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RESEARCH ARTICLE

Breeding season length and nest mortality drive cryptic life history variation in Dark-eyed Juncos (*Junco hyemalis*) breeding across a montane elevational gradient

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ABSTRACT

The manner in which individual life history traits respond to the environment and to each other, and how these traits combine to form overall patterns of life history variation, remains poorly characterized in wild populations. We monitored breeding Dark-eyed Juncos (*Junco hyemalis*) across a 700-m elevational range. We compared breeding season length, temporal patterns of breeding activity, adult body size, clutch size, brood size, nestling quality, and nest mortality among elevations. We also compared environmental measures across the studied elevations to determine whether abiotic factors explained life history trait variation. We used 12 microsatellite loci to test for genetic differentiation in populations at different elevations. Finally, we constructed a computer simulation to evaluate the combined effects of observed variation in life history traits. We found differences among elevations in breeding season length and in patterns of reproductive timing, which did not match each other and which were not explained solely by abiotic factors. We found no differences among elevations in adult body size, clutch size, brood size, or nestling quality. Nest mortality increased significantly with elevation. Genetic differentiation was too low to define distinct subpopulations. The simulation suggested that differences in mortality, in combination with differences in breeding season length, contributed to substantial differences in reproductive success among elevations. Thus, although individual life history traits showed little evidence of variation in response to the environment or to each other and little genetic differentiation, variation in breeding season length and in nest mortality were potential drivers of substantial elevational variation in overall life history in this system. These results demonstrate that individual life history traits may vary substantially in their patterns of variation, and that some life history traits may have disproportionate effects on overall life history.

Keywords: breeding phenology, elevation, *Junco hyemalis*, life history variation, nest mortality

La duración de la estación reproductiva y la mortalidad del nido generan variación críptica en la historia de vida de individuos de *Junco hyemalis* que se reproducen a lo largo de un gradiente de elevación montano

RESUMEN

La manera en la que los rasgos individuales de las historias de vida responden al ambiente y entre ellos, y cómo estos rasgos se combinan para formar patrones generales de variación de las historias de vida, permanece aún poco claro en las poblaciones silvestres. Monitoreamos individuos reproductivos de *Junco hyemalis* a lo largo de un rango de elevación de 700 m. Comparamos entre elevaciones la duración de la estación reproductiva, los patrones temporales de la actividad reproductiva, el tamaño corporal del adulto, el tamaño de la nidada, el tamaño de las crías, la calidad de los volantones y la mortalidad del nido. También comparamos mediciones ambientales entre las elevaciones para determinar si los factores bióticos pueden explicar la variación en los rasgos de la historia de vida. Usamos 12 loci microsatelitales para evaluar la existencia de diferenciación genética entre elevaciones. Finalmente, construimos una simulación computacional para evaluar los efectos combinados de la variación observada en los rasgos de la historia de vida. Encontramos diferencias entre elevaciones en la duración de la estación reproductiva y en los patrones de las fechas reproductivas, los que no coincidieron entre sí y los que no pudieron ser explicados solamente por factores abióticos. No encontramos diferencias entre elevaciones en el tamaño corporal del adulto, el tamaño de la nidada, el tamaño de las crías y la calidad del volantón. La mortalidad del nido aumentó significativamente con la elevación. La diferenciación genética fue demasiado baja para definir subpoblaciones distintas. La simulación sugirió que las diferencias en mortalidad, en combinación con las diferencias en la duración del período reproductivo, contribuyeron con las diferencias sustanciales encontradas entre elevaciones en el éxito reproductivo. De este modo, aunque los rasgos individuales de la historia de vida mostraron poca evidencia de variación en respuesta al ambiente o al otro, y poca diferenciación genética, la variación en la duración de la estación reproductiva y en la mortalidad del nido tienen

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el potencial de producir variación sustancial entre elevaciones en la historia de vida general en este sistema. Estos resultados demuestran que los rasgos individuales de la historia de vida pueden variar sustancialmente en sus patrones de variación, y que algunos rasgos de la historia de vida pueden tener efectos desproporcionados en la historia de vida en general.

Palabras clave: elevación, fenología reproductiva, *Junco hyemalis*, mortalidad del nido, variación en la historia de vida

INTRODUCTION

A central goal of evolutionary biology is to understand how environmental conditions shape phenotypic traits. Trait change in response to environmental variation may occur through genetic change or phenotypic plasticity (Gienapp et al. 2008). However, responses of traits to environmental variation are potentially complicated in situations where traits experience correlational selection, in which the selection for one trait depends on the phenotype of another trait or traits (Lande and Arnold 1983). In this case, phenotype is affected both by the external environment and by the phenotype of other relevant traits.

A classic case of such an interrelated system of traits is the collection of life history traits that make up an overall life history strategy. Life history strategies are comprised of behavioral, physiological, and anatomical traits that directly influence survival and reproductive success (Ricklefs and Wikelski 2002). These individual life history traits interact to affect the fitness of the whole organism (Scheiner and Istock 1991, Robinson et al. 2010). Correlated patterns of variation in life history traits were initially described using the terminology of *r*- and *K*-selection (Pianka 1970); more recently, life history strategies have been located along a fast–slow pace-of-life continuum, with "fast" species reproducing at a younger age, producing more offspring, investing less in each offspring, and experiencing greater mortality than "slow" species (Fisher et al. 2001, Ricklefs and Wikelski 2002). Gradients in life history speed have been observed latitudinally (Lack 1947, Robinson et al. 2010) and elevationally (Krementz and Handford 1984, Badyaev 1997, Bears et al. 2009) and have been attributed to adaptation to selection pressures arising from environmental variation. Such gradients provide an opportunity to explore the environmental effects on life history, as well as the patterns of covariation among life history traits.

Although some individual life history traits have been extensively characterized (e.g., clutch size in birds; Lack 1947, Krementz and Handford 1984, Badyaev 1997, Johnson et al. 2006, Altamirano et al. 2015, Dillon and Conway 2015), our understanding of the manner in which multiple life history traits respond to each other and to the environment remains limited. Studying life history traits in isolation from each other is inherently unrealistic, because they are potentially linked through correlational selection and/or shared underlying mechanisms (Scheiner and Istock 1991, Svensson et al. 2001, Robinson et al. 2010). A complete understanding of the dynamics of life history strategy variation is only possible through the study of multiple life history traits simultaneously (Robinson et al. 2010). Such an understanding would be valuable both for explaining historical and current patterns of life history variation, which include an incredible diversity of life history strategies across life forms (Jeschke and Kokko 2009), and for contributing to predictions about the future effects of climate change on populations and the ability of populations to adapt to these changes (Boyle et al. 2016).

Elevational gradients are useful systems within which to study life history variation, because they allow the observation of populations experiencing a considerable range of environmental conditions over a relatively small geographic area and within a single species (Boyle et al. 2016). In this study, we monitored the Dark-eyed Junco (*Junco hyemalis*), a common songbird, breeding across a 700-m elevational gradient in the Sierra Nevada of California, USA. We sought to answer 4 questions about this system: (1) Are patterns of life history trait variation correlated with patterns of environmental variation? (2) Do life history traits exhibit a consistent pattern of covariation with each other? (3) Is life history trait variation underlain by genetic differentiation? (4) Given observed levels of variation in the environment and individual life history traits, what degree of variation in overall life history is present? We measured environmental conditions across the 700-m elevational range, and compared the length of the breeding season, adult body size, clutch size, brood size, offspring quality, and nest survival among elevations. We also estimated genetic differentiation between populations at varying elevations. In addition, we used values drawn from our field observations to construct a computer simulation of populations breeding at different elevations, allowing us to observe how variation in individual factors, such as breeding season length and nest survival, combined to affect overall life history.

MATERIALS AND METHODS

Study System

Study species. The Dark-eyed Junco (hereafter, "junco") is a common passerine found throughout North America from sea level to the subalpine tree line (Nolan et al. 2002). The broad geographic range of this species necessitates juncos to survive and reproduce under a variety of environmental conditions. Juncos may respond to environmental variation through plasticity, e.g., by seasonal changes to their thermal properties (Swanson 1991), or through evolution, as in the rapid loss of a sexually selected trait from an isolated population of juncos that colonized a novel environment (Price et al. 2008). Juncos primarily nest on the ground, raising 1–3 broods of 3–5 nestlings per breeding season (Nolan et al. 2002). Because juncos do not build nests on snow (White 1973), the date of snowmelt directly influences the onset of breeding (Smith and Andersen 1985).

Study area. We conducted fieldwork at 8 primary field sites located in Stanislaus National Forest in the Sierra Nevada. These sites ranged in elevation from 1,960 to 2,660 m above sea level (asl). The primary habitat types were conifer forest (all elevations), open meadows dominated by grasses and California false hellebore (*Veratrum californicum*; all elevations), and rocky areas dominated by low scrub including big sagebrush (*Artemisia tridentata*) and manzanita (*Arctostaphylos* spp.; high elevation only). All of the sites experienced light-to-moderate human use, including camping, hiking, logging, and cattle grazing.

In addition to our primary field sites, we also performed fieldwork at several secondary sites (Appendix Table 8) to allow a more complete assessment of genetic structure.

In 2012–2014, California experienced low precipitation and record high temperatures that combined to effect a severe drought (Griffin and Anchukaitis 2014). This drought may have affected our study system, particularly at the lower elevations (Waring and Schwilk 2014).

Field Methods

We visited each primary field site every 1–10 days throughout the breeding season (May–September) in 2013 and 2014. In 2015 we conducted an abbreviated field season during May 12–14 and July 14–19 only. We captured adults in mist nets using conspecific playback, measured wing chord with a wing rule and tarsus length with digital calipers, measured mass to the nearest 0.1 g using an Ohaus HH120 digital pocket scale (Ohaus, Parsippany, New Jersey, USA), collected approximately 50 μl of blood from the brachial vein for genetic analysis, and applied a unique combination of 1 U.S. Fish and Wildlife Service aluminum leg band and either 3 (2013) or 2 (2014–2015) color bands made of acetal or darvic.

To monitor reproductive timing and success, we searched extensively for nests throughout the field season. For each nest found, we recorded the location using a hand-held GPS unit. We returned to nests periodically (number of visits per nest = 2.55 ± 1.42; interval between visits = 5.00 ± 2.76 days) to record clutch size, brood size, and survival (mean ± SE). To age nestlings, we created a photographic key of nestling appearance by age, calibrated using photographs of nestlings whose exact ages were known because they had been observed hatching.

When nestlings were 8–13 days old we banded them with 1 aluminum and 3 color bands (2013) or 1 aluminum band only (2014), collected blood from the brachial vein, and took morphological measurements. Nestlings were replaced in the nest afterward. Young fledglings were caught by hand and were processed in the same manner as nestlings.

We recorded all sightings of juncos, including their band combinations. Records of fledgling sightings included estimates of tail length to aid the estimation of fledgling age. We calibrated age estimates based on tail length using resightings of banded individuals of known age.

Temperature, Precipitation, and Snow

To relate observations of breeding phenology to ambient conditions, we downloaded data from weather stations through the National Climatic Data Center of the National Oceanic and Atmospheric Administration (NOAA). We used data from 13 weather stations (Appendix Table 9) located above 1,850 m asl in the Sierra Nevada in Alpine, Amador, Calaveras, Mariposa, and Tuolumne Counties. These weather stations were chosen for their proximity to our study area to ensure that the associated data were representative of conditions in our study sites. We downloaded the following daily weather measures: maximum temperature (T_{max}), minimum temperature (T_{min}), total precipitation, and snow depth. We assigned the weather data into 3 elevation bins: "low" (1,850–2,100 m), "mid" (2,240–2,460 m), and "high" (2,470–2,660 m). These elevation bins were also employed in our analysis of the temporal patterns of breeding activity and for constructing the simulation.

Statistical analyses were performed in R 3.1.2 (R Core Team 2014). To test whether elevations differed in their weather conditions, we ran generalized additive models (using function gam in package gamm4; Wood and Scheipl 2014) in which the weather measure of interest was the response variable, date was a nonlinear smooth term, and elevation bin was an independent variable.

Analysis of Life History

To analyze elevational patterns in clutch size and brood size, we ran generalized linear models with clutch size or brood size as the response variable, and hatching date (ordinal date), elevation, and an interaction between hatching date and elevation as potential explanatory variables. We modeled the error as Poisson-distributed because clutch size and brood size are integer counts.

To assess elevational patterns in adult body size, we used either wing chord or body mass as the response variable in linear models that included sex, ordinal date, elevation, and an interaction between ordinal date and elevation as potential explanatory variables.

To assess relationships between elevation and nestling quality, we calculated the residuals of a regression of individual chick body mass against wing chord length as a measure of condition (Ardia 2005, Schulte-Hostedde et al. 2005), and used those residuals as our response variable in a linear model that included chick age, hatching date (ordinal date), elevation, and an interaction between hatching date and elevation as potential explanatory variables. Hatching date was included in the model because nestling condition often declines over the course of the breeding season in altricial birds (Arnold et al. 2004, Bize et al. 2006, Verhulst and Nilsson 2008).

To compare the length of the breeding season among elevations, we assigned nests into the same 3 elevation bins used for weather data (see above). We calculated 2 measures of breeding season length: *potential* breeding season length, based on weather data, and *realized* breeding season length, based on our observations of nesting activity. We calculated 2 weather-based measures of potential breeding season length. The temperature-based potential breeding season length was the number of days between the first and last day of the year in which $T_{min} > 0°C$ in each elevation bin, based on the generalized additive model (run using function gam in package gamm4; Wood and Sheipl 2014) for that elevation bin, in which T_{min} was the response variable and date was a nonlinear smooth term. The additive model was employed to reduce the influence on our calculations of outlying weather measurements. The snow-based potential breeding season length was the number of days between the last day where snow depth was >0 mm in the spring and the first day that snow depth was >0 mm in the autumn.

In contrast to the weather-based potential breeding season lengths, realized breeding season length was calculated using our field observations of breeding activity. Realized breeding season length was the number of days between the 10^{th} and 90^{th} percentiles of first hatching dates in each elevation bin (Bears et al. 2009, Dillon and Conway 2015). We omitted nests from the 2015 field season from this analysis because our fieldwork did not span the entire potential breeding season in 2015. Because this calculation was based on the distribution of hatching dates only, it was shorter than the period of time during which juncos were engaged in breeding activity. To estimate the total length of time during which juncos were engaged in breeding activity, the number of days to lay (4 days) and incubate (13 days) eggs was added to the beginning of the realized breeding season, and the number of days caring for nestlings (11 days) and fledglings (14 days) was added to the end of the realized breeding season; values are means from Nolan et al. (2002).

To determine whether nest survival varied with elevation, we used a logistic exposure model (Shaffer 2004) to calculate daily nest survival rate. In addition to elevation, the model also included the median ordinal date of the period during which the nest was observed and the age of the nest (nest age = 1 on the day the first egg is laid) on that date as fixed effects.

Genetic Analysis

We extracted genomic DNA from whole blood using either Qiagen (Hilden, Germany) or Zymo (Irvine, California, USA) DNA extraction kits. We amplified the DNA at 12 microsatellite loci (Table 1) using the following PCR protocol: 3 min at 94°C; then 30 cycles of 30 s at 94°C, 1 min at the primer-specific annealing temperature T_a (see Table 1), and 90 s at 72°C; then 10 min at 72°C. We then genotyped the PCR products using an ABI 3730 DNA Analyzer (Applied Biosystems, Foster City, California, USA), estimating allele size with a GeneScan-500 LIZ size standard (Applied Biosystems). We viewed the genotyping results using GeneMapper 3.7 (Applied Biosystems).

We used STRUCTURE 2.3.4 (Pritchard et al. 2000, Hubisz et al. 2009) to look for genetic structure among adults in our populations using data from the 12 microsatellite loci. We assumed 1, 2, 3, or 4 populations and ran admixture models with a 25,000 burn-in period followed by 100,000 repetitions.

We used R package adegenet (Jombart 2008) to calculate pairwise F_{ST} (Holsinger and Weir 2009) between populations as well as overall F_{ST} and to run the *G*-statistic test for the significance of these F_{ST} values (Goudet et al. 1996). We included adults from both our primary and secondary field sites in these analyses.

Simulation

To explore the potential effects of variation in nest mortality rate and within-season variation in brood size on elevational patterns of reproductive success, we simulated a simplified version of our study system using NetLogo 5.3 (Wilensky 1999; see Supplemental Material for simulation code). In the base model, 3,000 breeding pairs laid 4 eggs each, incubated and hatched them, cared for and fledged nestlings, and then repeated this cycle until the breeding season ended. The breeding pairs were distributed evenly among 3 elevations, with each elevation differing in the length of the breeding season. The simulation reported the following results for each elevation: number of eggs laid, number of broods hatched, and number of independent offspring raised (i.e. the number of offspring still alive at the curtailment of parental care). The durations of laying, incubation, and care were derived from our field data and from Nolan et al. (2002), and were as

TABLE 1. Microsatellite loci used in the genetic analysis of Dark-eyed Junco populations along an elevational gradient in California, USA. Reverse primers were modified by the addition of a "pigtail" to the 5′ end, as in Makarewich et al. (2009). T_a = annealing temperature during PCR.

Locus	Forward 3′ to 5′	Reverse 5′ to 3′	T_a (°C)	Species of origin	Reference
Cuμ28	GAGGCACAGAAATGTGAATT	TAAGTAGAAGGACTTGATGGCT	55	*Catharus ustulatus*	Gibbs et al. (1999)
Dpμ01	TGGATTCACACCCCAAAATT	AGAAGTATATAGTGCCGCTTGC	55	*Setophaga petechia*	Dawson et al. (1997)
Dpμ16	ACAGCAAGGTCAGAATTAAA	AACTGTTGTGTCTGAGCCT	63	*Setophaga petechia*	Dawson et al. (1997)
Gf01b	AGAGGAAAAACTCCTGTGG	CTGCATGCAGACTGAAATTCT	59	*Geospiza fortis* & *Junco hyemalis*	Petren (1998), Rasner et al. (2004)
Gf05	AAACACTGGGAGTGAAGTCT	AACTATTCTGTGATCCTGTTACAC	56	*Geospiza fortis*	Petren (1998)
Gf06	GCTATTGAGCTAACTAAATAAACAACT	CACAAATAGTAATTAAAAGGAAGTACC	47	*Geospiza fortis*	Petren (1998)
Jh_mm4.1	TATCTGGTAATGTCTCTTGTC	AATTCCTGGACATGAATGAAG	58	*Junco hyemalis*	Price et al. (2008)
Jh_mm4.2	GAATGAAATTACTGGTGCATG	AGATAGGTAGAAGGCAGAAGC	60	*Junco hyemalis*	Price et al. (2008)
Jh_mmA03	ATGCTCCCCGCTCTCTCCTGC	TGCATCAAGTCCTTGAAGCAC	63	*Junco hyemalis*	Gerlach et al. (2012)
Jh_mmJu05	TGACCATGCCTTGGATATG	CATGGGAAACATGGACACTG	63	*Junco hyemalis*	Gerlach et al. (2012)
Mme7 §	TGCGAGCCTTTCCAAGTTTG	AACCCCACATGAAACAGGTCAC	54	*Melospiza melodia*	Jeffery et al. (2001)
Pdou3	CTGTTCATTAACTCACAGGT	AGTGAAACTTTAATCAGTTG	44	*Passer domesticus*	Neumann and Wetton (1996)

§ This locus is *Z*-linked, so females have only one allele.

follows: 4 days of laying (1 egg laid per day); 13 days of incubation; 11 days of nestling care; and 14 days of postfledging care. The duration of the breeding season at each elevation was taken from our field data (see Results for specific values). Because juncos are not known to lay more than 4 clutches per season (Nolan et al. 2002), pairs did not begin laying a new clutch if they had already laid >15 eggs. We simulated daily mortality by randomly selecting clutches and broods to be lost each day; a pair that lost a clutch or brood began breeding again at the laying stage on the third day following loss (based on a 2-day construction period for the replacement nest immediately followed by laying, as reported by Nolan et al. [2002]).

To calculate daily mortality rates for nests and broods at each elevation in the simulation, we ran a second logistic exposure model using our field data, again including nest age and date as fixed effects, but with elevation represented by 3 elevation bins rather than as a continuous measure. The base model daily mortality rates were the mean of observed daily nest mortality rates at nest day 13 (egg stage) and nest day 24 (nestling stage) across all 3 elevation bins.

We simulated a number of perturbations of this base model. Each version, including the base model, was run 5 times. The "staggered season onset" perturbation delayed the onset of breeding by a random number (0–10) of days for all breeding pairs. "Variable mortality" adjusted the number of randomly selected clutches or broods lost each day separately within each elevation, allowing mortality rates among elevations to differ; mortality rates were the observed daily nest mortality rates at nest day 13 (egg stage) and nest day 24 (nestling stage) for each elevation bin. The "late breeding penalty" reduced the number of fledglings by 1 in fledged broods when there were ≤20 days remaining in the breeding season, to account for reduced fledgling survival late in the season (Arnold et al. 2004, Bize et al. 2006, Verhulst and Nilsson 2008).

RESULTS

Sample Sizes for Life History Measures

Hatching dates were known or estimated for 156 breeding attempts in 2013–2014; these included nests with eggs or nestlings ($n = 100$) and young fledglings aged based on tail length ($n = 56$). We located a total of 109 nests in 2013–2015. Habitat was known for all nests. Depending on the timing of our observations, we knew the clutch size, the brood size, or both for any given nest (Table 2). Only nests which were visited at least twice were included in our analyses of nest survival; nests that were visited only once could be included in the hatching date and brood or clutch size datasets. We were able to band and measure nestlings in only a subset of broods due to nest mortality or

TABLE 2. Sample sizes of nests of Dark-eyed Juncos in California, USA, for each year or elevational range.

Year or elevation	Clutch size known	Brood size known	Included in survival analysis	Total nests
2013	23	48	43	53
2014	25	38	35	46
2015	7	4	6	10
1,960–2,193 m	17	25	21	36
2,194–2,427 m	22	35	34	42
2,428–2,660 m	16	30	29	31
Total	55	90	84	109

logistical challenges; a total of 187 nestlings in 67 broods were measured during the study. Mass and wing chord were measured for 191 adults, 27 of which were female and the rest male. The sex bias in our captures was due to the difference between the sexes in their response to conspecific playback: males responded aggressively to the apparent territorial intrusion, whereas females largely ignored the playback.

Elevational Differences in Temperature, Precipitation, and Snow

Daily maximum and minimum temperatures declined as elevation increased (Table 3). Precipitation did not differ among elevations. Snow depth was significantly greater at mid and high elevations than at low elevations.

The temperature-based potential breeding season length at low, mid, and high elevation was 261, 171 days, and 169 days, respectively (Figure 1). The mean snow-based potential breeding season length at low, mid, and high elevation was 208, 161, and 159 days, respectively (Figure 1).

Life History and Elevation

Realized breeding season length differed slightly among elevations (length at high, mid, and low elevation = 44, 50, and 58 days, respectively). The number of days during which juncos were engaged in breeding activity of any kind at high, mid, and low elevation was 86, 92, and 100 days, respectively (Figure 1).

Temporal patterns of breeding activity also differed among elevations, but did not transition smoothly (Figure 2). Whereas low and high elevations had a bimodal distribution of nest hatching dates, the distribution for mid elevations was unimodal. Additionally, in the 2

TABLE 3. High, mid, and low elevations in California, USA, differed significantly in maximum (max.) and minimum (min.) daily temperature and daily snow depth, but not in daily precipitation. Significant differences are indicated with an asterisk.

Variable	Elevation [a]	Estimate ± SE	t	P
Min. temperature	Mid	0.51 ± 0.09	5.7	<0.001*
	Low	5.70 ± 0.10	58.6	<0.001*
Max. temperature	Mid	1.17 ± 0.09	13.0	<0.001*
	Low	3.84 ± 0.10	38.8	<0.001*
Precipitation	Mid	0.23 ± 0.14	1.6	0.10
	Low	0.05 ± 0.16	0.3	0.76
Snow depth	Mid	0.03 ± 0.01	4.4	<0.001*
	Low	−0.26 ± 0.01	−27.8	<0.001*

[a] Estimates are in comparison with high elevation.

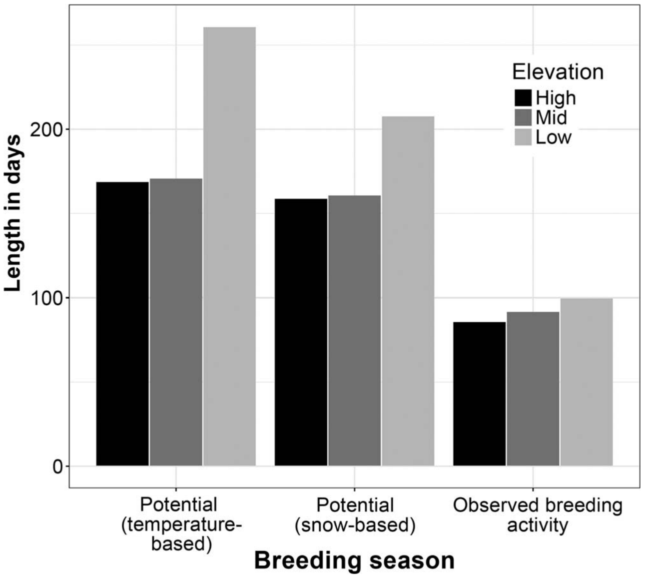

FIGURE 1. Potential breeding season length of Dark-eyed Juncos, based on either temperature or snow cover, showed a different pattern of elevational variation than did observed breeding season length.

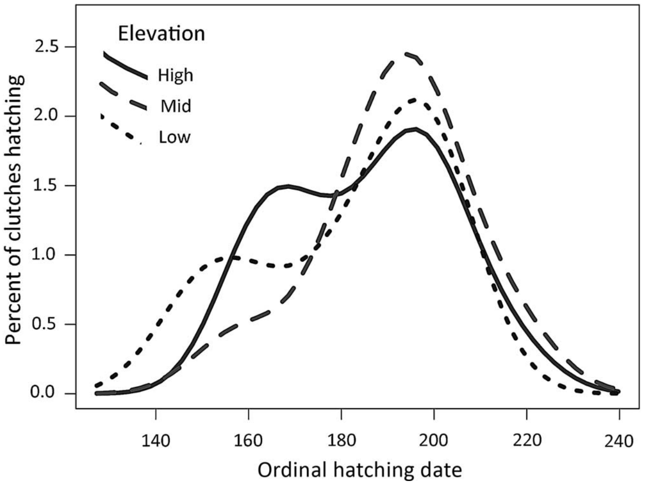

FIGURE 2. Kernel density plot of first hatching dates of Dark-eyed Juncos at low, mid, and high elevations. Ordinal date 140 = May 20, and ordinal date 240 = August 28.

TABLE 4. Daily nest survival of Dark-eyed Juncos across an elevational gradient in California, USA, increased with nest age and was higher at low elevation. Significant results are indicated with an asterisk.

Variable	Estimate ± SE	z	P
Nest age (days)	0.180 ± 0.056	3.3	0.001*
Ordinal date	0.023 ± 0.014	1.6	0.10
Elevation (m)	−0.002 ± 0.001	−2.0	0.04*

bimodal distributions, the relative heights of the peaks differed.

Daily nest survival rates were lower at younger nest ages and at higher elevations (Table 4). The estimated elevation difference was especially pronounced when nests were young, with the difference declining as nests aged (Figure 3, Table 5).

Neither clutch size, brood size, nor nestling quality was significantly related to elevation, hatching date, or the interaction between these 2 variables (Table 6). Adult body size (mass and wing chord) differed significantly between the sexes, but was not related to elevation, date, or the interaction between elevation and date. Nestling quality declined significantly with age, as was expected from ontogenetic changes in body proportions (Ricklefs 1979).

Genetic Structure

The overall F_{ST} among our populations was –0.003, which was not significant ($P = 0.80$). The STRUCTURE model with the highest probability was the single-population model, indicating that our genetic data did not exhibit strong spatial structure (Figure 4). Models assuming 2, 3, or 4 populations had lower probabilities and were unable to assign individuals to populations with any confidence.

Simulation

The base simulation model demonstrated that the relatively small differences in breeding season lengths observed among elevations, independent of any other variation, could result in elevational differences in reproductive success (Table 7, Figure 5). The addition of other sources of variation (staggered season onset or late breeding penalty) generally increased these elevational differences in reproductive success only slightly. An exception was the addition of elevationally variable nest mortality, which led to an increase in the number of eggs laid with increasing elevation and a decrease in the number of broods hatched and of independent offspring produced with increasing elevation.

The "realistic" model, which incorporated the sources of variation observed in our study system (staggered season onset, late breeding penalty, and variable mortality), showed moderate differences among elevations in the number of eggs laid, and considerable differences in the numbers of broods hatched and independent offspring produced. High elevation pairs in this model produced a mean of just 1.4 offspring surviving to independence from 0.7 broods hatched per season, whereas mid and low elevation pairs produced 3.5 independent offspring from 1.5 broods hatched and 5.6 independent offspring from 1.9 broods hatched, respectively (Table 7).

DISCUSSION

We found little evidence for a correlation between variation in life history traits and variation in the environment. The life history traits that we measured did not exhibit consistent patterns of variation across the

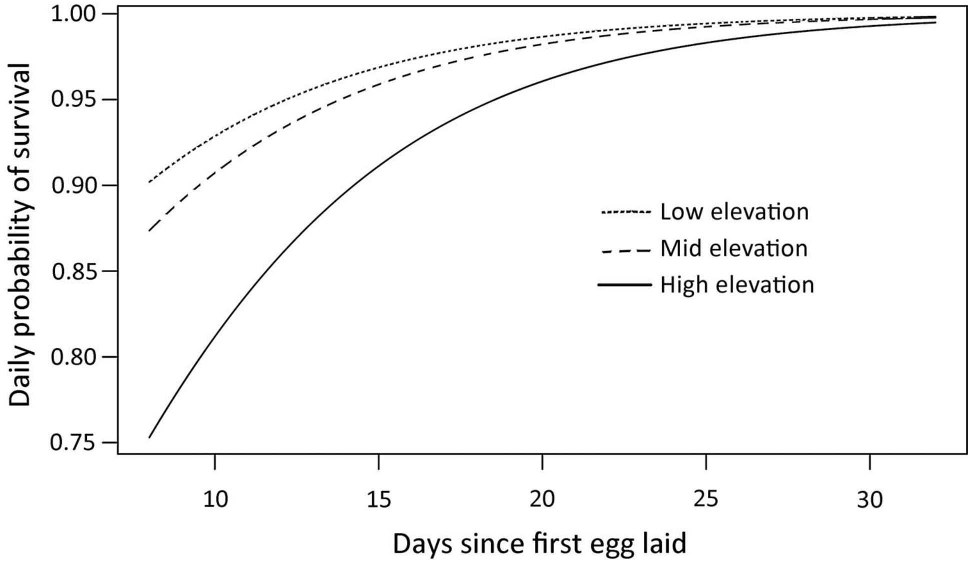

FIGURE 3. Daily nest survival of Dark-eyed Juncos increased with nest age and declined with elevation.

TABLE 5. Daily nest mortality rates calculated from a logistic exposure model for 2 nest ages representing the egg and nestling stages. These values were used in our simulation to evaluate the combined effects of observed variation in life history traits of Dark-eyed Juncos across an elevational gradient.

	Daily mortality rate (%) for the given nest age	
Elevation	13 days (eggs)	24 days (nestlings)
High	11.9	1.8
Mid	5.9	0.9
Low	2.9	0.4
Mean	6.9	1.0

elevational range. We also found no evidence for genetic structure among populations at different elevations. Our simulation of breeding juncos demonstrated that small differences in breeding season length could potentially have large effects on relative reproductive success, and that these differences were considerably amplified when combined with variation in nest mortality.

Environmental Conditions Do Not Explain Life History Trait Variation

Although substantial variation in temperature and snow depth was observed between elevations, a number of life history traits (clutch size, brood size, offspring quality, and adult body size) showed no variation among elevations. Potential breeding season length, calculated based on minimum daily temperature or snow depth, was >45 days longer at low elevation while differing by only 2 days between mid and high elevations. This did not match observed breeding activity, which differed by approximately even intervals between each elevation bin (8 days between low and mid elevations, 6 days between mid and high elevations). Environmental data also did not explain the differences in peak breeding activity, for which mid elevations appeared more different from low and high elevations than low and high elevations were from each other.

It may be that the length of the breeding season and the timing of breeding are more influenced by the biotic, rather than the abiotic, environment. While temperature and snow depth may limit the onset of breeding (White 1973), the most important environmental influence on the timing of breeding is probably the peak in arthropod food availability (Thomas et al. 2001, Verhulst and Nilsson 2008). Like most altricial passerines, nestling juncos are insectivores, and the degree of synchronization of peak nestling food demand with peak arthropod food availability is a key determinant of breeding success (Thomas et al. 2001). Additionally, because starvation is a major cause of mortality of newly independent juveniles (Sullivan 1989), and because adult juncos must undergo an energy-intensive molt immediately following breeding (White 1973, Wilson and Martin 2005), the cost of breeding later than the food peak extends beyond the nestling period.

These costs of breeding late render the late peaks in breeding activity observed in our low- and mid-elevation juncos perplexing. We saw no evidence that the small number of early breeders in these habitats preceded their food peak: nestlings in these nests achieved equal body mass to their later-hatched counterparts. However, it has been repeatedly shown that early breeders are of higher quality (Verhulst and Nilsson 2008), suggesting that early breeding is challenging. It may be that the food peaks at

TABLE 6. Elevation (m), date, and the interaction between elevation and date did not affect any of the following life history traits of Dark-eyed Juncos across an elevational gradient in California, USA: clutch size, brood size, nestling quality, adult mass, or adult wing chord. Males were lighter and had longer wings than females. Significant results are indicated with an asterisk.

Trait	Variable	Estimate ± SE	t	P
Clutch size	Elevation	$-2.0 \times 10^{-4} \pm 2.8 \times 10^{-3}$	−0.07	0.69
	Hatching date	$-7.0 \times 10^{-3} \pm 3.4 \times 10^{-2}$	−0.23	0.82
	Elevation*Hatching date	$-1.7 \times 10^{-6} \pm 1.5 \times 10^{-5}$	0.11	0.91
Brood size	Elevation	$1.5 \times 10^{-4} \pm 2.3 \times 10^{-3}$	0.06	0.95
	Hatching date	$-3.0 \times 10^{-3} \pm 2.9 \times 10^{-2}$	−0.11	0.91
	Elevation*Hatching date	$4.4 \times 10^{-7} \pm 1.3 \times 10^{-5}$	0.04	0.97
Nestling quality	Age	$-1.6 \times 10^{-1} \pm 4.5 \times 10^{-3}$	−3.64	<0.001*
	Elevation	$6.7 \times 10^{-5} \pm 3.5 \times 10^{-3}$	0.02	0.98
	Hatching date	$-1.6 \times 10^{-2} \pm 4.4 \times 10^{-2}$	−0.36	0.72
	Elevation*Hatching date	$-1.2 \times 10^{-6} \pm 1.9 \times 10^{-5}$	−0.06	0.95
Adult mass	Sex (Male)	−0.40 ± 0.19	−2.09	0.04*
	Elevation	$-4.2 \times 10^{-4} \pm 1.2 \times 10^{-3}$	−0.36	0.72
	Date	−0.010 ± 0.016	−0.62	0.54
	Elevation*Date	$2.7 \times 10^{-6} \pm 7.2 \times 10^{-6}$	0.37	0.71
Adult wing chord	Sex (Male)	3.40 ± 0.45	7.62	<0.001*
	Elevation	0.001 ± 0.002	0.46	0.65
	Date	0.013 ± 0.038	0.33	0.74
	Elevation*Date	$-5.8 \times 10^{-6} \pm 1.7 \times 10^{-5}$	−0.34	0.73

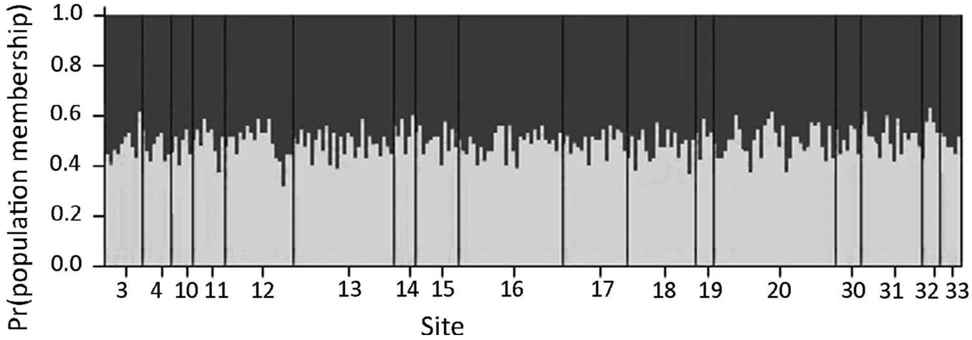

FIGURE 4. STRUCTURE plot of the probabilities of Dark-eyed Junco individuals belonging to either of 2 hypothetical populations (light and dark gray) based on 12 microsatellite loci. The even probabilities indicate a lack of population genetic structure. Population codes on the *x*-axis correspond to the codes in Appendix Table 8.

these elevations were sufficiently prolonged that juncos could delay breeding without a reduction in reproductive success, and that most juncos did so to avoid the elevated costs of early breeding. At high elevations the food peak was likely more compressed, accounting for the greater incidence of early breeding.

An alternative explanation for the late breeding peaks at low and mid elevations is that habitat structure changed dramatically over the course of the season, and juncos may have delayed breeding until optimal nest sites were created by the growth of sheltering plants. Juncos usually place nests under low cover (White 1973, Nolan et al. 2002). Much vegetative cover does not reach sufficient size until a period of time into the growing season. For example, California false hellebores, whose broad, low leaves often shelter junco nests, begin growing only when the ground thaws and do not reach sufficient size to shelter nests until several weeks later. Because nests must be hidden from the first egg day to protect eggs from depredation, juncos might delay the onset of breeding until preferred nest sites are available.

One potential complicating factor in our observations of elevational differences was the drought that occurred in our study area. Because drought effects are likely to be more severe at lower elevations than at higher elevations (Waring and Schwilk 2014), the drought may have reduced the breeding season length at low elevations while having little effect at higher elevations, reducing the overall differences in breeding season lengths. However, a study of juncos breeding in the Sierra Nevada at 1,950–2,100 m (corresponding to our low elevation bin), but not during a drought, found a similar breeding season length (54 days, recalculated from figure 4 in White (1973) in the same manner in which realized breeding season length was calculated for our own field data). This suggests that our low-elevation breeding season length (58 days) was normal for this location. Additionally, the drought did not appear to shift the breeding season substantially, as our observed breeding season largely matched that observed by White (1973): ordinal dates 154–208 (White 1973) vs. ordinal dates 147–205 (this study).

The only other trait besides timing of breeding that exhibited variation across elevations was nest mortality, which increased at higher elevations. Nest mortalities in our system were attributed to 3 causes: predation, human-

TABLE 7. Mean ± SE reproductive success (number of eggs laid, number of broods hatched, and number of fledglings raised to independence) per breeding pair of Dark-eyed Juncos at each of 3 elevations (low, mid, and high) in simulation models with different attributes. Models were each run 5 times with 1,000 breeding pairs per elevation. The base model included different breeding season lengths at each elevation and a single nest mortality rate across elevations. Subsequent models added modifications: SSO = staggered season onset; LBP = late breeding penalty; VM = variable daily nest mortality among elevations.

	Eggs laid			Broods hatched			Independent fledglings raised		
Model	Low	Mid	High	Low	Mid	High	Low	Mid	High
Base	14.54 ± 0.02	14.37 ± 0.03	13.93 ± 0.02	1.37 ± 0.00	1.35 ± 0.01	1.30 ± 0.01	3.98 ± 0.02	3.57 ± 0.02	3.27 ± 0.03
+ SSO	14.49 ± 0.02	14.10 ± 0.03	13.48 ± 0.04	1.35 ± 0.01	1.31 ± 0.01	1.25 ± 0.01	3.77 ± 0.01	3.36 ± 0.03	3.07 ± 0.02
+ LBP	14.55 ± 0.02	14.31 ± 0.02	13.90 ± 0.04	1.36 ± 0.01	1.34 ± 0.01	1.30 ± 0.01	3.68 ± 0.02	3.34 ± 0.02	3.03 ± 0.01
+ VM	11.67 ± 0.04	13.78 ± 0.05	15.44 ± 0.03	1.95 ± 0.01	1.50 ± 0.02	0.66 ± 0.03	6.51 ± 0.02	4.04 ± 0.03	1.50 ± 0.06
+ SSO, LBP, VM [‡]	11.58 ± 0.04	13.62 ± 0.03	15.13 ± 0.03	1.93 ± 0.01	1.45 ± 0.01	0.65 ± 0.01	5.63 ± 0.01	3.50 ± 0.02	1.40 ± 0.03

[‡] This model had the most similar attributes to those observed in the field in our study system.

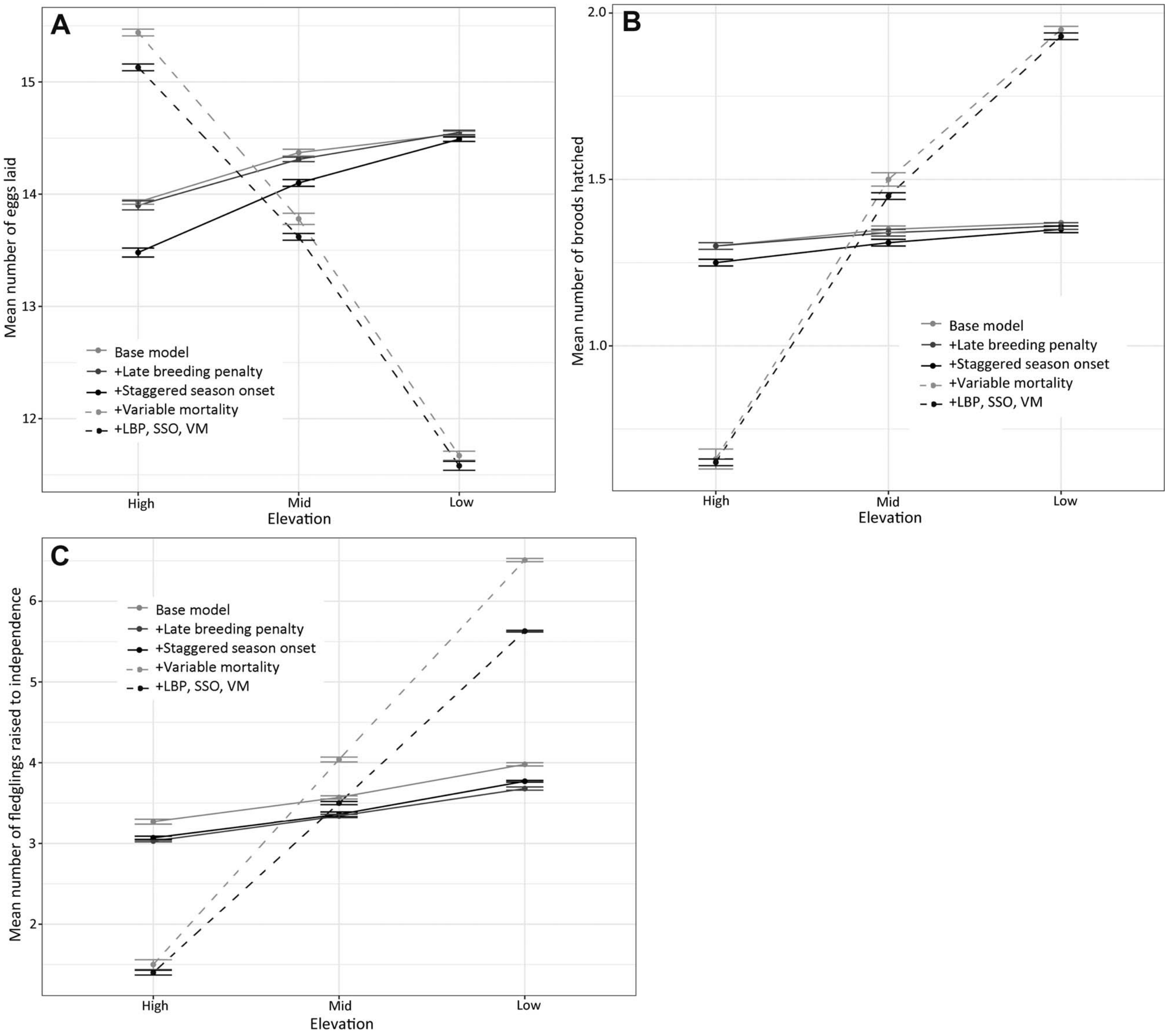

FIGURE 5. Mean reproductive success per Dark-eyed Junco breeding pair at each of 3 elevations in simulation models with different attributes. (**A**) Number of eggs laid; (**B**) Number of broods hatched; and (**C**) Number of fledglings raised to independence. Models were each run 5 times with 1,000 breeding pairs per elevation. Error bars indicate standard error. "Late breeding penalty" (LBP) models reduced the success of broods fledging late in the breeding season; "staggered season onset" (SSO) added random delays to the beginning of breeding; and "variable mortality" (VM) used different mortality rates for each elevation.

related activity, and severe weather. Commonly observed potential nest predators in our study system included chipmunks (*Tamias* spp.), American martens (*Martes americana*), black bears (*Ursus americanus*), garter snakes (*Thamnophis* spp.), and Steller's Jays (*Cyanocitta stelleri*), all of which were found across the studied elevational range. Human-related activity caused nest mortality primarily through nest trampling by grazing cows. Like depredation, human-related mortality is a threat across all elevations.

Severe weather, however, does occur with greater frequency at higher elevations (Johnson et al. 2007), and causes nest mortality in our system as well as others. Snowstorms and thunderstorms caused nest loss in high-elevation juncos breeding in Utah, USA (Smith and Andersen 1982). Heavy rainfall led to nest mortality in the Green-backed Tit (*Parus monticolus*), with survival further decreasing when cold temperatures accompanied the rain (Shiao et al. 2015). A late spring snowstorm at high elevation drove abandonment of 68% of nests by Red-faced Warblers (*Cardellina rubrifrons*; Decker and Conway 2009). Furthermore, severe weather can reduce reproductive success indirectly by negatively affecting parental energy stores. Storms adversely affected the fat stores and stress levels of White-ruffed Manakins (*Corapipo altera*), and this effect was greater in individuals at higher elevations (Boyle et al. 2010). It is possible that severe weather at high elevations contributed to their greater nest mortality.

We cannot rule out the possibility that our own nest monitoring activities increased predation at observed nests. We took precautions to minimize this possibility, such as not marking nest locations, visiting nests infrequently, and not approaching nests when potential predators were visible. In the course of nest searching we passed through large amounts of habitat; therefore, signs of our passage were not an accurate indicator of the presence of a nest. A multispecies meta-analysis of the effects of researcher monitoring on nest survival found no negative impact on survival (Ibáñez-Álamo et al. 2012). Nevertheless, it is possible that nest survival was compromised by our activities, and, if this effect was greater at higher elevations, it could provide an alternative explanation for the observed variation among elevations in nest mortality.

Life History Traits Do Not Consistently Covary

We found considerable variation in the elevational patterns of our focal life history traits. Breeding season length and nest mortality transitioned continuously and evenly across elevations, decreasing and increasing, respectively, approximately the same amount from our low to mid elevation sites and from our mid to high sites. The distribution of breeding activity was weakly bimodal at low elevation, unimodal at mid elevation, and strongly bimodal at high elevation, i.e. low elevation displayed a pattern intermediate between mid and high elevations. Clutch size, brood size, offspring quality, and adult body size did not vary significantly among elevations. When the differences in breeding season lengths were combined with observed variation in nest mortality rates, simulated reproductive success transitioned continuously and evenly between elevations, with each step up in elevation category resulting in ~2.1 fewer independent fledglings produced per year.

No Genetic Differentiation among Elevations

We found no evidence of genetic structure among populations at different elevations. Gene flow within and among junco populations is largely the result of natal dispersal, as breeding juncos are philopatric (Nolan et al. 2002). Previous work on juncos has documented natal dispersal distances of approximately 300–500 m, with females dispersing farther than males; these dispersal patterns resulted in spatial genetic structure that was detectable using neutral markers (Liebgold et al. 2013). Juncos differ considerably in migratory behavior across their range, however, and detailed studies of natal dispersal are lacking for most populations (Nolan et al. 2002). In our system, we rarely resighted individuals banded as juveniles in their natal sites in subsequent years (1/264 resighted = 0.4%), suggesting a lack of natal philopatry, but dispersal distances in our populations are not known.

Considering the lack of observed genetic structure, it is unlikely that differences among elevations in life history parameters reflect genetic divergence arising from reproductive isolation among elevations. However, the lack of differentiation in the neutral markers examined here does not exclude the possibility of elevational divergence in individual genes due to selection. Alternatively, differences among juncos breeding at different elevations may be due to plasticity: Substantial plasticity in the timing of breeding and the breeding season length of juncos has been previously demonstrated (Yeh and Price 2004).

Variation in Overall Life History Strategy

Our simulation of breeding juncos experiencing the same conditions that we observed in our field system demonstrated that even small differences in realized breeding season length could potentially have effects on relative reproductive success, and that these differences were considerably amplified when combined with elevational variation in nest mortality. Moreover, raising fledglings to independence was not equally costly among elevations. To produce 1 independent fledgling, a low-elevation breeding pair in our most realistic model laid on average 2.1 eggs, whereas a mid-elevation pair laid 3.9 eggs, and a high-elevation pair laid 10.8 eggs.

Variable nest mortality rates made the greatest contribution to differences in success among elevations. Variable nest mortality drove an elevational increase in the number of eggs laid—as clutches and broods were lost more frequently at high elevations, permitting more renesting attempts—and an elevational decrease in the number of broods hatched and independent offspring produced.

It is important to note that the final measure of reproductive success used in the simulation, the number of independent offspring produced, is not equivalent to the final measure of success used most frequently in field studies. Although the number of independent fledglings produced is a more accurate measure of overall reproductive success, hence its employment in our simulation, field studies overwhelmingly report offspring fledged from the nest as the final measure of reproductive success (Streby and Andersen 2013). This is a matter of practicality: It is considerably more challenging to follow the survival of fledglings, which may be both cryptic and highly mobile, than that of nestlings. However, substantial mortality occurs between fledging and independence from parental care (e.g., Sullivan 1989), with mortality rates increasing for offspring that fledge late in the season (Arnold et al. 2004, Bize et al. 2006, Verhulst and Nilsson 2008). Fledged offspring cannot all be assumed to survive to independence. Although a number of studies have pointed out the inaccuracy inherent in counting nests as "successful" prior to fledgling independence (Streby and Andersen 2011, 2013), they have primarily focused on inflated estimates of survival rather than reduced estimates of differences in survival. Studies should consider devoting extra resources to tracking fledglings if accurate values of either absolute or relative reproductive success are important.

Conclusions

Our results suggest that the dynamics of variation in life history traits are complex, with traits potentially, but not necessarily, responding to environmental variation as well as variation in other life history traits. Life history differences may arise over relatively small elevational ranges, even in the absence of substantial genetic differentiation; our simulation suggested that, in our system, these differences were driven by differences in breeding season length and, to a greater extent, by differences in nest failure rates among elevations. Although life history strategies are often conceptualized as responding to selection as a single phenotype, our results suggest a messier reality, in which overall life history strategy is determined by individual life history traits that exhibit a range of variabilities, relationships to the environment, and relationships to each other, and in which a few life history traits may have disproportionately large effects on overall life history strategy. Whether these patterns hold at the level of interspecific life history variation would be a valuable question for future research.

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Author contributions: Both authors conceived the idea, design, and experiment (supervised research, formulated question and/or hypothesis), and wrote the paper; K.L. performed the experiments (collected data, conducted the research), developed and/or designed the methods, and analyzed the data.

Data deposits: Data have been archived in the Dryad Data Repository at doi:10.5061/dryad.d88d8

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APPENDIX TABLE 8. Locations in California, USA, from which blood was collected from adult Dark-eyed Juncos for inclusion in the analysis of genetic structure. Locations marked with an asterisk (*) were primary field sites, at which substantial additional field work was conducted.

Site name	Code	Latitude	Longitude	County	Year(s) active
Pines	3	N 37°49.163′	W 120°05.677′	Tuolumne	2012
Fraser Flat	4	N 38°10.165′	W 120°04.345′	Tuolumne	2012
Sheep Ranch	10	N 38°11.953′	W 120°23.889′	Calaveras	2013–2015
P10	11	N 38°19.543′	W 120°14.673′	Calaveras	2013
P7*	12	N 38°22.541′	W 120°11.625′	Calaveras	2013–2015
Stanislaus River*	13	N 38°25.325′	W 120°02.907′	Calaveras	2012–2015
Logged*	14	N 38°24.434′	W 120°02.297′	Calaveras	2014–2015
Utica Reservoir*	15	N 38°25.544′	W 120°00.796′	Calaveras	2012–2015
Lake Alpine*	16	N 38°28.653′	W 120°00.422′	Alpine	2013–2015
P5*	17	N 38°29.223′	W 119°59.154′	Alpine	2013–2015
Mosquito Lake*	18	N 38°30.987′	W 119°54.864′	Alpine	2013–2015
P2	19	N 38°32.517′	W 119°53.253′	Alpine	2013
Ebbetts*	20	N 38°32.667′	W 119°48.717′	Alpine	2013–2015
Tioga Lakes	30	N 37°56.376′	W 119°14.458′	Mono	2012
Saddlebag	31	N 37°57.351′	W 119°16.023′	Mono	2012
Rock Creek	32	N 37°25.886′	W 118°44.806′	Mono	2012
Pack Station	33	N 37°27.290′	W 118°44.446′	Mono	2012

APPENDIX TABLE 9. Weather stations in the Sierra Nevada, California, USA, from which data were used in our study of life history variation in Dark-eyed Juncos breeding across an elevational gradient. Data were provided courtesy of the National Climatic Data Center, part of the National Oceanic and Atmospheric Administration (NOAA). The initial "GHCND:" has been omitted from station IDs. Elev. = elevation.

Station name	Station ID	Latitude	Longitude	Elev. (m)	Elev. bin
Spratt Creek	USS0019L39S	38.67	−119.82	1,864	Low
Yosemite Village 12 W	USW00053150	37.76	−119.82	2,018	Low
Crane Flat Lookout	USR0000CCRA	37.77	−119.82	2,025	Low
Poison Flat	USS0019L06S	38.51	−119.63	2,358	Med
Forestdale Creek	USS0019L43S	38.68	−119.96	2,444	Med
White Wolf	USR0000CWWO	37.86	−119.65	2,446	Med
Blue Lakes	USS0019L05S	38.61	−119.92	2,456	Med
Burnside Lake	USS0019L41S	38.72	−119.89	2,478	High
Monitor Pass	USS0019L40S	38.67	−119.61	2,533	High
Carson Pass	USS0019L45S	38.69	−119.99	2,546	High
Horse Meadow	USS0019L44S	38.84	−119.89	2,608	High
Tuolumne Meadows Ranger Station	USC00049063	37.88	−119.34	2,650	High
Ebbetts Pass	USS0019L19S	38.55	−119.80	2,672	High