Evolution, 2023, **77**(**9**), 1956–1966
https://doi.org/10.1093/evolut/qpad112
Advance access publication 22 June 2023
Original Article

Lower survival of hybrid grosbeaks, but not towhees, suggests a molt divide disfavors hybrids

Vanya G. Rohwer[1], Samantha J. Hagler[1,2], Benjamin M. Van Doren[2,3], Miguel Fuentes[4], Shawn M. Billerman[2]

[1]Cornell University Museum of Vertebrates, Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY, United States
[2]Cornell Lab of Ornithology, Ithaca, NY, United States
[3]Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY, United States
[4]Manning College of Information and Computer Sciences, University of Massachusetts–Amherst, Amherst, MA, United States

Corresponding author: Cornell University Museum of Vertebrates, Department of Ecology and Evolutionary Biology, Cornell University, 159 Sapsucker Woods Road, Ithaca, NY 14850, United States. Email: vgr7@cornell.edu

Abstract

Although avian hybrid zones in the Great Plains have been studied for almost 70 years, we know surprisingly little about the fitness costs to hybrids that keep these zones narrow. We compare age ratios in grosbeaks (*Pheucticus ludovicianus* and *P. melanocephalus*) and towhees (*Pipilo erythropthalums* and *P. maculatus*), two species pairs that differ in their life histories and molt schedules, to evaluate survival between hybrids and parentals. We then contrast molt and migratory divides as possible sources of selection against hybrids. Hybrid grosbeaks had 27%–33% lower survival relative to their parentals, whereas hybrid towhees had survival rates similar to parentals. Age ratio data for hybrid grosbeaks suggest high mortality in older birds, as expected if selection operates after the first year of life. This pattern is consistent with parental species of grosbeaks having contrasting molt schedules relative to migration, suggesting high mortality costs to hybrids driven by molt biology, which are expressed later in life. Contrasts in molt schedules are absent in towhees. While migratory divides may exist for towhees and grosbeaks, the low adult survival of hybrid grosbeaks suggest that molt may be an important and underappreciated source of selection maintaining this and other narrow avian hybrid zones.

Keywords: molt divide, migratory divide, survival, age ratios, grosbeak, towhee

Introduction

Narrow hybrid zones are thought to be maintained by a balance of selection against hybrids and dispersal of parentals into the zone (Barton & Hewitt, 1989). However, documenting fitness costs to hybrids is often challenging. Tracking individuals through time (Grant & Grant, 2008) or conducting reciprocal transplants across a hybrid zone (Arnold et al., 2012; Cooper et al., 2018; Mallet & Barton, 1989) is possible only in sedentary organisms or when fitness is assessed prior to migration or dispersal. When individuals are difficult to track through time, selection against hybrids is often inferred by the shape of character transition clines across the hybrid zone (Barton & Hewitt, 1985), by comparison of parentals and hybrids in performance assays (often done in captivity; Berthold & Querner, 1981; Du et al., 2017), or by inferring that evolved differences between parental species leave hybrids at a disadvantage (Coyne & Orr, 2004; Haldane, 1922; Price & Bouvier, 2002). These methods offer insights into challenging systems but mostly fail to directly compare hybrid and parental fitness.

Avian hybrid zones in the Great Plains of North America were formally described in the 1950s and 1960s, and spurred a history of taxonomic lumps and splits among hybridizing taxa (Short, 1965; Sibley & Short, 1959; Sibley & Short, 1964; Sibley &West, 1959; West, 1962; see Rising, 1983). None of these initial studies focused on the potential causes of selection against hybrids. Later, studies began to probe the fitness costs of hybrids, often by examining links between parental species and ecological variables (Moore & Price, 1993; Rising, 1969; Schaefer, 1980; Swenson, 2006). These studies often suggested ecological gradients as sources of selection against hybrids because recombination should disrupt gene complexes coadapted to environmental conditions. However, the continuum of environmental gradients seemed unlikely to generate the abrupt, almost binary character transitions observed in some hybridizing taxa of the Great Plains (e.g., grosbeaks and orioles). Studies that tracked reproductive success of hybrids or mixed pairs often found few reproductive costs when measuring hatching or fledgling success, suggesting that selection against hybrids occurred after young fledge (Anderson & Daugherty, 1974; Baker & Boylan, 1999; Moore & Koenig, 1986).

The discovery that the migratory routes and the timing and number of molts in the annual cycle of birds are heritable suggests that differences in these traits between hybridizing taxa could generate strong selection against hybrids (Berthold & Helbig, 1992; Berthold & Querner, 1981; Berthold et al., 1994; Guinner & Neusser, 1985; Helbig, 1991). While "migratory divides" are well known in the literature (Delmore & Irwin, 2014; Irwin & Irwin, 2005; Ruegg & Smith, 2002;

Received November 27, 2022; revisions received May 29, 2023; accepted June 21, 2023
Associate Editor: Catherine Linnen; Handling Editor: Miriam Zelditch

Scordato et al., 2020; van Bemmelen et al., 2019), "molt divides" have received little attention. Molt divides should occur in hybridizing species that differ in the timing of feather replacement (molt) relative to migration or in the number of molts completed annually (Rohwer & Irwin, 2011; Rohwer & Manning, 1990). Unlike the gradual selection generated by ecological gradients, intrinsic differences in migratory routes and molt schedules could create strong sources of selection against hybrids that could explain the abrupt step-like clines observed in some of these suture zones.

While clines provide inferences to the strength of selection against hybrids, they often fail to address *why* hybrids perform differently than parentals. Comparing adult survival between hybrids and their parentals examines a mechanism that could result in selection against hybrids. In migratory birds, estimating adult survival can be challenging if species are unamenable to mark–recapture methods, or if individuals disperse outside of study areas, confounding dispersal with mortality (Ricklefs, 1997; Ricklefs & Rohwer, 2005). One method to overcome these challenges is comparing age ratios: the number of adults relative to the number of both adult and younger age classes within a sample population (Ricklefs, 1997). Many birds can be assigned discrete age classes based on their annual replacement of feathers. To estimate adult survival using age ratios, the two relevant age classes are "SY" (a Second-Year individual that is 1 year old and breeding for the first time) or "ASY" (an After-Second-Year individual that is 2 (or more) years old and in their second (or later) breeding season). In many north temperate songbirds, both SY and ASY individuals have successfully migrated to and from their winter ranges, but only ASY individuals have replaced all their flight feathers in their postbreeding molt. SY individuals carry nearly all their flight feathers that they grew while in the nest and these feathers are often a browner color, have a slightly different shape, or show more evidence of wear compared to older ASY individuals that have replaced these feathers (Pyle, 1997, Supplementary Figure S1). After an SY's first breeding season they replace all flight and contour feathers and enter the ASY age class. Because the ASY age class encompasses a broad range of ages (any individual that is 2 years and older), populations should accumulate more ASY individuals. When age ratios between SY and ASY individuals are roughly equal or biased toward SY individuals, this is interpreted as low adult survival.

At least two studies have used age ratios to evaluate survival across hybrid zones (Rohwer, 2004; Toews et al., 2018). In the Hermit–Townsend's warbler system (*Setophaga occidentalis* and *S. townsendi*) of Washington and Oregon, United States, neither parental species differ strongly in life-history traits and hybrids had survival rates similar to both parentals (Rohwer, 2004). Similarly, despite a suspected migratory divide in the yellow-rumped warbler system (*Setophaga coronata*) in British Columbia, Canada, hybrids had similar survival rates compared to parentals (Toews et al., 2018). These and other studies highlight the utility of using age ratios for estimating survival in migratory species (Beissenger & Perry, 2007; Green, 2008; Ricklefs & Rohwer, 2005; Ricklefs et al., 2011) and suggest that contrasts in life histories beyond evolved differences in migratory behavior may be important for detecting selection against hybrids.

We use age ratios to evaluate the potential survival costs to hybrids in two Great Plains hybrid zones: grosbeaks (rose-breasted, *Pheucticus ludovicianus*, in the east, and black-headed, *P. melanocephalus*, in the west) and towhees (eastern, *Pipilo erythrophthalmus*, and spotted, *P. maculatus*, in the west). These species pairs differ in their evolutionary histories and the suspected costs of hybridization. Rose-breasted and black-headed grosbeaks diverged from each other ~1.56 million years ago (Pulgarín-R et al., 2013), are long-distance migrants that winter in Central and South America (Hill, 2022; Wyatt & Francis, 2020), and have different molt and migration schedules (Supplementary Figure S2, Rohwer et al., 2005). These parental differences, coupled with abrupt east–west character transition curves, suggest strong selection against hybrid grosbeaks (Figure 1) (Anderson & Daugherty, 1974; Mettler & Spellman, 2009; West, 1962). In contrast, eastern and spotted towhees diverged ~400,000 years ago (Johnson & Cicero, 2004), migrate short distances, molt on the breeding range prior to migrating south (Bartos Smith & Greenlaw, 2020; Greenlaw, 2020), and share many ecological traits. Gradual character transitions across the towhee zone (Sibley & West, 1959) suggests little selection against hybrids (Figure 1). Thus, we predicted that survival costs to hybrids should be most detectable in grosbeaks.

Next, we use age ratio and behavioral data from eBird observations to probe molt and migratory divides as sources of selection against hybrid grosbeaks and towhees. eBird observations show that parental species of both grosbeaks and towhees have contrasting migratory orientations, especially in the hybrid zone, suggesting a potential migratory divide across both hybrid zones (Helbig, 1991; Irwin & Irwin, 2005; Ruegg & Smith, 2002). By contrast, only parental species of grosbeaks differ in the timing and location of their annual, postbreeding molts, suggesting a potential molt divide in grosbeaks, but not towhees (Rohwer & Irwin, 2011). These two hypotheses generate different predictions for when selection should be strongest in hybrids.

For migratory divides, hybrid mortality should be strongest when hybrids migrate, for the first time, to and from the wintering grounds. To evaluate this prediction, data comparing the number of recently fledged hybrids that have yet to migrate (HY or Hatch Year individuals), with the number of hybrids that have completed their first migration to and from the wintering grounds and are breeding for the first time (the SY age class) are ideal. If migratory divides are a strong source of selection against hybrids, comparisons between HY (that have yet to migrate) and SY (that have returned from their first migrations) hybrids should have an excess of HY individuals, relative to parentals, especially if hybrid have poor migratory behaviors. Unfortunately, our data lack frequency information on HY individuals across hybrids and parentals. Nonetheless, if migratory divides predominate as a source of selection against hybrids, we might expect age ratios of hybrids to be biased toward ASY individuals, as high mortality of birds migrating for the first time should result in fewer SY individuals returning to the breeding grounds. Hybrids with appropriate migratory programs could survive multiple migrations, resulting in an accumulation of ASY hybrids. Because both grosbeak and towhees show similar contrasts in migratory orientation (see results below), we might expect similar age ratios between hybrids of both species pairs.

For molt divides, selection against hybrids should be strongest after the first year of life, when hybrids undergo, for the first time, their complete replacement of both flight and contour feathers. For birds as small as grosbeaks and towhees, the energetic costs of molt are high (Lindström et al., 1993;

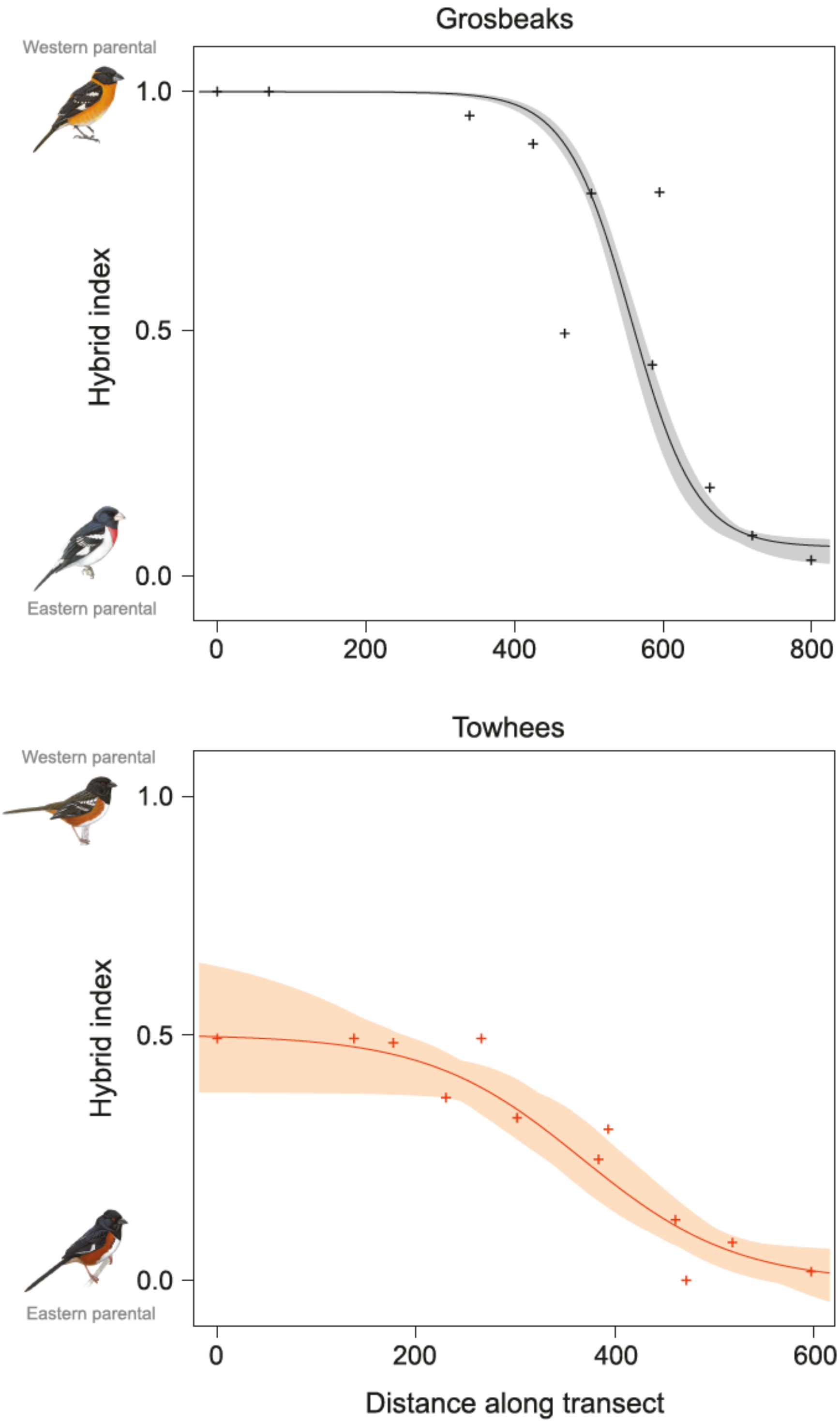

Figure 1. Clines from plumage-based hybrid indices for grosbeaks (top) and towhees (bottom) across the Great Plains hybrid zone. Grosbeaks show a steep, abrupt cline, whereas towhees show a gentle cline between parentals, suggesting strong selection against hybrids in grosbeaks, but not towhees. The westernmost sampling site (0 along the x-axis) was near Greeley, CO, for grosbeaks and near Crook, CO, for towhees; for both species pairs, Blair was the easternmost sample site.

Murphy & King, 1991; Murphy & Taruscio, 1995). During the first year of life, recently fledged grosbeaks and towhees will replace the body feathers that they grew in the nest (Pyle, 1997). In both parental species of grosbeaks, adults feed recently fledged individuals throughout the duration of this body feather molt (VGR, personal observation), shielding young birds from the true energetic costs of molt. We suspect this is true for towhees, but data are lacking. Both the extent of this molt (only body feathers) and the observation that parents feed young throughout it, suggest minimal energetic costs of molt during the first year of life. Neither grosbeak or towhee species undergo a complete replacement of both body and flight feathers until after the first year of life. Importantly, parental species of grosbeaks, but not towhees, have contrasting schedules of molt relative to their fall migration, such that rose-breasted grosbeaks first molt within the breeding range before their migration to wintering areas, whereas black-headed grosbeaks first migrate to northwestern Mexico then undergo their postbreeding molt of flight and body feathers, before continuing south to their wintering grounds (Supplementary Figure S2, Rohwer et al., 2005). High energetic costs of molt and the binary contrasts in the timing and location of the postbreeding molt between parental species of grosbeaks suggest that hybrids may inherit poor combinations of molt-related genes (Rohwer & Irwin, 2011; Rohwer & Manning, 1990). By contrast, both species of towhees molt on the breeding range prior to migration suggest little role for molt divides in this hybrid zone. Thus, if molt divides predominate, hybrid mortality should be highest in grosbeaks and occur after the first year of life when the costs of molt are most strongly expressed. After nearly 70 years of study and few data to suggest what selects against hybrids, our data suggests strong mortality selection operating after the first year of life in the grosbeak, but not towhee, hybrid zone, consistent with the molt divide hypothesis.

Methods

Study species and specimens

We examined 261 grosbeak and 383 towhee specimens collected along river transects through their Great Plains hybrid zones in Nebraska, South Dakota, and Colorado, from May through July, 1953–1957 (with the exception of one towhee, collected in 1948). Most specimens came from the ~700 km east–west Platte River transect, from the eastern border of Nebraska to Greeley, Colorado in the west. In both species pairs, SY and ASY males are difficult to distinguish in the field (Supplementary Figure S1), reducing the likelihood of a collecting bias toward one age class (Ricklefs, 1997; Ricklefs & Rohwer, 2005). We examined only males because too few females were collected for reliable survival estimates.

Assigning hybrid scores

We used plumage characters to assign individuals as hybrids or phenotypically pure parentals (Supplementary Material: Generating hybrid indices from plumage characters). Eastern and spotted towhees differ primarily in the amount of white on their back and wings. Following Sibley and West (1959), these differences were ranked from 0 to 4, where 0 indicated phenotypic eastern towhees (black backs) and 4 indicated phenotypic spotted towhees (extensive white on back and wings). Plumage characters for grosbeaks were separated into two groups based on color, following West (1962). Breast, belly, and underwing vary from rose-red to rich yellow and were scored together from 0 to 4. Similarly, rump and neck color vary from brown to black coloration and were scored together from 0 to 4. For both plumage groups, 0s indicated pure rose-breasted grosbeaks and 4s indicated pure black-headed grosbeaks, and their sum was our hybrid index.

For grosbeaks, pure parental rose-breasted grosbeak scored 0–1, pure parental black-headed grosbeak scored 7–8, and hybrids scored 2–6. For towhees, pure parental eastern towhees scored 0, pure parental spotted towhees scored 4, and hybrids scored 1–3. For our cline analyses (see below), these hybrid scores were standardized from 0 (pure eastern parental) to 1 (pure western parental). This classic approach of using plumage characters to evaluate hybrid ancestry correlates well with photographic measures of phenotype, at least in one other species (Aguillon & Rohwer, 2022).

Assigning age classes

We assigned specimens to SY or ASY age classes by differences in feather color, shape, wear, and number of replaced feathers, following Pyle (1997) (Supplementary Figure S1 for examples of age classes). SJH aged all specimens. All grosbeaks were easily and accurately assigned to SY and ASY age classes. For towhees, five specimens were challenging to age, and for these individuals, SMB and VGR helped age these specimens.

While differences in feather characters can be observed on specimens in the hand, they are difficult to see in the field in both species pairs. Grosbeaks often sing from high perches and towhees often skulk in thick vegetation, behaviors that minimize potential collecting biases driven by age-differences in plumage. More importantly, survival estimates in this study represent relative measures between hybrids and parentals for males only, and not species-level estimates of survival. None of the plumage characters used for assigning age class contributed to an individual's hybrid score and these specimens were not collected with song playback. Finally, SY and ASY grosbeaks show some, though minor, variation in the extent of body feathers replaced prior to the breeding season (the prealternate molt), which could influence our assessment of hybrid individuals. Any possible influence of age on hybrid score in grosbeaks would result in underestimates of the number of SY hybrids, producing conservative estimates of the survival differences we detected (see results below).

Calculating adult survival

We calculated adult survival for each parental species and their hybrids by comparing age ratios following Ricklefs (1997), where Survival = ASY/(ASY + SY). ASY is the number of individuals in their second or later breeding season and SY is the number of individuals in their first breeding season. When populations are stable ($\lambda = 1$), age ratios may be thought of as the proportion of adults (age > 1 year) that survive annually.

Survival estimates from age ratios come with assumptions (Ricklefs, 1997). For example, samples of SY to ASY individuals are assumed to be proportional to their abundance in the population. If one age class is sampled disproportionately relative to the other, this can bias survival estimates. Age ratios also assume equal likelihood of mortality between SY and ASY individuals, and that individuals of different ages within the ASY age class have similar survival probabilities. Increased mortality of young birds is assumed to have already occurred (e.g., within the first 6 months of life), making these survival estimates applicable to adults only, and not earlier life stages. Ricklefs (1997) provides a detailed review of potential sources of bias when using age ratios to estimate survival, many of which are not applicable to this data set (i.e., continuous breeding seasons, one sex overrepresented in collections compared to the other, sex-specific differences in survival, etc.).

Comparison with core breeding ranges

Differences in age ratios between hybrids and parentals could represent selection against hybrids if parentals have higher survival than hybrids. If parental survival within the hybrid zone is low, this could indicate that (a) habitat quality within the hybrid zone is poor or (b) competitive interactions among SY and ASY males that are establishing breeding territories results in the displacement of subordinate SY males to the periphery of their breeding range, as reported for other species (Graves, 1997; Rohwer, 2004; Studds et al., 2008). Either of these scenarios could bias estimates of parental survival such that they would appear lower compared to core regions located centrally within the breeding range, potentially obscuring differences in survival between parentals and hybrids, or complicating interpretations of hybrid survival, habitat quality, and the relative importance of ecological gradient hypotheses. To control for this, we included samples of eastern and western parental species of both towhees and grosbeaks collected outside of the hybrid zone from central regions of their breeding range. For spotted towhees, we use individuals from Wyoming, southern Montana, eastern Colorado, Utah, Nevada, and California corresponding to the *curatus*, *falcinellus*, *arcticus*, *montanus* subspecies, of which the *arcticus* and *montanus* subspecies are thought to be the western parentals in this hybrid system (Sibley & West, 1959). For the three other species (eastern towhees, rose-breasted, and black-headed grosbeaks), we choose individuals collected broadly from central regions of their breeding range, from similar temperate latitudes as the hybrid zone (see Table 1).

We tested for (a) differences in adult survival between hybrids and parentals from within the hybrid zone and (b) differences in adult survival between parentals inside and outside of the hybrid zone. We used binomial tests of proportions in all comparisons (Crawley, 2005) using R (R Core Team, 2022), and accounted for multiple comparisons made from the same data sets using False Discovery Rates following Pike (2011). Additional analyses of survival in hybrid zone specimens gave similar results and are summarized in Supplementary Materials (see sections: Using GLM approaches to analyze age ratio data, Supplementary Table S1, and Summaries of age ratio data, Supplementary Tables S2–S7).

Evaluating migratory divides using migration models

We estimated timing and direction of migration for grosbeaks and towhees using BirdFlow models (Fuentes et al., 2023), which uses species distribution maps from the eBird Status and Trends project (Fink et al., 2020) to infer individual movement across a species' range. Briefly, BirdFlow fits a probabilistic graphical model to a time series of relative abundance maps to estimate the most likely species movements that occurred to produce that time series. From a BirdFlow model, we can generate predictions of the routes that individuals in a population are likely to follow. BirdFlow results should be interpreted cautiously, as they are model predictions, not observations. Fuentes et al. (2023) validated the modeling approach using GPS and satellite tracking data from 11 species of birds. For towhees and grosbeaks, we used model hyperparameters validated for another species of the same order (order Passeriformes; wood thrush, *Hylocichla mustelina*). Fuentes et al. (2023) found that the following sets of hyperparameters performed well on this passerine songbird: model (1) entropy weight = 0.02 and distance exponent = 0.4 and model (2) entropy weight = 0.04 and distance exponent = 0.7. We applied models with both sets of hyperparameters to grosbeak and towhee species to ensure that our conclusions were not sensitive to small differences in hyperparameter selection. We present the results from model 1 in the main text and the results from model 2 in Supplementary Materials.

After fitting BirdFlow models for grosbeak and towhee species, we used the model to simulate fall migration trajectories starting in week 26 of the year (approximately the last week of June) through week 52. For each species, we simulated 1,000 trajectories outside of the hybrid zone and 1,000 trajectories within the hybrid zone. We defined the hybrid zone as a rectangle between 37 and 49° N and −105 and −95° W. For each simulated individual trajectory, we considered it to be in a migratory state once it moved 150 km in the direction of its destination. We recorded the time at which the simulated bird crossed this threshold and calculated initial migration orientation as the angle from the starting location to the crossing point. We ignored simulated birds that did not move far enough to satisfy this condition (e.g., year-round residents in towhees).

We compared fall migration departure timing, orientation, and distance for each of the four focal species, both within and outside of the hybrid zone. For orientation, we evaluated circular means and circular differences at varying distances from the center of the hybrid zone (defined as 100° W), and predicted that orientation should differ most strongly between

Table 1. Summary of grosbeak and towhee age classes and adult survival estimates within and outside of the hybrid zone. Pure western phenotype within the hybrid zone indicates black-headed grosbeaks and spotted towhees, and pure eastern phenotypes indicate rose-breasted grosbeaks and eastern towhees; in all cases of "pure western/eastern phenotypes," these individuals showed no phenotypic signs of introgression. Survival estimates (±1 SE) were calculated using the number of After-Second-Year (ASY) and Second-Year (SY) individuals following Ricklefs (1997).

	Outside zone	Inside hybrid zone			Outside zone
	Western population	Pure western phenotype	Hybrid	Pure eastern phenotype	Eastern population
Grosbeaks					
Adults (ASY)	133	75	33	59	58
Young (SY)	60	37	35	22	36
Survival	0.69 ± 0.03	0.67 ± 0.04	0.49 ± 0.06	0.73 ± 0.05	0.62 ± 0.05
Towhees					
Adults (ASY)	73	27	161	48	86
Young (SY)	84	22	106	19	23
Survival	0.46 ± 0.04	0.55 ± 0.07	0.60 ± 0.03	0.72 ± 0.06	0.79 ± 0.04

parentals from the hybrid zone as this region is shifted further east or west, depending on parental species, from the north–south axis of migration.

Geographic cline analyses

To independently validate evidence of selection from the age ratio analyses and to assess the distribution of parental towhees and grosbeaks across the landscape, we used the Metropolis–Hastings Markov chain Monte Carlo algorithm as implemented in the "hzar" package (Derryberry et al., 2014) in R (R Core Team, 2022), which allowed us to fit a series of geographic cline models to hybrid scores assessed using phenotype. For both the towhee and grosbeak cline models, we tested four models: (a) no tails, (b) right tail, (c) left tail, and (d) two tails, each with a chain length of 2×10^7 and a burn-in of 2×10^6, randomized the initial value for each fit request, and selected the best model using AIC_C scores as the final model for each hybrid zone.

Results

Survival of hybrids

Grosbeaks scoring as hybrids had lower survival than parentals from within the hybrid zone (black-headed within the hybrid zone vs. hybrids $\chi^2 = 5.25$, $p = .022$; rose-breasted within the hybrid zone vs. hybrids $\chi^2 = 8.25$, $p = .008$; Figure 2, Table 1). Survival of hybrids was 27.5% lower than that of black-headed adults and 33.4% lower than that of rose-breasted adults collected within the hybrid zone. Comparing survival between parentals collected within and outside of the hybrid zone revealed no differences, suggesting that settlement patterns along the east–west breadth of the breeding range are not affected by despotic behaviors (black-headed $\chi^2 = 0.05$, $p = .82$; Rose-breasted $\chi^2 = 1.96$, $p = .32$).

In contrast, we found no striking differences in adult survival between hybrids and parental towhees collected within the hybrid zone (spotted and hybrids: $\chi^2 = 0.27$, $p = .60$; eastern and hybrids $\chi^2 = 2.48$, $p = .23$). Instead of mortality selection against hybrids, survival in towhees appears to vary in a gradient-like fashion from lower survival in the west to higher survival in the east, as might be predicted from the greater variation in winter weather in the west (Figure 2, Table 1). We found no significant differences in the survival of parental species collected inside and outside of the hybrid zone (spotted $\chi^2 = 0.79$, $p = .37$; eastern $\chi^2 = 0.84$, $p = .37$).

Our survival estimates for grosbeaks and towhees are comparable to others (Supplementary Material: Comparing survival estimates with those found in the literature, Supplementary Table S8).

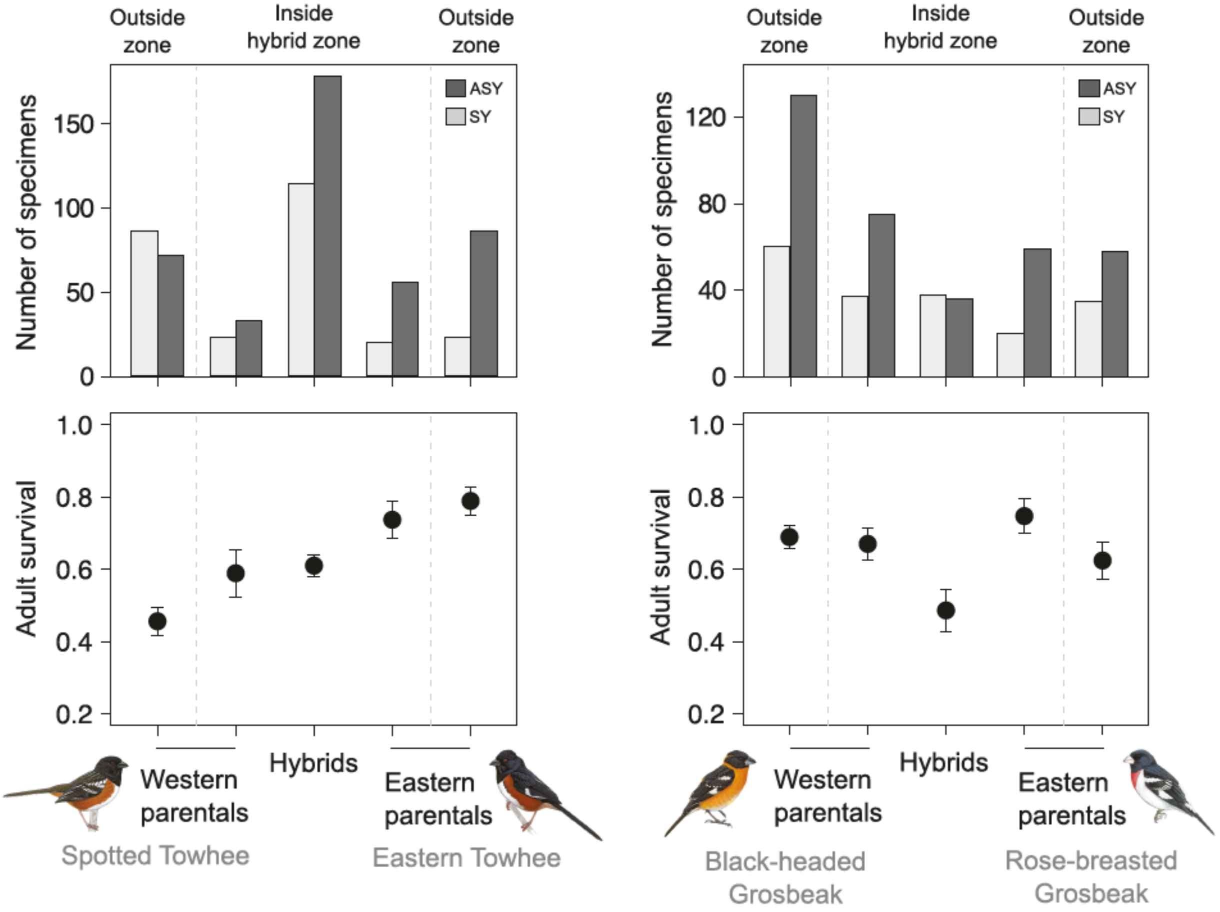

Figure 2. Hybrid grosbeaks have lower survival compared to both parentals, and this difference is driven by lower survival of After-Second-Year (ASY; older) birds, as indicated by the low number of ASY hybrids in the grosbeak bar plot. Hybrid towhees are abundant in the hybrid zone and showed no pronounced differences in survival between parentals, but survival may be lower in hybrids compared with eastern towhees from within the zone. Top bar plots show the number of ASY and Second-Year (SY) individuals examined across species and show the data used to generate adult survival estimates (± 1 SE) in the points below each set of bars.

Molt and migratory divides

Age ratios show that the lower adult survival in hybrid grosbeaks is driven by the presence of fewer ASY hybrids within the zone, consistent with selection acting later in life (Figure 2). Only hybrid grosbeaks had more SY compared with ASY individuals. These contrasts suggest that selection against hybrid grosbeaks occurs after the first annual cycle when the costs of molt divides should be first expressed.

BirdFlow simulations suggest that a migratory divide exists for both species pairs in the Great Plains (Figure 3). Migratory orientations for parental species of grosbeaks and towhees differed most strongly in individuals from within the hybrid zone (Figure 4, Supplementary Figure S3), while birds breeding away to the east and west showed much smaller differences in migratory orientations. Simulated departure dates from the breeding range were similar between the towhees but different between grosbeaks because black-headed grosbeaks depart earlier than rose-breasted grosbeaks to molt in west Mexico (Figure 5, Supplementary Figure S4). Migration distances also differed between grosbeaks, especially within the hybrid zone, with rose-breasted grosbeaks migrating longer distances. Migration distances differed little between eastern and spotted towhees inside or outside of the hybrid zone (Figure 5, Supplementary Figure S4).

Geographic clines

Geographic cline analyses revealed strikingly different patterns for the towhee and grosbeak hybrid zone consistent with the results from our calculations of adult survival. Estimates for cline center for towhees and grosbeaks based on hybrid scores were 218.4 km (174.0–271.9 km) and 243.0 km (232.8–253.2 km) west of Blair, Nebraska, respectively. Estimates of cline width for the towhee and grosbeak hybrid zone based on hybrid scores were 279.2 km (198.0–390.2 km) and 160.8 km (136.9–190.6 km), respectively. The width estimate for the towhee cline was over 100 km wider than the grosbeak cline, and also had an extremely broad confidence interval, perhaps an indication of the weak signal of transition across the hybrid zone for towhees compared with the abrupt transition in the grosbeaks or the incomplete sampling toward the western limits of the towhee hybrid zone.

Discussion

We compared survival estimates and molt and migratory divide hypotheses as sources of selection against hybrids in the grosbeak (*Pheucticus*) and towhee (*Pipilo*) hybrid zones of the central Great Plains, United States. Adult survival was lower in hybrid grosbeaks, but not in hybrid towhees, suggesting strong selection against hybrid grosbeaks, but not towhees. The lower survival in hybrid grosbeaks suggests that selection against hybrids is most pronounced after the first annual cycle, consistent with the molt divide hypothesis (Rohwer & Irwin, 2011). BirdFlow models, clearly show pronounced differences in the migratory behavior of parentals in both towhees and grosbeaks, but evaluating mortality costs to hybrids that might be associated with intermediate migratory

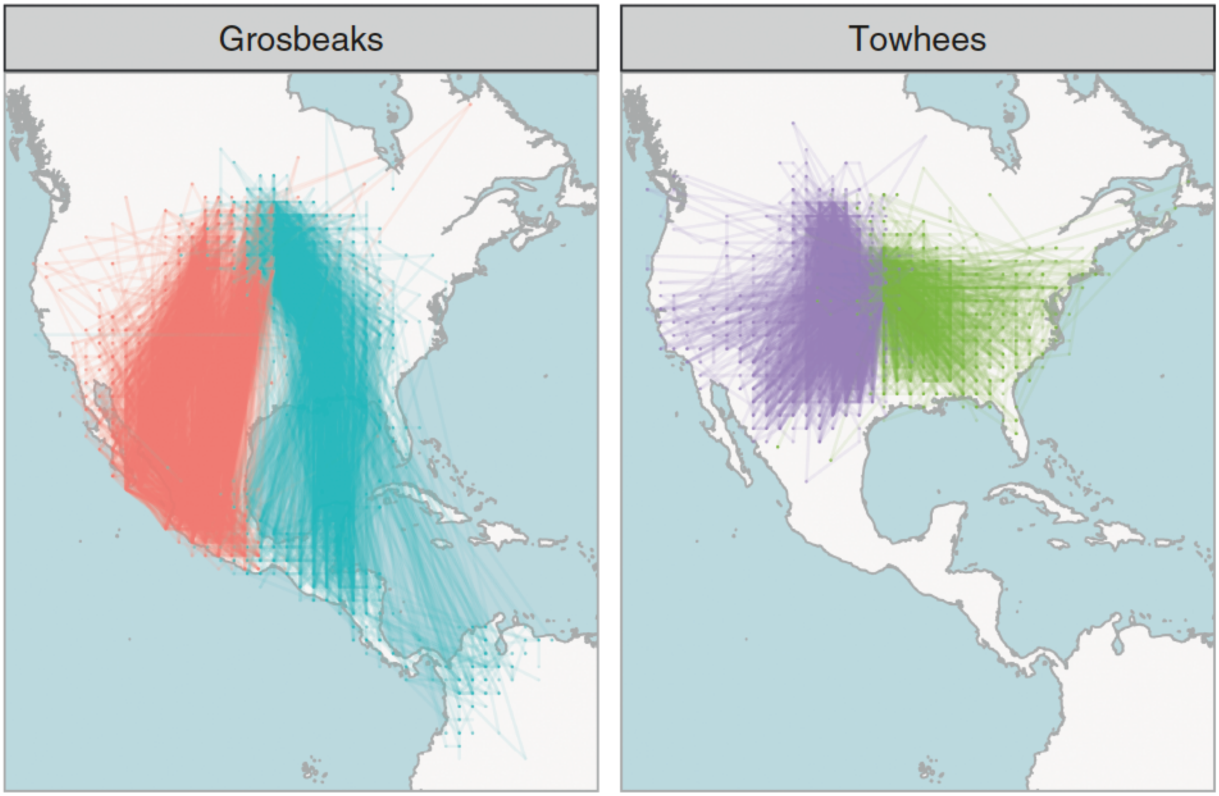

Figure 3. Simulated fall migration trajectories for grosbeaks and towhees originating within the hybrid zone. Both species pairs clearly show different migratory orientation and routes. For grosbeaks, orange represents black headed and blue represents rose breasted. For towhees, purple represents spotted and green represents eastern.

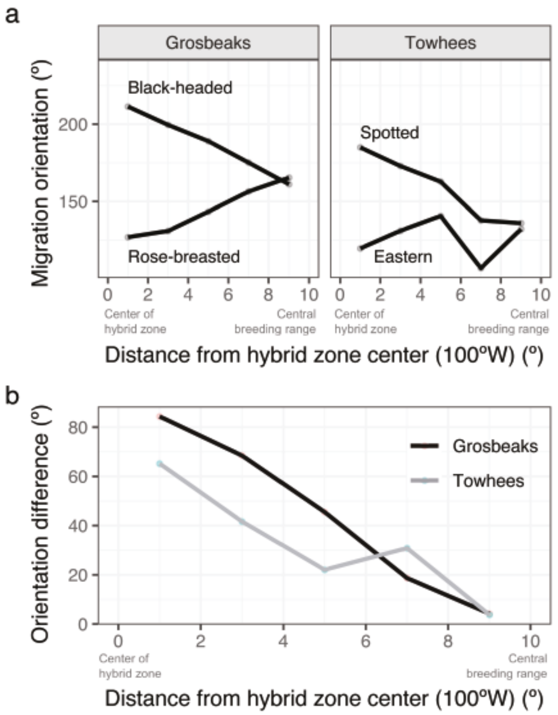

Figure 4. Grosbeaks and towhees from the hybrid zone show the strongest differences in orientation compared with individuals closer to the range center, creating potential for a migratory divide. (A) Average modeled migration orientation with increasing distance from the hybrid zone and (B) The difference between species at each distance evaluated. The predicted differences in orientation are strongest within the hybrid zone and decline toward the center of the breeding range, suggesting that orientation could be an important factor in selecting against hybrids in east–west contact zones.

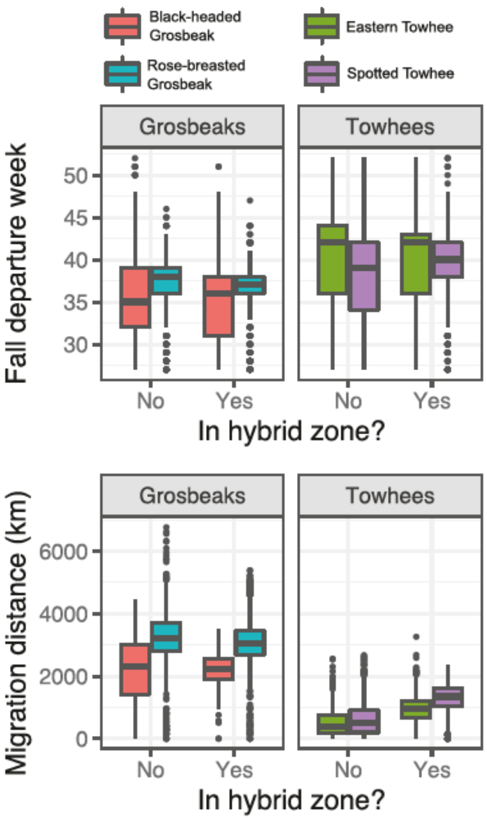

Figure 5. Contrast in timing of departure and migration distance, using modeled data from eBird, during the fall south-bound migration between hybridizing grosbeaks and towhees.

behavior is difficult when looking at adult survival instead of survival during the first year of life. That adult survival costs were detectable in hybrid grosbeaks, but not towhees, are consistent with contrasts in cline widths (Figure 1), life-history differences in molt biology, and divergence times between parental species of grosbeaks and towhees.

Our results suggest that molt divides may play an important role in maintaining the narrow grosbeak hybrid zone. Low adult survival of hybrid grosbeaks is driven by a lack of older, ASY birds, suggesting that selection is operating after the first year of life (Figure 2). SY hybrids have successfully completed two migrations and survived the nonbreeding period. If costs to hybrids are associated with their complete annual molts, then these costs should be expressed, for the first time, after the first year of life and result in fewer ASY birds, consistent with patterns of hybrid survival in grosbeaks (Figure 2). The molt divide hypothesis seems especially plausible in grosbeaks for two reasons. First, costs associated with molt are mostly deferred until later in life because parents feed young during their first replacement of body feathers, shielding them from the true costs of feather replacement. Second, after the first year of life, parental species differ in the timing and location of their molts: Rose-breasted grosbeaks molt on their breeding grounds immediately after breeding, while black-headed grosbeaks first migrate to the Mexican monsoon region, then undergo their molt (Supplementary Figure S2, Rohwer et al., 2005). These contrasts in molt schedules suggest that hybrids may molt in food-limited locations, molt while migrating, or undergo too many or too few molts annually (Rohwer & Irwin, 2011; Rohwer & Manning, 1990). Few other contrasts in life histories between parental species of grosbeaks are as stark as differences in molt-migration biology to account for the high mortality of hybrids required to generate the steep clines across this hybrid zone.

Our evaluation of the migratory divides hypothesis lacks data from recently fledged hybrids and parentals that have yet to undergo migration (Hatch Year or HY individuals). Comparing the number of HY individuals, prior to their first south-bound migration, to the number of SY individuals, which have recently returned from their first north-bound migration, would allow estimates of survival for both hybrids and parentals during the first year of life, which encompasses two migrations for the towhees and grosbeaks. We speculate that migratory divides alone may not be a substantial source of selection against hybrid grosbeaks because the number of hybrid SY individuals was comparable to or exceeded the number of parental SY individuals (Figure 2). If migratory divides are a strong source of selection against hybrids, we should expect individuals with intermediate or poor migratory programs, which are migrating for the first time (HY individuals), to be less likely to return to the breeding grounds as SY individuals, resulting in relatively low numbers of SY hybrids. Comparing numbers alone fails to account for collecting effort that may have been directed toward hybrids, but, the narrow hybrid zone, relatively low frequency of hybrids, and suspected assortative mating in grosbeaks (Anderson & Daughtery, 1974; West, 1962), suggests that hybrids are not producing disproportionate numbers of HY individuals compared to parentals. Thus, the relatively high frequency of SY hybrids, relative to parentals, suggests that mortality may not be disproportionately high during the first year of life in hybrid grosbeaks, when migration first occurs. While our inferences are speculative, they highlight the need for tests comparing age ratios of HY and SY age classes across hybrids and parentals of grosbeaks and other avian hybrid zones (see Toews et al., 2018).

Other mechanisms surely contribute to selection against hybrids. If hybrids suffer reproductive costs either through lower pairing success or fewer young produced, as suggested for female grosbeaks (Anderson & Daughtery, 1974), then this cost should further select against hybrids. However, reproductive costs do not predict differences in hybrid survival across age classes. Lower reproductive success of hybrids should result in fewer backcrossed individuals overall, but hybrids and parentals should have similar age ratios of SY to ASY birds. Alternatives such as compromised immune function, which may express costs later in life after accumulated challenges to the immune system, could further contribute to selection against hybrids and generate similar patterns of excess SY birds (Rice et al., 2021; Wiley et al., 2009).

An alternate explanation of our age ratio results could be the dispersal of ASY hybrids out of the hybrid zone. This seems unlikely for several reasons. First, hybrid grosbeaks are rarely seen outside of the hybrid zone (Supplementary Materials: Dispersal of hybrid grosbeaks across geography, Supplementary Figures S5–S6). Second, the grosbeaks we examined for this study were collected across a nearly 700 km transect from the eastern edge of Nebraska to central/eastern Colorado (West, 1962). Yet, almost no hybrids were collected outside of three localities (Silver Creek, Grand Island, Elm Creek) spanning ~160 km in the center of the hybrid zone. Third, a growing literature suggests that males breeding for the first time settle toward the northern reaches of the breeding range (Graves, 1997; Studds et al., 2008) or in less-suitable habitat (Anderson & Daugherty, 1974; Hill, 1988; Rohwer, 2004), neither of which seem to apply to the Platte River transect. Together, these observations suggest dispersal of ASY hybrid grosbeaks away from their first breeding sites is unlikely to have generated the deficiency of ASY hybrids we found within this hybrid zone.

Survival in towhees is lowest in the west and highest in the east. This pattern suggests that differences in survival between hybrids and eastern towhees collected within the hybrid zone may not reflect selection against hybrids. In some years, sampling effort of the towhee hybrid zone was concentrated in the central and eastern parts of the zone (Supplementary Material: Summaries of age ratio data, Supplementary Table S5), and this uneven sampling effort may weaken comparisons in survival data between hybrids and western parentals. Compared to grosbeaks, the wider towhee hybrid zone (Sibley & West, 1959, Figure 1) and high frequency of hybrids compared to phenotypically pure parentals (Figure 2) suggest weak, if any, mortality selection against hybrids. We speculate that environmental heterogeneity of the intermontane west, where survival is lowest, poses harsher, less predictable conditions on spotted towhees. By contrast, more stable and predictable climatic conditions in the east may allow higher survival for eastern towhees.

Our finding that hybrid grosbeaks, but not towhees, suffer ~27%–33% lower adult survival than either of their parentals from within the hybrid zone provides the first data on potential costs of hybridization in grosbeaks. The deficiency of ASY hybrids compared to parentals suggests that selection against hybrid grosbeaks is most pronounced after the first year of life, consistent with the molt divides hypothesis (Rohwer & Irwin, 2011), as the costs of molt are most strongly expressed after the first breeding season when hybrids replace their entire plumage without assistance from their parents. In contrast to grosbeaks, hybrid towhees showed no apparent survival costs, which we attribute to parental species being recently diverged and sharing many ecological and life-history traits. After nearly 70 years of study, the low adult survival in hybrid grosbeaks seems to be the first source of selection supported by data that could be keeping this zone narrow.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

All data have been uploaded to Dryad: doi:10.5061/dryad.c866t1gc3

Author contributions

V.G.R., S.H., and S.M.B. conceived the study. S.H. and S.M.B. scored specimens. V.G.R., S.H., and S.M.B. conducted age ratio analyses, and B.M.V.D. and M.F. conduced BirdFlow analyses. V.G.R., S.H., and B.M.V.D. wrote the initial draft. All authors reviewed and approved the manuscript.

Conflict of interest: The authors declare no conflict of interest.

Acknowledgments

This work would not have been possible without the efforts of David West and Charles Sibley who sampled these hybrid zones in the 1950s. We thank the Cornell University Museum of Vertebrates (CUMV), Paul Sweet at the AMNH, and Carla Cicero at the MVZ for access to specimens. Sievert Rohwer provided helpful discussion and feedback on earlier versions of this work, and Catherine Linnen and two anonymous reviewers helped clarify the text, improve organization, and strengthen analyses. S.H. was supported by a CALS Alumni Award and the Sally Merrill Sutcliffe Endowment for Cornell Students at the Cornell Lab of Ornithology. B.M.V.D. was supported by a Cornell Presidential Postdoctoral Fellowship. S.M.B. was supported by a National Science Foundation Postdoctoral Research Fellowship in Biology under grant 1612277. BirdFlow models were supported by NSF grant 2210980.

References

Aguillon, S. M., & Rohwer, V. G. (2022). Revisiting a classic hybrid zone: Movement of the northern flicker hybrid zone in contemporary times. *Evolution*, 76(5), 1082–1090. https://doi.org/10.1111/evo.14474

Anderson, B. W., & Daugherty, R. J. (1974). Characteristics and reproductive biology of grosbeaks (*Pheucticus*) in the hybrid zone in South Dakota. *The Wilson Bulletin*, 86, 1–11.

Arnold, M. L., Ballerini, E. S., & Brothers, A. N. (2012). Hybrid fitness, adaptation and evolutionary diversification: Lessons learned from Louisiana Irises. *Heredity*, 108(3), 159–166. https://doi.org/10.1038/hdy.2011.65

Baker, M. C., & Boylan, J. T. (1999). Singing behavior, mating associations and reproductive success in a population of hybridizing lazuli and indigo buntings. *The Condor*, 101(3), 493–504. https://doi.org/10.2307/1370179

Barton, N. H., & Hewitt, G. M. (1985). Analysis of hybrid zones. *Annual Review of Ecology and Systematics*, 16(1), 113–148. https://doi.org/10.1146/annurev.es.16.110185.000553

Barton, N. H., & Hewitt, G. M. (1989). Adaptation, speciation and hybrid zones. *Nature*, 341(6242), 497–503. https://doi.org/10.1038/341497a0

Bartos Smith, S., & Greenlaw, J. S. (2020). Spotted towhee (*Pipilo maculatus*), version 1.0. In P. G. Rodewald (Ed.), *Birds of the world*. Cornell Lab of Ornithology. https://doi.org/10.2173/bow.spotow.01

Beissinger, S., & Peery, M. Z. (2007). Reconstructing the historic demography of an endangered seabird. *Ecology*, 88, 296–305.

Berthold, P., & Helbig, A. J. (1992). The genetics of bird migration: Stimulus, timing, and direction. *Ibis*, 134, 35–40.

Berthold, P., Mohr, G., & Querner, U. (1994). Vererbung einer populationsspezifischen Mauser bei Kreuzung von Mönchsgrasmucken (*Sylvia atricapilla*) verschiedener Populationen. *Journal für Ornithologie*, 135, 233–236.

Berthold, P., & Querner, U. (1981). Genetic basis of migratory behavior in European warblers. *Science*, 212(4490), 77–79. https://doi.org/10.1126/science.212.4490.77

Cooper, B. S., Sadghifar, A., Nash, W. T., Comeault, A. A., & Matute, D. R. (2018). A maladaptive combination of traits contributes to the maintenance of a *Drosophilia* hybrid zone. *Current Biology*, 28, 2940–2947.

Coyne, J. A., & H. A. Orr. (2004). *Speciation*. Sinauer Associates.

Crawley, M. J. (2005). *Statistics: An introduction using R*. Wiley & Sons.

Delmore, K. E., & Irwin, D. E. (2014). Hybrid songbirds employ intermediate routes in a migratory divide. *Ecology Letters*, 17(10), 1211–1218. https://doi.org/10.1111/ele.12326

Derryberry, E. P., Derryberry, G. E., Maley, J. M., & Brumfield, R. T. (2014). HZAR: Hybrid zone analysis using an R software package. *Molecular Ecology Resources*, 14(3), 652–663. https://doi.org/10.1111/1755-0998.12209

Du, S. N. N., Khajali, F., Dawson, N. J., & Scott, G. R. (2017). Hybridization increases mitochondrial production of reactive oxygen species in sunfish. *Evolution*, 71(6), 1643–1652. https://doi.org/10.1111/evo.13254

Fink, D., Auer, T., Johnston, A., Ruiz-Gutierrez, V., Hochachka, W. M., & Kelling, S. (2020). Modeling avian full annual cycle distribution and population trends with citizen science data. *Ecological Applications*, 30(3), e02056. https://doi.org/10.1002/eap.2056

Fuentes, M., Van Doren, B. M., Fink, D., & Sheldon, D. (2023). BirdFlow: Learning seasonal bird movements from Citizen Science Data. *Methods in Ecology and Evolution*, 14, 923–938.

Grant, B. R., & Grant, P. G. (2008). Fission and fusion of Darwin's finches populations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 2821–2829.

Graves, G. R. (1997). Geographic clines in age ratios of black-throated blue warblers (*Dendroica caerulescens*). *Ecology*, 78(8), 2524–2531. https://doi.org/10.2307/2265911

Green, R. E. (2008). Demographic mechanism of a historical bird population collapse reconstructed using museum specimens. *Proceedings of the Royal Society of London B: Biological Sciences*, 275(1649), 2381–2387. https://doi.org/10.1098/rspb.2008.0473

Greenlaw, J. S. (2020). Eastern towhee (*Pipilo erythrophthalmus*), version 1.0. In P. G. Rodewald (Ed.), *Birds of the world*. Cornell Lab of Ornithology. https://doi.org/10.2173/bow.eastow.01

Guinner, E., & Neusser, V. (1985). Die Jugendmauser europäis- cher und afrikanischer Schwarzkehlchen (*Saxicola torquata tubicula* und *axillaris*) sowie yon F1-Hybriden. *Journal für Ornithologie*, 126, 219–220.

Haldane, J. B. S. (1922). Sex ratio and unisexual sterility in animal hybrids. *Journal of Genetics*, 12(2), 101–109. https://doi.org/10.1007/bf02983075

Helbig, A. J. (1991). Inheritance of migratory direction in a bird species: A cross-breeding experiment with SE- and SW-migrating blackcaps (*Sylvia atricapilla*). *Behavioral Ecology and Sociobiology*, 28, 9–12.

Hill, G. E. (1988). Age, plumage brightness, territory quality and reproductive success in the black-headed grosbeak. *The Condor*, 90(2), 379–388. https://doi.org/10.2307/1368566

Hill, G. E. (2022). Black-headed grosbeak (*Pheucticus melanocephalus*), version 2.0. In S. M. Billerman & B. K. Keeney (Eds.), *Birds of the world*. Cornell Lab of Ornithology. https://doi.org/10.2173/bow.bkhgro.02

Irwin, D. E., & J. H. Irwin. (2005). Siberian migratory divides: The role of seasonal migration in speciation. In R. Greenberg & P. P. Marra (Eds.), *Birds of two worlds: The ecology and evolution of migration* (pp. 27–40). Johns Hopkins University Press.

Johnson, N. K., & Cicero, C. (2004). New mitochondrial DNA data affirm the importance of Pleistocene speciation in North American birds. *Evolution*, 58(5), 1122–1130. https://doi.org/10.1111/j.0014-3820.2004.tb00445.x

Lindström, A., Visser, G. H., & Daan, S. (1993). The energetic cost of feather synthesis is proportional to basal metabolic rate. *Physiological Zoology*, 66, 490–510.

Mallet, J., & Barton, N. H. (1989). Strong natural selection in a warning-color hybrid zone. *Evolution*, 421, 431.

Mettler, R. D., & Spellman, G. M. (2009). A hybrid zone revisited: Molecular and morphological analysis of the maintenance, movement, and evolution of a Great Plains avian (Cardinalidae: *Pheucticus*) hybrid zone. *Molecular Ecology*, 18(15), 3256–3267. https://doi.org/10.1111/j.1365-294X.2009.04217.x

Moore, W. S., & Koenig, W. D. (1986). Comparative reproductive success of yellow-shafted, red-shafted, and hybrid flickers across a hybrid zone. *Auk*, 103, 42–51.

Moore, W. S., & J. T. Price. (1993). The nature of selection in the northern flicker hybrid zone and its implications for speciation theory. In R. G. Harrison (Ed.), *Hybrid zones and the evolutionary process* (pp. 196–225). Oxford University Press.

Murphy, M. E., & J. R. King. (1991). Nutritional aspects of avian molt. In B. D. Bell (Ed.), *Acta XX Congressus Internationalis Ornithologici* (pp. 2168–2193). Congress Trust Board.

Murphy, M. E., & Taruscio, T. G. (1995). Sparrows increase their rates of tissue and whole-body protein synthesis during the annual molt. *Comparative Biochemistry and Physiology A*, 111, 385–396.

Pike, N. (2011). Using false discovery rates for multiple comparisons in ecology and evolution. *Methods in Ecology and Evolution*, 2, 278–282.

Price, T. D., & Bouvier, M. M. (2002). The evolution of F1 postzygotic incompatibilities in birds. *Evolution*, 56(10), 2083–2089.

Pulgarín-R, P. C., Smith, B. T., Bryson, R. W., Jr., Spellman, G. M., & Klicka, J. (2013). Multilocus phylogeny and biogeography of the new world *Pheucticus* grosbeaks (Aves: Cardinalidae). *Molecular Phylogenetics and Evolution*, 69(3), 1222–1227. https://doi.org/10.1016/j.ympev.2013.05.022

Pyle, P. (1997). *Identification guide to North American birds, Part I: Columbidae to Ploceidae*. Slate Creek Press.

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://doi.org/https://www.R-project.org/

Rice, A. A., Curry, R. L., & Weckstein, J. D. (2021). Haemosporidian prevalence and community composition vary little across a chickadee hybrid zone. *Ornithology*, 138(3), 1–13.

Ricklefs, R. E. (1997). Comparative demography of New World populations of thrushes (*Turdus* spp.). *Ecological Monographs*, 67(1), 23–43. https://doi.org/10.2307/2963503

Ricklefs, R. E., & Rohwer, S. (2005). Comparative demography of New World populations of thrushes (*Turdus* spp.): Comment. *Ecology*, 86(9), 2541–2544. https://doi.org/10.1890/05-0066

Ricklefs, R. E., Tsunekage, T., & Shea, R. E. (2011). Annual adult survival in several new world passerine birds based on age ratios in museum collections. *Journal fuer Ornithologie*, 152, 481–495.

Rising, J. D. (1969). A comparison of metabolism and evaporative water loss of Baltimore and Bullock orioles. *Comparative Biochemistry and Physiology*, 31(6), 915–925. https://doi.org/10.1016/0010-406x(69)91801-5

Rising, J. D. (1983). The Great Plains hybrid zones. In R. F. Johnston (Ed.), *Current ornithology* (vol. 1, pp. 131–157). Springer.

Rohwer, S. (2004). Using age ratios to infer survival and despotic breeding dispersal in hybridizing warblers. *Ecology*, 85(2), 423–431. https://doi.org/10.1890/02-0380

Rohwer, S., Butler, L. K., & Froehlich, D. R. (2005). Ecology and demography of east-west differences in molt scheduling in Neotropical migrant passerines. In R. Greenberg & P. P. Marra (Eds.), *Birds of two worlds* (pp. 87–105). Johns Hopkins University Press.

Rohwer, S., & Irwin, D. E. (2011). Molt, orientation, and avian speciation. *The Auk*, 128(2), 419–425. https://doi.org/10.1525/auk.2011.10176

Rohwer, S., & Manning, J. (1990). Differences in timing and number of molts for Baltimore and Bullock's Orioles: Implications to hybrid fitness and theories of delayed plumage maturation. *The Condor*, 92(1), 125–140. https://doi.org/10.2307/1368391

Ruegg, K. C., & Smith, T. B. (2002). Not as the crow flies: A historical explanation for circuitous migration in Swainson's thrush (*Catharus ustulatus*). *Proceedings of the Royal Society of London Series B: Biological Sciences*, 269, 1375–1381.

Schaefer, V. H. (1980). Geographic variation in the insulative qualities of nests of the Northern Oriole. *Wilson Bulletin*, 92, 466–474.

Scordato, E. S. C., Smith, C. C. R., Semenov, G. A., Lui, Y., Wilkins, M. R., Liang, W., Rubtsov, A., Sundev, G., Koyama, K., Turbek, S. P., Wunder, M. B., Stricker, C. A., & Safran, R. J. (2020). Migratory divides coincide with reproductive barriers across replicated avian hybrid zones above the Tibetan Plateau. *Ecology Letters*, 23, 231–241.

Short, L. L. Jr (1965). Hybridization in the flickers (*Colaptes*) of North America. *Bulletin of the American Museum of Natural History*, 129, 306–428.

Sibley, C. G., & Short, L. L., Jr. (1959). Hybridization in the buntings (*Passerina*) of the Great Plains. *The Auk*, 76(4), 443–463. https://doi.org/10.2307/4082312

Sibley, C. G., & Short, L. L. (1964). Hybridization in the Orioles of the Great Plains. *The Condor*, 66(2), 130–150. https://doi.org/10.2307/1365391

Sibley, C. G., & West, D. A. (1959). Hybridization in the rufous-sided towhees of the Great Plains. *The Auk*, 76(3), 326–338. https://doi.org/10.2307/4081810

Studds, C. E., Kyser, T. K., & Marra, P. P. (2008). Natal dispersal driven by environmental conditions interacting across the annual cycle of a migratory songbird. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 2929–2933.

Swenson, N. G. (2006). GIS-based niche models reveal unifying climatic mechanisms that maintain the location of avian hybrid zones in a North American suture zone. *Journal of Evolutionary Biology*, 19(3), 717–725. https://doi.org/10.1111/j.1420-9101.2005.01066.x

Toews, D. P. L, Lovette, I. J., Irwin, D. E., & Brelsford, A. (2018). Similar hybrid composition among different age and sex classes in the Myrtle-Audubon's warbler hybrid zone. *The Auk*, 135(4), 1133–1145. https://doi.org/10.1642/auk-18-45.1

van Bemmelen, R. S. A., Kolbeinsson, Y., Ramos, R., Gilg, O., Alves, J. A., Smith, M., Schekkerman, H., Lehikoinen, A., Petersen, I. K., Þórisson, B., Sokolov, A. A., Välimäki, K., van der Meer, T., Okill, J. D., Bolton, M., Moe, B., Hanssen, S. A., Bollache, L., Petersen, A., … Tulp, I. (2019). A migratory divide among red-necked phalaropes in the western Palearctic reveals contrasting migration and wintering movement strategies. *Frontiers in Ecology and Evolution*, 7, 86. https://doi.org/10.3389/fevo.2019.00086

West, D. A. (1962). Hybridization in the grosbeaks (*Pheucticus*) of the Great Plains. *The Auk*, 79, 399–424.

Wiley, C., Qvarnström, A., & Gustafsson, L. (2009). Effects of hybridization on the immunity of collared *Ficedula albicollis* and pied flycatchers *F. hypoleuca*, and their infection by haemosporidians. *Journal of Avian Biology*, 40, 352–357.

Wyatt, V. E., & Francis C. M. (2020). Rose-breasted grosbeak (*Pheucticus ludovicianus*), version 1.0. In A. F. Poole & F. B. Gill (Eds.), *Birds of the world*. Cornell Lab of Ornithology. https://doi.org/10.2173/bow.robgro.01