all analyses (Zuur et al. 2009). In each case, we included species and year (scaled and centered) as random effects. For each climate index (temperature, precipitation, NPI, and MEI), we first chose the time scale that best explained each response variable by comparing Akaike information criterion (AIC) values for each model of each index and time scale (3 months, 6 months, 9 months, and 12 months; Burnham and Anderson 2002). There were no correlations between pairs of climate indices.

We created a global model including the best time scale for each of the four climate indices, year, diet, migratory distance, the interactions between diet and year and diet and each climate index, and the interactions between migratory distance and year and migratory distance and each climate index as fixed effects, with year and species as random effects to predict passage date or energetic condition of each bird. Including year as a fixed effect enabled us to test for an overall trend in migratory timing. Interaction terms were included to test whether the effects of year or climate on migratory timing or energetic condition were dependent on diet or migratory distance. We compared all subsets of the global model using AIC to choose the top model (Burnham and Anderson 2002). Lower ranked models were considered parsimonious if they were ΔAIC ≤ 2 of the top model, contained informative parameters, and were not a subset of the higher ranked model (Burnham and Anderson 2002, Arnold 2010). Coefficients and 85% confidence intervals are presented before back-transformation. We report predicted effect size for each variable whose 85% confidence interval of the coefficient failed to overlap zero after back-transformation (Arnold 2010).

We conducted all statistical analyses in Program R (version 2.15.2, R Foundation for Statistical Computing, Vienna, Austria). We used functions on the lme4 package for mixed-model analyses (version 1.0-4, D. Bates, M. Maechler, B. Bolker, and S. Walker). We calculated standard errors with the function described in the package psych

(version 1.2.12, W. Revelle). All means are presented with ±SE.

RESULTS

We captured a total of 48,602 individuals of 17 songbird species over a 13-year study period (2000–2012). Mean passage date for songbird species was 9 September, but ranged among species from 11 August for Dusky Flycatchers (*Empidonax oberholseri*) to 28 September for Oregon Juncos (*Junco hyemalis, oreganus* group; Table 11.1). Mean energetic condition for songbirds was 4.15 ± 0.005 g/mm³. We counted 25,096 individuals of migrating raptors. Mean passage date for raptors was 22 September, but ranged from 19 September for Cooper's Hawks (*Accipiter cooperii*) to 23 September for Sharp-shinned Hawks (*A. striatus*; Table 11.1). We captured a total of 9,795 individuals of two raptor species. Mean energetic condition for the raptors was 2.21 ± 0.004 g/mm³.

There were no significant trends in any of the climate indices at any time scale over the duration of our study (Table 11.2). In predicting passage date, the 3-month time scale was chosen for temperature, 9-month for precipitation, 9-month for NPI, and 3-month for MEI (Table 11.2). In predicting energetic condition, the 9-month time scale was chosen for temperature, 12-month for precipitation, 12-month for NPI, and 12-month for MEI (Table 11.2).

The top model predicting migratory passage date included 3-month temperature, 9-month precipitation, 9-month NPI, and 3-month MEI, year, diet, migratory distance, the interactions between diet and year and diet and each climate index, and the interactions between migratory distance and year and migratory distance and each climate variable (Table 11.3). There was no overall trend in migratory timing among all species over the study period (Figure. 11.2). Frugivores exhibited the largest trend in timing, shifting 1.48 d/y later over the study period. Insectivores shifted 0.27 d/y earlier, granivores shifted 0.38 d/y later, and avivores had no shift in timing (Figure 11.2). Short-distance migrants showed no trend in autumn migratory timing, whereas long-distance migrants trended later at our study site (0.53 d/y; Figure 11.2).

Each of the climate indices retained in the top model exhibited effects on the migratory timing of birds at Lucky Peak (Table 11.4). For each 0.1°C

TABLE 11.2

Mean values, standard error, and results of statistical tests evaluating trends in four climate indices measured at four time scales across the Northern Rockies Bird Conservation Region in western North America from 2000 to 2012.

Index	3 Months	6 Months	9 Months	12 Months
Temperature	$15.5 \pm 0.19°C$[a]	$12.2 \pm 0.16°C$	$7.2 \pm 0.18°C$[b]	$5.4 \pm 0.15°C$
	$F_{1,11} = 0.12,$ $P = 0.74$	$F_{1,11} = 0.53,$ $P = 0.48$	$F_{1,11} = 0.10,$ $P = 0.76$	$F_{1,11} = 0.23,$ $P = 0.64$
Precipitation	96.4 ± 8.7 mm	282.5 ± 12.3 mm	484.5 ± 14.4 mm[a]	710.4 ± 13.4 mm[b]
	$F_{1,11} = 4.54,$ $P = 0.06$	$F_{1,11} = 0.002,$ $P = 0.96$	$F_{1,11} = 0.05,$ $P = 0.82$	$F_{1,11} = 0.18,$ $P = 0.68$
NPI	1015.8 ± 0.19	1015.5 ± 0.18	1013.3 ± 0.26[a]	1012.6 ± 0.27[b]
	$F_{1,11} = 0.001,$ $P = 0.97$	$F_{1,11} = 0.002,$ $P = 0.97$	$F_{1,11} = 0.72,$ $P = 0.41$	$F_{1,11} = 2.46,$ $P = 0.15$
MEI	0.08 ± 0.20[a]	0.10 ± 0.13	-0.02 ± 0.13	-0.06 ± 0.15[b]
	$F_{1,11} = 0.76,$ $P = 0.40$	$F_{1,11} = 0.60,$ $P = 0.45$	$F_{1,11} = 0.62,$ $P = 0.45$	$F_{1,11} = 0.64,$ $P = 0.44$

NOTES: Trends measured with linear regression with an alpha value of 0.05 but no trends were present in any climate variable measured at any time scale.

[a] Time scale chosen as best for predicting migratory passage date.

[b] Time scale chosen as best for predicting mean energetic condition.

TABLE 11.3

Top model, closest model, and "null" model from AIC model selection of various climate indices predicting Julian passage date of migratory birds past Lucky Peak, Idaho.

Model	K	AIC	ΔAIC	w_i	Cum. w_i	LL
npi9 + mei3 + Temp3 + Precip9 + diet:npi9 + diet:mei3 + diet:Temp3 + diet:Precip9 + distance:npi9 + distance:mei3 + distance:Temp3 + distance:Precip9 + diet:year + distance:year + diet + distance + year	33	612910.4	0.00	1	1	−306422.2
npi9 + mei3 + Temp3 + Precip9 + diet:npi9 + diet:mei3 + diet:Temp3 + diet:Precip9 + diet:year + distance:year + diet + distance + year	29	612925.4	15.01	0	1	−306433.7
NULL (distance:year + diet:year + distance + diet + year)	13	613333.6	423.26	0	1	−306653.8

NOTES: Each model includes additional random effects for year and species. Models with AIC weights less than 0.01 are not shown. npi9 = 9-month North Pacific index; mei3 = 3-month multivariate El Niño/southern oscillation index; Temp3 = 3-month temperature index from northwestern Rocky Mountains bird conservation region; Precip9 = 9-month precipitation index from northwestern Rocky Mountains bird conservation region.

increase in the 3-month temperature index there was a predicted shift in timing of 0.56 d earlier in frugivores, 0.19 d earlier in granivores, and 0.21 d earlier in short-distance migrants (Figure 11.3). For each 0.1-mm increase in the 9-month precipitation index there was a predicted shift in timing of 0.003 d later for insectivores, 0.002 d later for avivores, 0.0007 d earlier for granivores and 0.002 d later for long-distance migrants (Figure 11.3). For each unit increase in the 9-month NPI there was a predicted shift in timing of 0.50 d earlier for avivores, 0.96 d later for granivores, 0.19 d earlier for
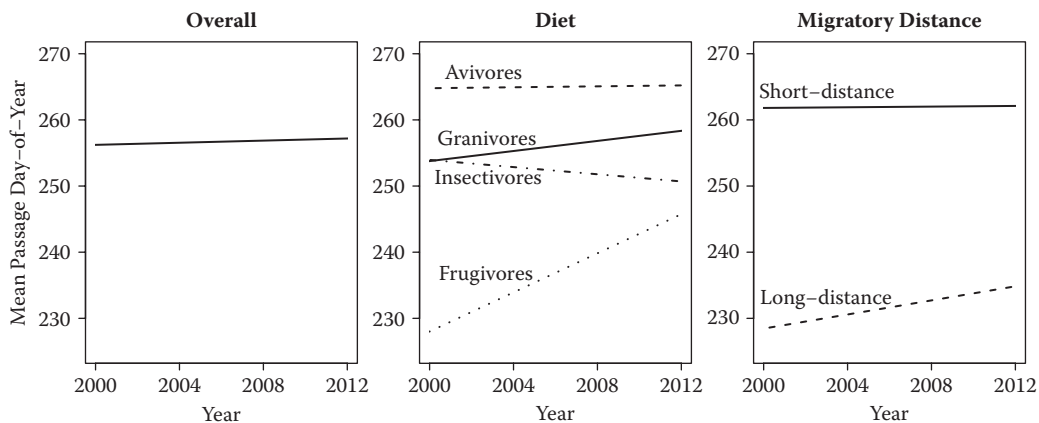
Figure 11.2. Mean passage dates during a 13-year study at Lucky Peak in southwest Idaho, 2000–2012. We present all sampled birds combined, all sampled birds separated by diet, and all sampled birds separated by migratory distance. No change was detected for the overall population, avivores, or short-distance migrants (confidence interval overlaps zero).

TABLE 11.4

Subset of model coefficients interactions and 85% confidence intervals from top model-predicting Julian passage date of migratory birds past Lucky Peak, Idaho.

Predictor variable	Avivore	Frugivore	Granivore	Insectivore	Short distance	Long distance
3-Month temperature	−0.01 (−0.32, 0.29)	**−3.92** **(−4.52, −3.33)**	**−1.36** **(−1.70, −1.02)**	0.08 (−0.20, 0.35)	**−0.45** **(−0.84, −0.06)**	0.30 (−0.07, 0.67)
9-Month precipitation	**−0.72** **(−0.99, −0.45)**	0.33 (−0.21, 0.87)	**−1.95** **(−2.25, −1.64)**	**1.59** **(1.34, 1.84)**	0.31 (−0.03, 0.65)	**1.43** **(1.12, 1.76)**
9-Month North Pacific index	**−0.64** **(−0.94, −0.34)**	−0.05 (−0.58, 0.48)	**0.74** **(0.42, 1.05)**	0.18 (−0.11, 0.46)	**−0.75** **(−1.14, −0.36)**	**0.55** **(0.17, 0.93)**
3-Month multivariate El Niño/ southern oscillation index	−0.02 (−0.35, 0.31)	**3.00** **(2.34, 3.66)**	**1.96** **(1.59, 2.34)**	**−0.65** **(−0.97, −0.34)**	**0.87** **(0.43, 1.31)**	**−1.09** **(−1.51, −0.66)**

NOTES: All predictor variables were scaled and centered. Bold text indicates coefficients whose 85% confidence intervals did not overlap zero.

short-distance migrants, and 0.59 d later for long-distance migrants (Figure 11.3). Last, for each unit increase in the 3-month MEI there was a predicted shift in timing of 3.22 d later for frugivores, 1.80 d later for granivores, 0.90 d earlier for insectivores, 1.40 d later for short-distance migrants, and 0.20 d later for long-distance migrants (Figure 11.3).

The top model-predicting energetic condition included 9-month temperature, 12-month precipitation, 12-month NPI, and 12-month MEI, year, diet, migratory distance, and the interactions between diet and year and diet and each climate index, and the interaction of migratory distance and year (Table 11.5). In general, energetic condition has improved over the study period at a rate of 0.014 g/mm³/y (Figure 11.4). However, differing trends became apparent when analyzed by diet and migratory distance (Figure 11.4). Granivores exhibited the largest trend in energetic condition, increasing at a rate of 0.038 g/mm³/y over the study period. Insectivores increased at a rate of 0.01 g/mm³/y, frugivores declined at a rate of 0.01 g/mm³/y, and avivores exhibited no trend in energetic condition. Short-distance migrants
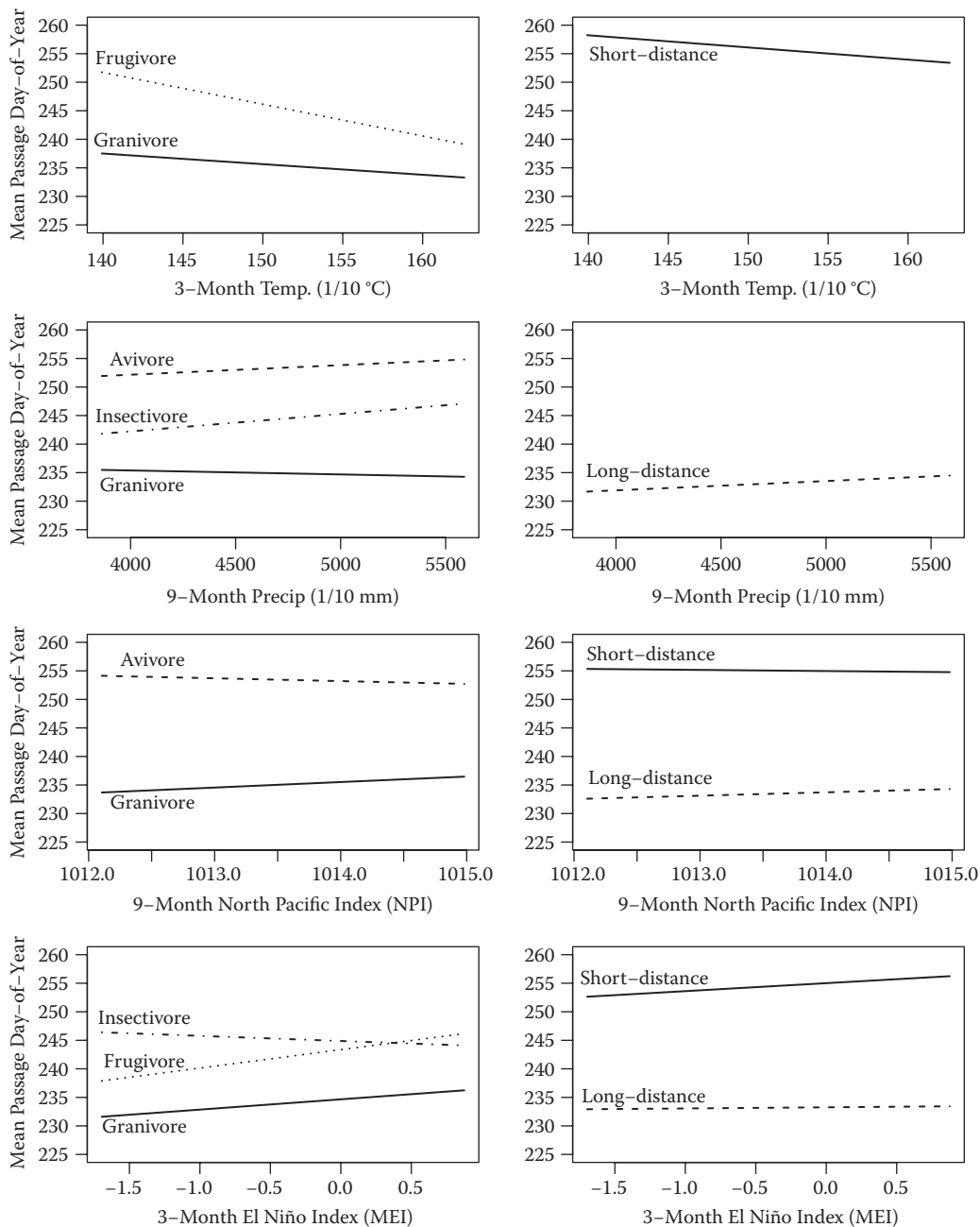
Figure 11.3. Predicted effect sizes of each of the four climate variables represented in the top ranked model for mean passage date of migratory birds by Lucky Peak in southwest Idaho, 2000–2012. Effect sizes were calculated separately by primary diet and then by migratory distance. For each sample, all other covariates in the top model are held at their mean values. Trend lines are shown for groups where confidence interval of the coefficient did not overlap zero.

increased at a rate of 0.013 g/mm³/y, whereas long-distance migrants increased at a rate of 0.01 g/mm³/y (Figure 11.4).

Each of the climate indices retained in the top model exhibited effects on the energetic condition

of birds at Lucky Peak and Boise Peak (Table 11.6). For each 0.1°C increase in the 9-month temperature index there was a predicted shift in energetic condition of 0.005 g/mm³ decrease for granivores, a 0.004 g/mm³ decrease for frugivores,

TABLE 11.5

Top model, closest model, and "null" model from AIC model selection of various climate indices predicting energetic condition of migratory birds past Lucky Peak, Idaho.

Model	K	AIC	ΔAIC	w_i	Cum. w_i	LL
npi12 + mei12 + Temp9 + Precip12 + diet:npi12 + diet:mei12 + diet:Temp9 + diet:Precip12 + diet:year + distance:year + diet + distance + year	29	56476.63	0.00	0.63	0.63	−28209.30
npi12 + mei12 + Temp9 + diet:npi9 + diet:mei3 + diet:Temp3 + diet:year + distance:year + diet + distance + year	25	56477.95	1.33	0.32	0.95	−28213.96
npi12 + mei12 + Temp9 + diet:npi12 + diet:mei12 + diet:Temp9 + distance:npi12 + distance:mei12 + distance:Temp9 + diet:year + distance:year + diet + distance + year	28	56482.83	6.21	0.03	0.98	−28213.40
npi12 + mei12 + Temp9 + Precip12 + diet:npi12 + diet:mei12 + diet:Temp9 + diet:Precip12 + distance:npi12 + distance:mei12 + distance:Temp9 + distance:Precip12 + diet:year + distance:year + diet + distance + year	33	56483.33	6.70	0.02	1.00	−28208.64
NULL (distance:year + diet:year + distance + diet + year)	13	56558.53	81.90	0	1	−28266.26

NOTES: Each model includes additional random effects for year and species. Models with AIC weights less than 0.01 are not shown. npi9 = 9-month North Pacific index; mei3 = 3-month multivariate El Niño/southern oscillation index; Temp3 = 3-month temperature index from northwestern Rocky Mountains bird conservation region; Precip9 = 9-month precipitation index from northwestern Rocky Mountains bird conservation region.
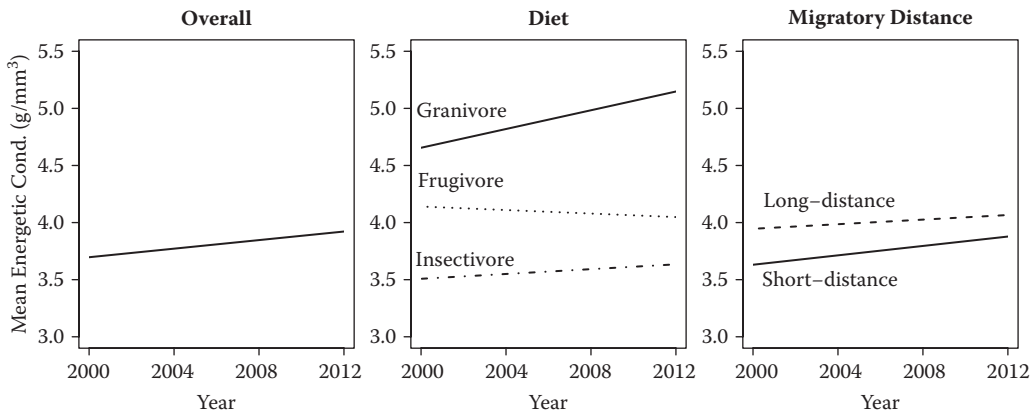

Figure 11.4. Mean energetic condition of birds during a 13-year study at Lucky Peak in southwest Idaho, 2000–2012. Condition is shown for all sampled birds combined, all sampled birds separated by diet, and all sampled birds separated by migratory distance. Overall, energetic condition tended to be higher but no trend was present for avivores.

and a 0.001 g/mm³ decrease for insectivores. For each 0.1 mm increase in the 9-month precipitation index, there was a predicted shift in energetic condition of 3.6×10^{-5} g/mm³ decrease for frugivores and a 4.4×10^{-7} g/mm³ decrease for insectivores. For each unit increase in the 12-month NPI there was a predicted increase in energetic condition of 0.04 g/mm³ for frugivores and 0.02 g/mm³ for granivores. Last, for each unit increase in the 12-month MEI there was a predicted shift in energetic condition of 0.06 g/mm³ increase for granivores and a 0.01 g/mm³ decrease for insectivores.

TABLE 11.6

Subset of model coefficient interactions and 85% confidence intervals from top model predicting energetic condition of migratory birds past Lucky Peak and Boise Peak, Idaho.

Predictor variable	Avivore	Frugivore	Granivore	Insectivore
9-Month temperature	0.0002 (−0.0119, 0.0124)	**−0.0023** **(−0.0366, −0.0100)**	**−0.0340** **(−0.0428, −0.0252)**	**−0.0079** **(−0.0160, 0.0001)**
12-Month precipitation	0.0121 (−0.0008, 0.0250)	**−0.0293** **(−0.0441, −0.0146)**	−0.0084 (−0.0176, 0.0009)	**−0.0124** **(−0.0211, −0.0036)**
12-Month North Pacific index	−0.0054 (−0.0180, 0.0072)	**0.0479** **(0.0362, 0.0595)**	**0.0239** **(0.0150, 0.0327)**	0.0074 (−0.0009, 0.0157)
12-Month multivariate El Niño/southern oscillation index	0.0110 (−0.0034, 0.0255)	−0.0059 (−0.0216, 0.0099)	**0.0169** **(0.0065, 0.0272)**	**−0.0184** **(−0.0282, −0.0085)**

NOTES: All predictor variables were scaled and centered. Bold text indicates coefficients whose 85% confidence intervals did not overlap zero.

DISCUSSION

Global climate change could have dramatic impacts on bird species, particularly migratory species with life histories that require use of multiple geographically dispersed habitat types, and are often dependent upon synchronized availability of prey. To better understand the connection between climate and species life histories, long-term avian monitoring projects are important (Porzig et al. 2011). We used 13 years of data for 19 species of birds to explore trends in migratory timing, energetic condition, and the effects of year-to-year variation in climate on these trends. While climate change has occurred around the globe and in the western United States, the Northern Rockies Bird Conservation Region has not experienced any significant trends in climate over the duration of our study.

Contrary to our initial hypothesis, and to other studies of migratory timing based on migration distance (Jenni and Kéry 2003, Van Buskirk et al. 2009, Rosenfield et al. 2011), we found no trend in the timing of autumn migration for short-distance migrants, but long-distance migrants tended to migrate later. We detected no significant trends in climate over the duration of our 13-year study, and we might expect little change in migratory timing of the short-distance migrants. However, long-distance migrants are exposed to a greater diversity of environments where greater change might be evident, which could explain their response. The magnitude and direction of trends in timing vary by the diet of the individuals.

The avivore raptors showed no trend in timing, whereas the frugivores shifted more than 15 days later over the duration of our study. As there were no overall trends present in climate over the duration of the study, the trends in timing by diet must be influenced by other factors not measured or climatic factors operating on different scales than we evaluated.

We hypothesized that annual climate variation would explain annual variation in timing and energetic condition as we expect regional climate directly to impact food resources, which is believed to be the ultimate driver of migratory behavior (Newton 2008). Our results showed relationships between annual variation in climate and annual variation in both timing and energetic condition. Furthermore, the strength and direction of these relationships varied by the diet of migrant birds. Generally, higher average within-year temperatures were correlated with birds migrating earlier—specifically granivores, frugivores, and short-distance migrants—with a corresponding decrease in energetic condition of these species in warmer years. Changes in condition could be the results of less availability and palatability of seeds and fruits. Insectivores showed no correlation between annual temperatures and timing, but did show a decrease in energetic condition in years with warmer average temperatures. The result is counter to our expectations as ectothermic arthropods are expected to be more active and at higher abundances in warmer years (Tulp and Schekkerman 2008). Increased precipitation was correlated with many species migrating

later, with the exception of the granivores, which migrated earlier in years of greater precipitation. Increased precipitation has been shown to influence arthropod abundance and fruit abundance positively, which in turn would be expected to influence the insectivores and frugivores to migrate later. However, the earlier migration of granivores in wet years was unexpected because summer precipitation has been shown to increase seed production (Dunning and Brown 1982). Also unexpected was a decrease in body condition of insectivores and frugivores in wetter years.

We included the hemispheric climate models to capture general climate influences not captured by temperature and precipitation. Retention in the top model indicated that hemispheric climatic conditions had some explanatory power for patterns of bird migration. The NPI in general had the least predictive power of the two measures, which may explain why this index is not used more broadly in ecological studies. The MEI exhibited larger influences, particularly on frugivores and short-distance migrants; however, the direction of the influence contradicts our expectations based upon the results of the temperature index. However, during our study, there were no strong El Niño events.

We further hypothesized that factors influencing songbird migration would similarly influence raptors that feed on songbirds. Raptors exhibited no trend in migratory timing and no trend in condition. Raptor responses to annual climate variation were negligible. Rosenfield et al. (2011) documented a delayed migration of Sharp-shinned Hawks in the midwestern United States, but we did not detect a significant shift in the timing of passage for Sharp-shinned Hawks or Cooper's Hawks. The difference may be the result of the longer duration of their study (35 years) than our study (13 years), which can improve the ability to detect gradual trends. Additionally, generalist raptors may have more flexibility to shift among various prey sources while maintaining their migratory timing and their average energetic condition, especially if different guilds of prey are responding in opposite directions and thus collectively maintaining a relatively constant food source throughout the autumn migration. However, as shifts within their prey populations continue, a mismatch in timing between their migration and that of their prey could eventually exist, requiring a response.

Some species shifted timing while holding energetic condition constant, while others held timing constant while shifting condition. Our results suggest that different species may have different abilities to adapt to annual variation, possibly integrating day length, fat stores, and other environmental factors in their decision to migrate (Sandberg and Moore 1996, Helm et al. 2009). Individuals not reaching a minimum threshold of body condition may perish before reaching our study site.

Our study focused on correlations between a limited number of climate factors and migratory behaviors of a diverse set of birds. Our results confirmed a number of hypotheses but contradicted others. Clearly, the timing and condition of migrants are subject to many ecological forces and cannot be fully explained by a few climate indices. The findings of this study could be enhanced by the direct measurement of food availability on the breeding grounds and en route to our monitoring station.

In conclusion, timing of autumn migration is changing for a number of avian species migrating through the western United States. The magnitude of these changes varies by diet and by migratory distance, but is not as predicted by previous research. The annual variation in timing for a given class of migrants is predicted by regional temperature and precipitation, and by hemispheric climate indices. We did not measure food availability, but the predictive effect of climate on migratory timing of birds is mostly consistent with its presumed effect on food availability. Energetic condition measurements supported the food hypotheses in some, but not all cases. The different responses of species to annual variation in climate suggest that different species integrate different cues in their decision to migrate.

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