Molt, Orientation, and Avian Speciation

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MOLT, ORIENTATION, AND AVIAN SPECIATION

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A MAJOR GOAL of ornithology is to understand the processes that drive avian diversification (Price 2008). There is growing interest in and evidence for a potential role of seasonal migratory behavior in causing selection against hybrids and thereby promoting speciation (Helbig 1991; Bensch et al. 1999, 2009; Ruegg and Smith 2002; Bearhop et al. 2005; Irwin and Irwin 2005; Irwin 2009a, b; Rolshausen et al. 2009). Successful seasonal migration requires a finely tuned set of behavioral, morphological, and physiological traits; although learning has a role, many of these traits have been shown to have a genetic basis (Berthold and Querner 1981, Berthold 1996, Pulido 2007, Newton 2008). Thus, there is the potential for two closely related taxa to differ in their "migratory program" (Pulido 2007); hybrids between these groups might have a combination of genes that is suboptimal. Here, we focus on the potential importance of two aspects of the migratory program in avian speciation: (1) migratory orientation, which has received much focus as a potential driver of avian speciation; and (2) the timing of molt with respect to migration, which has previously received comparatively little attention. We provide the first comprehensive summary of patterns of divergence in these two traits in pairs of closely related North American taxa, with the goal of determining the possible importance of these two factors in causing selection against hybrids and thereby promoting speciation.

When populations isolated in allopatry meet in secondary contact, whether they merge depends on whether there is partial premating isolation or selection against hybrids (Coyne and Orr 2004, Price 2008). If there is no selection against hybrids, the strength of premating isolating factors (e.g., song differences) can gradually decrease, leading to fusion of the populations. Thus, selection against hybrids plays a critical role in the speciation process, by preventing fusion of differentiated forms and by favoring the evolution of stronger premating isolation. For most pairs of avian taxa in North America, the causes of selection against hybrids are unknown. Although there are a variety of possibilities (e.g., intrinsic genetic incompatibilities, mismatch between morphology of hybrids and environmental niche, inferior mating display of hybrids), there are few data with which to test these. Here, we review the potential importance of molt-scheduling divides and migratory-orientation divides (hereafter "orientation divides") as general sources of selection against hybrids and suggest tests that could further evaluate these hypotheses.

SPECIATION AND THE MIGRATORY PROGRAM

Most analyses of migration and speciation have focused on the role of migratory orientation in promoting speciation. Orientation divides occur when adjacent breeding populations take different routes to their wintering grounds; hybrids might take an intermediate and inferior route (Helbig 1991; Bensch et al. 1999, 2009; Ruegg and Smith 2002; Irwin and Irwin 2005; Ruegg 2007; Irwin 2009a). Such divides may facilitate speciation by causing selection against hybrids and potentially lead to selection that favors the strengthening of premating isolating mechanisms. Although fitness costs of migration in hybrids have not yet been measured in any particular case, reduced survival of hybrids due to intermediate migratory behavior seems highly plausible because many orientation divides take parental populations around alternate sides of major areas of inhospitable habitat, such as the Mediterranean Sea and the Sahara Desert (Helbig 1991, Bensch et al. 1999), the Tibetan Plateau (Irwin and Irwin 2005), and the deserts, mountains, and grasslands of the American West and Midwest. Orientation divides have now been described for adjacent pairs of taxa that breed in Europe and winter in Africa (Helbig 1991, Bensch et al. 1999, Helbig et al. 2001), that breed in northern Asia and winter in India or China (Irwin and Irwin 2005), and that breed in North America and winter farther south in the Americas (Ruegg and Smith 2002, Toews and Irwin 2008). In these cases, orientation divides appear to have formed partly as a result of postglacial range expansions, with seasonal migratory routes now retracing routes of northward expansion out of glacial refugia. These ancestral routes are stabilized by the present distribution of habitat, with favorable routes separated by ecological barriers.

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While migratory orientation may play an important role in many avian speciation events, there are other aspects of seasonal migration that may be equally important. One of these is the timing of molt. Each year after breeding, birds undergo a full or nearly full replacement of their plumage (the "prebasic molt"; Pyle 1997, Rohwer et al. 2005). Some species do this on the breeding grounds before migrating south, whereas others migrate south before molting. Others undergo parts of the molt in different places or have molt scheduling that differs between individuals (e.g., juvenile vs. adult). Molt divides occur when closely related populations or species pairs come into contact and differ either in the scheduling of molt and migration or in the number of molts they undergo each year (Rohwer et al. 2005). Hybrids could be selected against if they have a suboptimal combination of genes encoding for molt and migration timing. In White-crowned Sparrows (*Zonotrichia leucophrys*), the energetic cost of a complete molt is about equivalent to a complete turnover of body protein (Murphy and King 1991, Murphy and Taruscio 1995), whereas for large birds that fly while molting, the temporal costs of molt are high because feather growth rate increases with body size only half as fast as feather length increases with body size (Rohwer et al. 2009a). The selection against hybrids that we envision occurring across molt divides is likely due to excessive time and energy costs either of molting too many or too few times or of attempting to molt in regions where food supplies are insufficient for energetic demands.

In recent years, Rohwer and his students have demonstrated that >50% of Neotropical migrant passerine species that breed in western North America migrate to the region of the Mexican Monsoon immediately after breeding. There they spend two to three months exploiting the seasonal pulse of food generated by the monsoon to undergo their annual postbreeding molt before continuing on to their wintering areas. By contrast, more than 95% of Neotropical migrant passerines breeding in eastern North America molt on their breeding grounds before migrating to their Neotropical winter range (Rohwer et al. 2005, 2007, 2009b). When west–east species pairs with differences in their molt scheduling come into contact and interbreed, the fall molt of hybrids may be scheduled suboptimally. Like the eastern species, hybrids might molt on the breeding grounds before migrating, even though late summer droughts that characterize much of western North America apparently have favored moving to the monsoon region of northwestern Mexico for the annual molt. Alternatively, like the western species, hybrids might migrate before molting but go all the way to the winter range, where resources may be insufficient for molting. Either of these hypothetical F_1 hybrids could have lower fitness than parentals, resulting in selection against hybrids. Even more costly recombinations, achieved in F_1 hybrids or through hybrid × hybrid matings, might produce hybrids that molt twice in the same fall, once before migrating and a second time after migrating (as has apparently been documented for a hybrid Bullock's × Baltimore Oriole; Rohwer and Manning 1990; for scientific names, see Tables 1 and 2), or hybrids that do not molt in either place.

The number of molts in the annual cycle could have similar effects on hybrids. Some eastern passerines have both spring and fall molts, whereas some western passerines have only a single (postbreeding) molt in the annual cycle, presumably because conditions in their wintering range on the west side of Central America are too dry in spring to support an additional molt. Thus, differences in the presence or absence of a spring molt is another contrast between some western and eastern species pairs that could disfavor hybrids. For example, Indigo Buntings, Baltimore Orioles, and Rose-breasted Grosbeaks are eastern species with two episodes of molting per year in adults or in first-year birds, whereas their western counterparts, Lazuli Buntings, Bullock's Orioles, and Black-headed Grosbeaks, molt just once a year, or have very limited spring molts (Rohwer 1986, Rohwer and Manning 1990, Young 1991, Pyle 1997, D. R. Froehlich unpubl. data). Hybrids between these species pairs might undertake an inappropriate number of molts for their wintering area, reducing their fitness to below that of parentals.

Molt and Orientation Divides in North America

To assess the potential importance of molt and orientation divides as sources of selection against hybrids, we reviewed the literature on closely related western and eastern North American passerine and near-passerine long-distance migrants, summarizing what is known about migratory direction and molt scheduling. To confine our study to those pairs that had most clearly been separated into western and eastern groups for long periods, we included only species pairs in which one taxon was distributed (in the breeding season) primarily west of the Rocky Mountains and another taxon primarily east of the Rocky Mountains (except for western and eastern Painted Buntings, with two isolated populations east and south of the Rocky Mountains). All migrate far enough south that at least a substantial number of individuals winter south of the U.S. border. Molt divides were assessed from Rohwer et al. (2005), Pyle (1997), and Butler et al. (2006). Orientation divides have been little studied in North America but seem reasonable to infer on the basis of known breeding and wintering ranges, migratory routes, and contacts between western and eastern breeding populations, as inferred for Swainson's Thrushes by Ruegg and Smith (2002).

We divided these cases into two tables to highlight those cases that have well-studied contact zones (Table 1) and to provide a list (Table 2) of other cases that might be investigated further. Several points need to be made about these data. First, these tables are intended only to establish the plausibility of differences in molt and orientation as sources of selection against hybrids; a full test of that relationship will have to await future work. Second, our comparison of west–east pairs need not be restricted to sister taxa, because hybrid zones often develop between closely related taxa that are not sisters; investigating causes of reproductive isolation between them is not contingent upon their being sisters. Thus, the *Icterus* and *Passerina* pairs in Table 1 and the *Myiarchus* and *Piranga* pairs in Table 2 are closely related, but not sister taxa (Omland et al. 1999, Klicka et al. 2001, Joseph et al. 2004, Shepherd and Burns 2007). Third, a number of the pairs in Table 2 may be less well studied precisely because they are not known to form hybrid zones. Thus, Table 2 places the data in Table 1 in a larger context by identifying a set of west–east pairs for which molt and orientation divides may be less likely as current sources of selection against hybrids, either because the pairs have little or no contact (e.g., hummingbirds, buntings, Nashville Warblers) or because they are not as closely related as other pairs (e.g., tanagers).

Among the 12 taxon pairs that have well-studied contact zones (Table 1), a striking pattern emerges: all have either orientation

TABLE 1. Well-studied west–east contact zones between closely related pairs of North American long-distance migrants. All of these cases involve molt or orientation divides, which may cause strong selection against hybrids.

Species pair	Hybrid zone?	Molt scheduling divide?	Molt number divide?	Orientation divide?	References
Red-breasted–Yellow-bellied sapsucker (*Sphyrapicus ruber–S. varius*)[a]	Yes, narrow	In first year	No	Strong	Cicero and Johnson 1995, Pyle 1997, Seneviratne and Irwin unpubl. data
Red-naped–Yellow-bellied sapsucker (*S. nuchalis–S. varius*)[a]	Yes, narrow	In first year	No	Moderate	Cicero and Johnson 1995, Pyle 1997
Western–Eastern Warbling Vireo (*Vireo gilvus*)	Hybrids rare	Yes	No	Weak	Johnson et al. 1988, Voelker and Rohwer 1998
Pacific–Winter wren (*Troglodytes pacificus–T. troglodytes*)	Hybrids rare	No	No	Likely strong	Toews and Irwin 2008
Western–Eastern Marsh Wren (*Cistothorus palustris*)	Narrow contact, hybrids unknown	No	Apparently (more study needed)	Likely moderate	Kroodsma 1989, 2005
Swainson's Thrush (*Catharus ustulatus*)	Yes, narrow	No	No	Strong	Ruegg and Smith 2002, Ruegg 2007
Audubon's–Myrtle warbler (*Dendroica [coronata] auduboni–D. coronata*; both members of Yellow-rumped Warbler)	Yes, narrow	No	No	Moderate	Hubbard 1969, Brelsford and Irwin 2009
MacGillivray's–Mourning warbler (*Oporornis tolmiei–O. philadelphia*)	Yes, narrow	No	No	Strong	Irwin et al. 2009
Townsend's–Black-throated Green warbler (*Dendroica townsendi–D. virens*)	Yes, narrow	No	No	Strong	D. P. L. Toews and D. E. Irwin unpubl. data
Black-headed–Rose-breasted grosbeak (*Pheucticus mel anocephalus–P. ludovicianus*)	Hybrids rare	Yes	No	Weak	Pyle 1997, Rohwer et al. 2005, Mettler and Spellman 2009
Lazuli–Indigo bunting (*Pas serina amoena–P. cyanea*)	Hybrids rare	Yes	Yes	Weak	Emlen et al. 1975, Rohwer 1986, Young 1991
Bullock's–Baltimore oriole (*Icterus bullockii–I. galbula*)	Yes, narrow	Yes	Degree only	Weak	Rising 1970, Rohwer and Manning 1990

[a]There is also a narrow hybrid zone between Red-breasted and Red-naped Sapsuckers (*S. rubber–S. nuchalis*), not included in the table because they are both west of the Rockies (for details, see Johnson and Johnson 1985, Cicero and Johnson 1995).

divides (8 cases) or molt scheduling divides (at least 6 cases). Interestingly, specific cases tend to have either migratory or molt divides, but rarely both (2–3 cases). In all of these cases, there is evidence of substantial reproductive isolation between western and eastern taxa, as indicated by either a lack of hybrids or the presence of a narrow hybrid zone. A sufficiently narrow hybrid zone can be taken as evidence of selection against hybrids or some other form of selection maintaining the discreteness of the taxa (Barton and Hewitt 1989). In the case of the Audubon's and Myrtle warblers, there is little if any assortative mating yet substantial selection against hybrids (Brelsford and Irwin 2009). Among 14 additional taxon pairs with less well-studied contact zones (in which reproductive isolation has not been adequately assessed; Table 2), there are two cases of moderate or strong orientation divides and three cases of molt scheduling divides.

These patterns suggest that orientation divides and molt scheduling divides could be important in generating selection against hybrids between many west–east species pairs in North America and that molt and orientation have roughly equal potential as possible sources of selection against hybrids. Which sort of divide applies to a species pair has a strong geographic component. The late summer drought that drives the evolution of molt migrations to the American southwest mainly affects migrants with more southern distributions in the western United States (Table 1; Rohwer et al. 2005), whereas most of the inferred orientation divides apply to populations that have recently expanded northward out of western and eastern refugia following the retreat of continental glaciers. Populations derived from eastern refugia have developed broad west–east distributions; they have done so first by moving north out of their southern refugia, and then by expanding west across the boreal forests of North America, meeting a western group that occurs well north of the more southern region of the inland west that becomes so dry in late summer.

Table 2. Other, less-studied west–east pairs of closely related North American long-distance migrants that come into close or actual contact. For some of these, molt and orientation divides may play a role in generating selection against hybrids.

Species pair	Range contact?	Molt scheduling divide?	Molt number divide?	Orientation divide?	References
Chimney–Vaux's swift (*Chaetura pelagica–C. vauxi*)	Allopatric	No	No	Weak	Pyle 1997
Black-chinned–Ruby-throated hummingbird (*Archilochus alexandri–A. colubris*)	Parapatric	No	No	Moderate	Pyle 1997
Western–Eastern wood-peewee (*Contopus virens–C. sordidulus*)	Some sympatry	No	No	Weak	Pyle 1997
Ash-throated–Great Crested flycatcher (*Myiarchus cinerascens–M. crinitus*)	Some sympatry	Yes	No	Weak	Pyle 1997, Butler et al. 2006
Cassin's–Blue-headed vireo (*Vireo cassinii–V. solitarius*)	Parapatric	No	No	Weak	Pyle 1997, Rohwer et al. 2008
Plumbeous–Blue-headed vireo (*V. plumbeus–V. solitarius*)	Allopatric	No	No	Weak	Pyle 1997
Western–Eastern Orange-crowned Warbler (*Vermivora celata*)	Parapatric	No	No	Weak	Pyle 1997
Western–Eastern Nashville Warbler (*V. ruficapilla*)	Allopatric	No	No	Weak	Pyle 1997
Western–Eastern Wilson's Warbler (*Wilsonia pusilla*)	Allopatric	No	No	Weak	Pyle 1997
Western–Eastern Yellow-breasted Chat (*Icteria virens*)	Parapatric	No	No	Weak	Pyle 1997
Western–Scarlet tanager (*Piranga ludoviciana–P. olivacea*)	Allopatric	Yes	Yes	Weak	Pyle 1997
Western–Eastern Painted Bunting (*Passerina ciris*)	Parapatric	Yes	No	Strong	Thompson 1991
Hooded–Orchard oriole (*Icterus cucullatus–I. spurius*)	Some sympatry	Unknown	No	Weak	Pyle 1997

Unlike gradual clinal adaptation to environmental gradients, which is often suggested as a source of selection against hybrids (e.g., Rising 1969, Schaefer 1980, Moore and Price 1993), both molt divides and orientation divides are derived from discrete, intrinsic differences between closely related species or populations. At least in the case of molt divides, there apparently is no clinal variation across the ranges of western and eastern populations, despite the differences between them (Rohwer and Manning 1990, Rohwer and Johnson 1992). When the ranges of populations with such fixed and dramatic differences in migration and life-history scheduling come into contact, the sharp differences in the fitness landscapes for parentals should tend to place hybrids in the fitness trough between alternative parental fitness peaks (see Irwin and Irwin 2005, Irwin 2009b). The consequence should be selection against hybrids that, in contrast to gradual clinal variation across environmental gradients, could easily be strong enough to favor the reinforcement of premating isolating mechanisms. The widths of the oriole, grosbeak, bunting, and Yellow-rumped Warbler hybrid zones have not increased over decades (Hubbard 1969; Rising 1973, 1983; Emlen et al. 1975; Baker and Johnson 1998; Brelsford and Irwin 2009; Mettler and Spellman 2009), which strongly suggests that selection against hybrids is ongoing and strong. Furthermore, some studies of the oriole zone suggest that hybrids may be less common in this zone than they were when it was first sampled, possibly indicating the development of premating isolating

mechanisms (Corbin and Sibley 1977). We suggest that the molt divide within the orioles, grosbeaks, and buntings is likely responsible for generating this strong selection against hybrids. Likewise, the orientation divide between Audubon's and Myrtle warblers may generate the 18% selection against hybrids that was estimated from an analysis of linkage disequilibrium in molecular markers (Brelsford and Irwin 2009).

A Call for Research

It is important to emphasize that these comparative data test neither molt divides nor orientation divides as sources of selection against hybrids, but only evaluate their plausibility and domain (molt divides tend to be southern and orientation divides tend to be northern). The data in Tables 1 and 2 suggest that the two hypotheses have about equal relevance as potential sources of selection against hybrids in North America, and they point to species pairs appropriate for field or experimental tests. We note that many other factors (e.g., intrinsic genetic incompatibilities, differences in communication systems, different adaptations to habitat) might contribute to reproductive isolation in these cases.

European studies of orientation divides suggest ways to approach testing the importance of these factors as drivers of speciation in North American birds. The orientation divides within European populations of Blackcaps (*Sylvia atricapilla*) and Willow

Warblers (*Phylloscopus trochilus*) have been studied in detail. For these species, we know that adjacent populations take a western route around the Mediterranean Sea and the Sahara Desert and an eastern route around these same barriers (Helbig 1991, Bensch et al. 1999). The contact zones between the forms are narrow, which suggests selection against hybrids (Helbig 1991; Bensch et al. 1999, 2009; Irwin 2009a, b). Further, for the Blackcap, we know that the direction of orientation is under genetic control, because the migratory orientation of F_1 hybrids is intermediate to that of their parents (Berthold and Querner 1981, Helbig 1991, Berthold and Helbig 1992). All that is missing from these systems is a direct demonstration that hybrids have lower survival during migration than parentals (Irwin 2009b). A challenge with these two systems is that hybrids cannot easily be recognized in the field because the parental forms are of similar appearance. Thus, the possibility that hybrids have lower survival than parentals across either migratory or molt divides may better be studied using age ratios in species pairs in which (1) hybrids and parentals differ enough in appearance that they can easily be recognized; and (2) first-year, second-year, and after-second-year birds can be distinguished (Ricklefs 1997, Rohwer 2004).

The excellent breeding studies of orientation divides (e.g., Helbig 1991) offer models for the sort of tests that should be done to establish whether molt divides generate important sources of selection against hybrids. We need to know whether the scheduling of molt in the annual cycle is under genetic or environmental control. Captive breeding studies of two Old World species have provided evidence that both the number of molts and the duration of a molt are under genetic control (Guinner and Neusser 1985, Berthold et al. 1994). Presumably the scheduling of molt and migration in North American species pairs is also under genetic control, because some of the species pairs characterized by molt divides meet and hybridize, either sporadically (Lazuli and Indigo buntings: Sibley and Short 1959, Emlen et al. 1975, Kroodsma 1975) or in narrow west–east zones in the Great Plains (Bullock's and Baltimore orioles: Rising 1970; Black-headed and Rose-breasted grosbeaks: West 1962, Mettler and Spellman 2009), and their differences in molt scheduling appear to persist in this common environment (Rohwer and Johnson 1992). The relative rarity of hybrids in these contacts and the narrowness of the zones between the grosbeaks and between the orioles suggest strong selection against hybrids. Furthermore, hybrids are rare or not known in other closely related pairs that feature molt divides, such as western and eastern Warbling Vireos (Murray et al. 1994, Voelker and Rohwer 1998) or the allopatric populatons of western and eastern Painted Buntings (Thompson 1991), both of which might be possible to hybridize in captivity. Establishing the genetic control of the scheduling of molt in these species will require captive breeding followed by demonstration that migratory restlessness precedes the molt in western molt migrants and follows the molt in their eastern counterparts. It is less clear what to expect of hybrids. Will they show an intermediate period of migratory restlessness followed by a molt that takes place before they would have arrived in the monsoon region? Or will they overlap molt and migratory restlessness? Phenotypic plasticity and the endocrine controls of molt and migration (Dawson 2008, Lessels 2008) suggest that neither may be plausible, but further progress in this field simply requires descriptions of the results of breeding experiments. Further, issues like molting twice, once before and once after the fall migratory restlessness, as found in an oriole that appeared to be a hybrid (Rohwer and Manning 1990), or perhaps not molting at all, might be observed in F_1 hybrids or recombinants produced by breeding F_1 hybrids with each other.

Evolution of Molt and Orientation Divides

If molt and orientation divides generate selection against hybrids, an intriguing question arises: how did western and eastern pairs of taxa evolve these differences, given that there is now selection against intermediates? Did either taxon actually have to evolve across a fitness valley? We suggest not, at least for recently differentiated species pairs, as long as they had southern ranges when divergence in molt scheduling or orientation began. For this reason, we think that molt scheduling and orientation divides were most likely to have arisen when the pair of species in question, regardless of whether they are sisters, diverged in these characteristics during Pliocene and Pleistocene glacial cycles, which generated southern ranges that periodically retreated northward (Weir and Schluter 2004). The critical component of our model is that, as breeding ranges move northward, the two taxa evolve differences in migratory orientation or the scheduling of molt and migration.

On secondary contact these key differences could cause selection against hybrids that have a mixture of genes for the two optimal migratory programs. Such parallel south-to-north expansion and divergence in various traits has been documented in Greenish Warblers (*P. trochiloides*) of Asia (Irwin and Irwin 2005, Irwin et al. 2005) and Willow Warblers of northern Europe (Bensch et al. 2009, Irwin 2009a); in these cases, the pattern of divergence could be reconstructed because the taxa are still connected by a chain of intermediate forms to the south. It is likely that migratory divergence during northward expansions is a very common phenomenon and may commonly contribute to speciation. This may help explain why speciation rates in birds appear to be higher at more northern latitudes than at more tropical latitudes (Weir and Schluter 2007).

For east–west species pairs that differentiated before the Pleistocene (Klicka and Zink 1997, Johnson and Cicero 2004, Weir and Schluter 2004, Lovette 2005), traits and ranges of ancestral species are more difficult to reconstruct, because of the greater span of time involved and the uncertainty about climate reconstructions during that time (Lunt et al. 2008). However, climate was variable to some degree throughout the Pliocene (Lunt et al. 2008), and the basic scenario outlined above, of an ancestral species with short or no migration becoming geographically separated and evolving into two northern forms with different migratory behavior, could still apply. Other scenarios are also possible. For example, an eastern migratory species that expanded west across the boreal forests of North America might eventually have moved south into the forests of the Rocky Mountains or the coastal ranges and ceased to migrate. If it became a migrant again during later glacial cycles, its orientation or molt scheduling might differ from that of its eastern relative. Alternatively, a southern resident related to an eastern migrant might move northward and begin to migrate. The key concept is that divergence in migratory orientation or the scheduling of molt and migration can occur without crossing a fitness valley when breeding ranges are moving northward; glacial cycles make the northward movement of ranges easy to envision, but ranges could move north for many reasons.

Literature Cited

Baker, M. C., and M. S. Johnson. 1998. Allozymic and morphometric comparisons among Indigo and Lazuli buntings and their hybrids. Auk 115:537–542.

Barton, N. H., and G. M. Hewitt. 1989. Adaptation, speciation and hybrid zones. Nature 341:497–503.

Bearhop, S., W. Fiedler, R. W. Furness, S. C. Votier, S. Waldron, J. Newton, G. J. Bowen, P. Berthold, and K. Farnsworth. 2005. Assortative mating as a mechanism for rapid evolution of a migratory divide. Science 310:502–504.

Bensch, S., T. Andersson, and S. Åkesson. 1999. Morphological and molecular variation across a migratory divide in Willow Warblers, *Phylloscopus trochilus*. Evolution 53:1925–1935.

Bensch, S., M. Grahn, N. Müller, L. Gay, and S. Åkesson. 2009. Genetic, morphological, and feather isotope variation of migratory Willow Warblers show gradual divergence in a ring. Molecular Ecology 18:3087–3096.

Berthold, P. 1996. Control of Bird Migration. Chapman & Hall, London.

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

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

Berthold, P., and U. Querner. 1981. Genetic basis of migratory behavior in European warblers. Science 212:77–79.

Brelsford, A., and D. E. Irwin. 2009. Incipient speciation despite little assortative mating: the Yellow-rumped Warbler hybrid zone. Evolution 63:3050–3060.

Butler, L. K., S. Rohwer, and M. Rogers. 2006. Prebasic molt and molt-related movements in Ash-throated Flycatchers. Condor 108:647–660.

Cicero, C., and N. K. Johnson. 1995. Speciation in sapsuckers (*Sphyrapicus*): III. Mitochondrial-DNA sequence divergence at the cytochrome-*b* locus. Auk 112:547–563.

Corbin, K. W., and C. G. Sibley. 1977. Rapid evolution in orioles of the genus *Icterus*. Condor 79:335–342.

Coyne, J. A., and H. A. Orr. 2004. Speciation. Sinauer Associates, Sunderland, Massachusetts.

Dawson, A. 2008. Control of the annual cycle in birds: Endocrine constraints and plasticity in response to ecological variability. Philosophical Transactions of the Royal Society of London, Series B 363:1621–1633.

Emlen, S. T., J. D. Rising, and W. L. Thompson. 1975. A behavioral and morphological study of sympatry in the Indigo and Lazuli buntings of the Great Plains. Wilson Bulletin 87:145–179.

Guinner, E., and V. Neusser. 1985. Die Jugendmauser europäischer und afrikanischer Schwarzkehlchen (*Saxicola torquata tubicula* und *axillaris)* sowie yon F$_1$-Hybriden. Journal für Ornithologie 126:219–220.

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.

Helbig, A. J., M. Salomon, S. Bensch, and I. Seibold. 2001. Male-biased gene flow across an avian hybrid zone: Evidence from mitochondrial and microsatellite DNA. Journal of Evolutionary Biology 14:277–287.

Hubbard, J. P. 1969. The relationships and evolution of the *Dendroica coronata* complex. Auk 86:393–432.

Irwin, D. E. 2009a. Incipient ring speciation revealed by a migratory divide. Molecular Ecology 18:2923–2925.

Irwin, D. E. 2009b. Speciation: New migratory direction provides route toward divergence. Current Biology 19:R1111–R1113.

Irwin, D. E., S. Bensch, J. H. Irwin, and T. D. Price. 2005. Speciation by distance in a ring species. Science 307:414–416.

Irwin, D. E., A. Brelsford, D. P. L. Toews, C. MacDonald, and M. Phinney. 2009. Extensive hybridization in a contact zone between MacGillivray's and Mourning warblers (*Oporornis tolmiei* and *O. philadelphia*) detected using molecular and morphometric analyses. Journal of Avian Biology 40:539–552.

Irwin, D. E., and J. H. Irwin. 2005. Siberian migratory divides: The role of seasonal migration in speciation. Pages 27–40 *in* Birds of Two Worlds: The Ecology and Evolution of Migration (R. Greenberg and P. P. Marra, Eds.). Johns Hopkins University Press, Baltimore, Maryland.

Johnson, N. K., and C. Cicero. 2004. New mitochondrial DNA data affirm the importance of Pleistocene speciation in North American birds. Evolution 58:1122–1130.

Johnson, N. K., and C. B. Johnson. 1985. Speciation in sapsuckers (*Sphyrapicus*): II. Sympatry, hybridization, and mate preference in *S. ruber daggetti* and *S. nuchalis*. Auk 102:1–15.

Johnson, N. K., R. M. Zink, and J. A. Marten. 1988. Genetic evidence for relationships in the avian family Vireonidae. Condor 90:428–445.

Joseph, L., T. Wilke, E. Bermingham, D. Alpers, and R. Ricklefs. 2004. Toward a phylogenetic framework for the evolution of shakes, rattles, and rolls in *Myiarchus* tyrant-flycatchers (Aves: Passeriformes: Tyrannidae). Molecular Phylogenetics and Evolution 31:139–152.

Klicka, J., A. J. Fry, R. M. Zink, and C. W. Thompson. 2001. A cytochrome-*b* perspective on *Passerina* bunting relationships. Auk 118:611–623.

Klicka, J., and R. M. Zink. 1997. The importance of recent ice ages in speciation: A failed paradigm. Science 277:1666–1669.

Kroodsma, D. E. 1989. Two North American song populations of the Marsh Wren reach distributional limits in the central Great Plains. Condor 91:332–340.

Kroodsma, D. [E.] 2005. The Singing Life of Birds. Houghton Mifflin, New York.

Kroodsma, R. L. 1975. Hybridization in buntings (*Passerina*) in North Dakota and eastern Montana. Auk 92:66–80.

Lessells, C. M. 2008. Neuroendocrine control of life histories: What do we need to know to understand the evolution of phenotypic plasticity? Philosophical Transactions of the Royal Society of London, Series B 363:1589–1598.

Lovette, I. J. 2005. Glacial cycles and the tempo of avian speciation. Trends in Ecology & Evolution 20:57–59.

Lunt, D. J., G. L. Foster, and A. M. Haywood. 2008. Late Pliocene Greenland glaciation controlled by a decline in atmospheric CO_2 levels. Nature 454:1102–1105.

Mettler, R. D., and G. M. Spellman. 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 18:3256–3267.

Moore, W. S., and J. T. Price. 1993. Nature of selection in the Northern Flicker hybrid zone and its implications for speciation theory. Pages 196–225 *in* Hybrid Zones and the Evolutionary Process (R. G. Harrison, Ed.). Oxford University Press, New York.

Murphy, M. E., and J. R. King. 1991. Nutritional aspects of avian molt. Pages 2168–2193 *in* Acta XX Congressus Internationalis Ornithologici (B. D. Bell, Ed.). Congress Trust Board, Wellington, New Zealand.

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

Murray, B. W., W. B. McGillivray, J. C. Barlow, R. N. Beech, and C. Strobeck. 1994. The use of cytochrome *b* sequence variation in estimation of phylogeny in the Vireonidae. Condor 96:1037–1054.

Newton, I. 2008. The Migration Ecology of Birds. Elsevier, London.

Omland, K. E., S. M. Lanyon, and S. J. Fritz. 1999. A molecular phylogeny of the New World orioles (*Icterus*): The importance of dense taxon sampling. Molecular Phylogenetics and Systematics 12:224–239.

Price, T. 2008. Speciation in Birds. Roberts, Greenwood Village, Colorado.

Pulido, F. 2007. The genetics and evolution of avian migration. BioScience 57:165–174.

Pyle, P. 1997. Identification Guide to North American Birds, Part 1: Columbidae to Ploceidae. Slate Creek Press, Bolinas, California.

Ricklefs, R. E. 1997. Comparative demography of New World populations of thrushes (*Turdus* spp.). Ecological Monographs 67:23–43.

Rising, J. D. 1969. A comparison of metabolism and evaporative water loss of Baltimore and Bullock orioles. Comparative Biochemistry and Physiology 31:915–925.

Rising, J. D. 1970. Morphological variation and evolution in some North American orioles. Systematic Zoology 19:315–351.

Rising, J. D. 1973. Morphological variation and status of the orioles *Icterus galbula*, *I. bullockii*, and *I abeillei*, in the northern Great Plains and in Durango, Mexico. Canadian Journal of Zoology 51:1267–1273.

Rising, J. D. 1983. The progress of oriole hybridization in Kansas. Auk 100:885–897.

Rohwer, S. 1986. A previously unknown plumage of first-year Indigo Buntings and theories of delayed plumage maturation. Auk 103:281–292.

Rohwer, S. 2004. Using age ratios to infer survival and despotic breeding dispersal in hybridizing warblers. Ecology 85:423–431.

Rohwer, S., L. K. Butler, and D. R. Froehlich. 2005. Ecology and demography of east–west differences in molt scheduling of Neotropical migrant passerines. Pages 87–105 *in* Birds of Two Worlds: The Ecology and Evolution of Migration (R. Greenberg and P. P. Marra, Eds.). Johns Hopkins University Press, Baltimore, Maryland.

Rohwer, S., and M. S. Johnson. 1992. Scheduling differences of molt and migration for Baltimore and Bullock's orioles persist in a common environment. Condor 94:992–994.

Rohwer, S., and J. Manning. 1990. Differences in timing and number of molts for Baltimore and Bullock's orioles: Implications to hybrid fitness and theories of delayed plumage maturation. Condor 92:125–140.

Rohwer, S., A. G. Navarro, and G. Voelker. 2007. Rates versus counts: Fall molts of Lucy's Warblers (*Vermivora luciae*). Auk 124:806–814.

Rohwer, S., R. E. Ricklefs, V. G. Rohwer, and M. M. Copple. 2009a. Allometry of the duration of flight feather molt in birds. PLoS Biol 7: e1000132.

Rohwer, V. G., S. Rohwer, and J. H. Barry. 2008. Molt scheduling of western Neotropical migrants and up-slope movement of Cassin's Vireo. Condor 110:365–370.

Rohwer, V. G., S. Rohwer, and M. F. Ortiz-Ramirez. 2009b. Molt biology of resident and migrant birds of the monsoon region of west Mexico. Ornithologia Neotropical 20:565–584.

Rolshausen, G., G. Segelbacher, K. A. Hobson, and H. M. Schaefer. 2009. Contemporary evolution of reproductive isolation and phenotypic divergence in sympatry along a migratory divide. Current Biology 19:2097–2101.

Ruegg, K. 2007. Genetic, morphological, and ecological characterization of a hybrid zone that spans a migratory divide. Evolution 62:452–466.

Ruegg, K. C., and T. B. Smith. 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 269:1375–1381.

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

Shepherd, T. M., and K. J. Burns. 2007. Intraspecific genetic analysis of the Summer Tanager *Piranga rubra*: Implications for species limits and conservation. Journal of Avian Biology 38:13–27.

Sibley, C. G., and L. L. Short, Jr. 1959. Hybridization in the buntings (*Passerina*) of the Great Plains. Auk 76:443–463.

Thompson, C. W. 1991. The sequence of molts and plumages in Painted Buntings and implications for theories of delayed plumage maturation. Condor 93:209–235.

Toews, D. P. L., and D. E. Irwin. 2008. Cryptic speciation in a Holarctic passerine revealed by genetic and bioacoustic analyses. Molecular Ecology 17:2691–2705.

Voelker, G., and S. Rohwer. 1998. Contrasts in scheduling of molt and migration in Eastern and Western warbling vireos. Auk 115:142–155.

Weir, J. T., and D. Schluter. 2004. Ice sheets promote speciation in boreal birds. Proceedings of the Royal Society of London, Series B 271:1881–1887.

Weir, J. T., and D. Schluter. 2007. The latitudinal gradient in recent speciation and extinction rates of birds and mammals. Science 315:1574–1576.

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

Young, B. E. 1991. Annual molts and interruption of the fall migration for molting in Lazuli Buntings. Condor 93:236–250.