# Divergence Between Subspecies Groups of Swainson's Thrush (Catharus ustulatus ustulatus and C. u. swainsoni)

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## CHAPTER 6

# DIVERGENCE BETWEEN SUBSPECIES GROUPS OF SWAINSON'S THRUSH (*CATHARUS USTULATUS USTULATUS* AND *C. U. SWAINSONI*)

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Abstract.—Swainson's Thrush (*Catharus ustulatus*) is a long-distance Nearctic–Neotropical migrant that includes two major subspecies groups: the russet-backed group (*C. u. ustulatus*) of the Pacific Coast and the olive-backed inland group (*C. u. swainsoni*) (American Ornithologists' Union [AOU] 1998, Evans Mack and Yong 2000). The two groups are most easily distinguished by differences in plumage characteristics, breeding and wintering location, and some vocalizations (Evans Mack and Yong 2000). Historical controversy over the taxonomic treatment of the *ustulatus* and *swainsoni* groups suggests that they have previously been considered on the border between subspecies and recently diverged sister species (reviewed in Bond 1963). Several authors emphasize the differences between the groups in breeding habitat and the lack of intergradation in regions where they co-occur (Bent 1949, Phillips 1991). Other authors emphasize their similarities, citing extensive intergradation along the eastern slope of the Sierra Nevada (Grinnell and Miller 1944). In the past decade, a number of studies have brought further clarity to the extent of genetic, behavioral, ecological, and acoustic divergence between the *ustulatus* and *swainsoni* subspecies groups. Here, I review these recent advances in our knowledge, identify future research questions, and discuss potential implications of divergence on the taxonomic treatment of the two groups according to the AOU's guidelines for naming species (AOU 1998, Johnson et al. 1999). *Received 25 July 2006, accepted 9 February 2007.*

Resumen.—*Catharus ustulatus* es un migrador de larga distancia, Neártico–Neotropical. Incluye dos grupos importantes de subespecies: en la costa del Pacífico, el grupo de "espalda café-rojizo", *C. u. ustulatus,* y, en el interior, el grupo de "espalda olivácea", *C. u. swainsoni* (American Ornithologists' Union 1998, Evans Mack and Yong 2000). Ambos grupos se diferencian fácilmente por las características del plumaje, sitios de reproducción y área de invernada, además de vocalizaciones (Evans Mack and Yong 2000). La controversia sobre el tratamiento taxonómico de los grupos *ustulatus* y *swainsoni,* sugiere que han sido previamente considerados en el límite entre subespecies y especies hermanas que recientemente divergieron (revisado en Bond 1963). Varios autores enfatizan las diferencias entre los grupos en áreas de reproducción y la falta de intergradación en las regiones en que coexisten (Bent 1949, Phillips 1991). Otros autores subrayan sus similitudes, aludiendo además a una extensiva intergradación en la vertiente este de la Sierra Nevada (Grinnell and Miller 1944). En la década pasada, varios estudios clarificaron los niveles de divergencia genética, de comportamiento, acústicas y ecológica entre los grupos de subespecie *ustulatus* y *swainsoni.* En este estudio, reviso los trabajos anteriores, identifico futuras preguntas de investigación, y discuto las implicaciones taxonómicas para ambos grupos de acuerdo con las reglas establecidas por la Unión de Ornitólogos Americanos (American Ornithologists' Union 1998, Johnson et al. 1999).

## Evolutionary History

Recent genetic data have helped shed light on the evolutionary history within the genus *Catharus* as well as on intraspecific variation within the Swainson's Thrush (*C. ustulatus*). Two independently derived molecular phylogenies of the genus *Catharus* using different loci suggest that the Swainson's Thrush is the oldest lineage in the genus and is sister to all other species of *Catharus*, including several resident and short-distance migratory species from the Neotropics (Outlaw et al. 2003, Winker and

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Pruett 2006). The five morphologically similar long-distance migratory species within the genus *Catharus* do not form a monophyletic clade, which indicates that migratory behavior has evolved multiple times within the genus and that the morphology of the North American long-distance migratory species exhibits strong evolutionary convergence (Winker and Pruett 2006). Outlaw et al. (2003) suggested that the Swainson's Thrush diverged from other *Catharus* species ~4 mya, and the combined data sets indicate that species of *Catharus* most likely diverged somewhere in the Neotropics.

An analysis of population structure within the Swainson's Thrush (Ruegg and Smith 2002) using a rapidly evolving region of the mitochondrial genome, the control region, focused on genetic differentiation between the two major subspecies groups (Fig. 1): the russet-backed group of the Pacific Coast (*C. u. ustulatus*) and the olive-backed inland group (*C. u. swainsoni*) (American Ornithologists' Union [AOU] 1998, Evans Mack and Yong 2000). These data showed that divergence between the subspecies groups is lower than reported levels of divergence between many sister species, but similar to estimates of divergence between well-differentiated subspecies of birds. Individuals of *ustulatus* and *swainsoni* from across the breeding range are separated by five diagnostic mutations with a net sequence divergence of 0.7% (Fig. 2; Ruegg and Smith 2002). By comparison, Johnson and Cicero (2004) found that estimates of mitochondrial DNA (mtDNA) sequence divergence in 39 pairs of avian sister species ranged from 0.0% to 8.2%, with an average divergence of 1.9%. Alternatively, control-region divergence between some well-differentiated subspecies ranges from 0.07% to 4.8%: 0.07% between Brewer's Sparrow (*Spizella breweri breweri*) and Timberline Sparrow (*S. b. taverneri*) subspecies

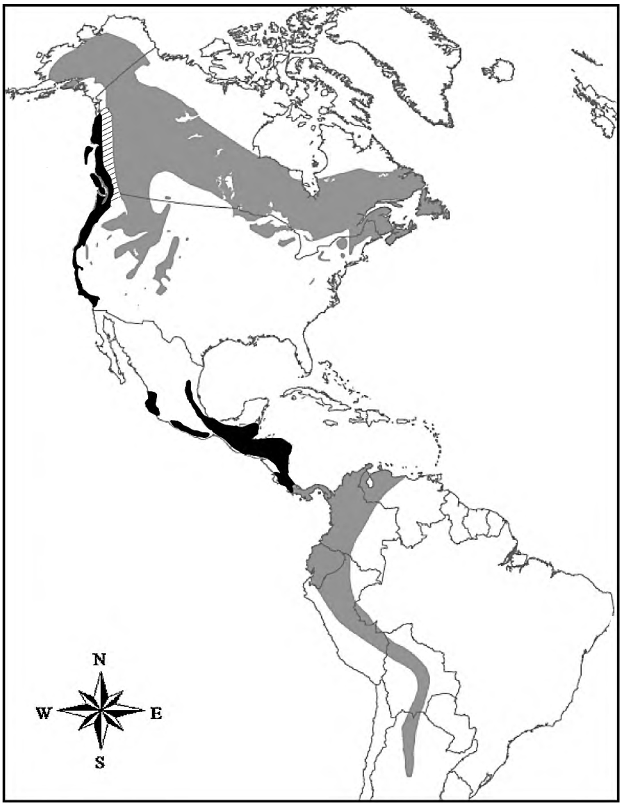

FIG. 1. Breeding and wintering ranges of coastal *ustulatus* (black) and inland *swainsoni* (gray) subspecies groups and potential contact zones (black and white stripes) in Swainson's Thrush (based on a range map from the Cornell Laboratory of Ornithology, with range data by Nature-Serve).

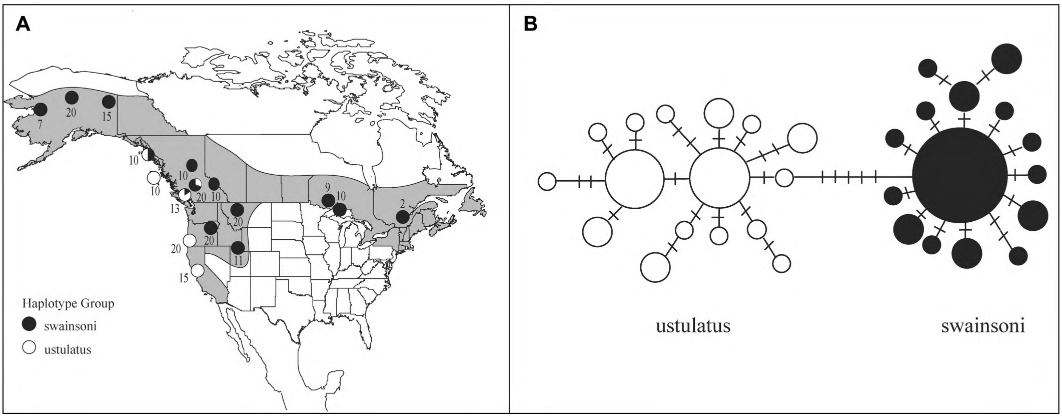

FIG. 2. Summary of genetic analysis based on mtDNA control-region haplotypes from Ruegg and Smith (2002). (A) Frequency of coastal *ustulatus* (white circles) and inland *swainsoni* (black circles) haplotypes in 17 breeding populations. (B) Haplotype network with bars across branches indicating single nucleotide changes. Four sizes of circle are used to represent the number of individuals sharing the same haplotype (smallest, 1 individual; medium-small, 2–4 individuals; medium-large, 5–11 individuals; largest, 44 individuals).

(Klicka et al. 1999), 0.1% between Bluethroat (*Luscinia svecica*) subspecies (Questiau et al. 1998), and 1.7–4.8% between seven subspecies of Common Chaffinch (*Fringilla coelebs*; Marshall and Baker 1998).

Nuclear genetic distances between *ustulatus* and *swainsoni* populations from the Pacific Northwest of North America (two *ustulatus*, two *swainsoni*, and one mixed population) are lower than microsatellite genetic distances between other designated species but within the range of genetic distances between other subspecies and populations. Microsatellite-based genetic distances, in which an $F_{ST}$ of 1 represents no gene flow and an $F_{ST}$ of 0 represents complete mixing, ranged from 0.018 to 0.043 between pure *ustulatus* and *swainsoni* populations (Ruegg et al. 2006b). In comparison, $F_{ST}$-based estimates of genetic distance among some species of birds range from 0.054 (Shy Albatross [*Thalassarche cauta*] and White-capped Albatross [*T. steadi*]; Abbott and Double 2003) to 0.069 (five species of gulls [*Larus* spp.]; Crochet et al. 2003), whereas $F_{ST}$-based genetic distances among some well-differentiated subspecies and populations range from 0.014 to 0.075 (0.014 for populations of Yellow Warblers [*Dendroica petechia*] from across North America [Gibbs et al. 2000]; 0.018 among populations of Chestnut-backed Chickadees [*Poecile rufenscens*; Burg et al. 2006]; and 0.075 among subspecies of North American Steller's Jays [*Cyanocitta stelleri*; Burg et al. 2005]). In conclusion, mitochondrial and nuclear genetic divergence between the *ustulatus* and *swainsoni* subspecies groups is somewhat lower than estimates of genetic divergence between some other avian sister species, but is within the range of genetic divergence between other well-defined subspecies of birds.

It is generally accepted that divergence between many well-differentiated subspecies and recently diverged sister species of birds can be attributed to geographic isolation during the mid- to late Pleistocene (Avise and Walker 1998, Johnson and Cicero 2004, Lovette 2005). Paleoecological data suggest that suitable songbird habitat was present in the east and west, south of the glacier's edge, and that the center of the country was occupied by tundra and desert that likely would have been inhospitable to a songbird (Pielou 1991). Genetic data combined with climate models of the distribution of the *ustulatus* and *swainsoni* subspecies groups at the last glacial maximum (LGM) are concordant with paleoecological data and suggest that the most likely distribution of populations at the LGM would have been western coastal and southeastern regions (Ruegg et al. 2006a; Fig. 3). In light of the hypothesized distribution at the LGM, regions of parapatry between the *ustulatus* and *swainsoni* subspecies groups likely represent regions of secondary contact following postglacial range expansions.

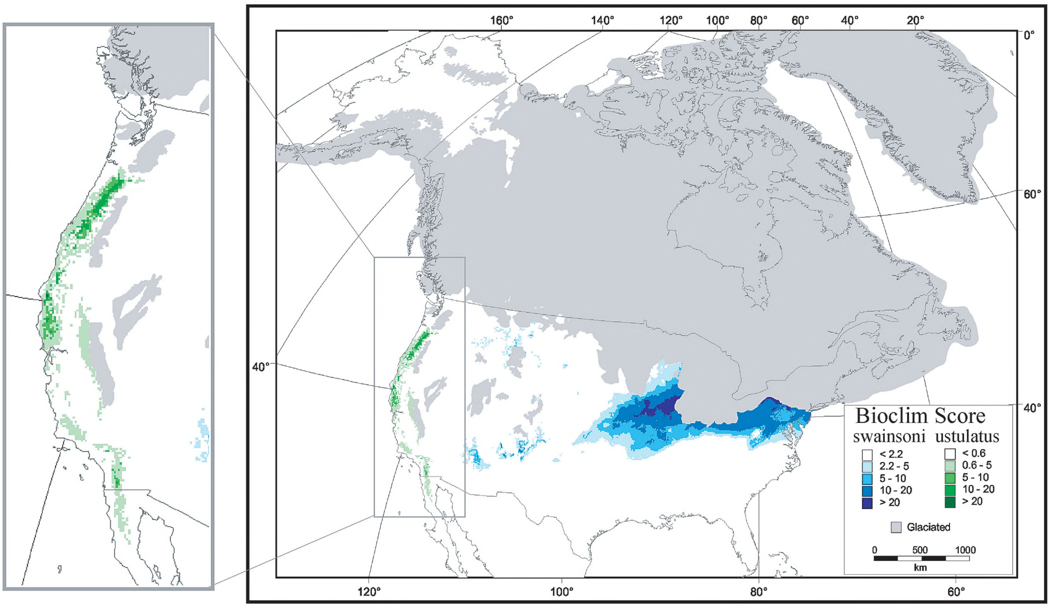

FIG. 3. Model of the distribution of coastal and inland populations at the last glacial maximum, based on climate data (adapted from Ruegg et al. 2006a).

## MIGRATORY ROUTES

Genetic, banding recapture, and subspecies distributional data confirm that the *ustulatus* and *swainsoni* subspecies groups of Swainson's Thrush follow distinct migratory pathways and overwinter in largely allopatric locations (Ramos and Warner 1980, Phillips 1991, Ruegg and Smith 2002). Coastal *ustulatus* populations migrate along a western route to wintering locations in southern Mexico and Central America, whereas inland *swainsoni* populations follow an eastern migratory pathway to wintering locations in Panama and South America (Fig. 1). Distributional records indicate that *ustulatus* populations follow the same migratory route for both fall and spring migration, but that *swainsoni* populations follow different migratory routes in spring and fall. During spring migration, *swainsoni* populations are found throughout the central United States, whereas during fall migration, *swainsoni* populations shift their primary migration route eastward (Evans Mack and Yong 2000).

Northwestern *swainsoni* breeding populations do not follow the shortest migratory route to the wintering grounds. Instead, banding recapture and genetic data indicate that individuals migrate along an eastern route toward ancestral breeding grounds in the east before migrating south to the wintering grounds (Ruegg and Smith 2002). Ruegg and Smith (2002) suggested that the migratory pathway of northwestern *swainsoni* breeding populations is an artifact of their postglacial range expansion and noted that it may not represent the most efficient route to the wintering grounds. Two lines of evidence support this hypothesis: (1) the migratory pathway of northwestern *swainsoni* populations mirrors the postglacial expansion of the boreal forest at the end of the LGM (Ruegg and Smith 2002), and (2) genetic signatures of population expansion and climatic models of the change in distribution since the LGM both support the idea that the *ustulatus* and *swainsoni* subspecies groups expanded out of eastern and western regions following the recession of ice sheets from North America (Ruegg and Smith 2002, Ruegg et al. 2006a). An alternative (and not mutually exclusive) explanation to this historical hypothesis is that the current migratory pathway of northwestern *swainsoni* populations is adaptive because of favorable ecological conditions or favorable trade winds along the route. Given how fast selection is known to act on migration patterns in other species (Berthold et al. 1992), one would expect that nonadaptive migration patterns would change over time so that members of the *swainsoni* lineage would begin taking the shortest route by migrating down the Pacific Coast.

Although the migration patterns of *ustulatus* and northwestern and eastern *swainsoni* populations are relatively well documented, the patterns of migration in Rocky Mountain breeding populations remain less clear. Current data are inadequate to determine whether Rocky Mountain and northwestern *swainsoni* populations expanded out of the same region at the end of the LGM, or even to map the current migratory pattern of Rocky Mountain populations. Available genetic data indicate that Rocky Mountain populations are indistinguishable from other *swainsoni* populations, thus suggesting that they share a similar evolutionary history. However, further research is needed to help clarify questions regarding the migration routes in Rocky Mountain populations of the *swainsoni* subspecies group.

## Breeding Habitat and Climate Zones

The *ustulatus* and *swainsoni* groups occupy different habitat types across their extensive breeding range, which has led some authors to suggest that ecological specialization may play a role in maintaining subspecies boundaries (Bent 1949). Populations of *ustulatus* are riparian woodland specialists during the breeding season (Grinnell and Miller 1944, Bent 1949, Verner and Boss 1980). Their connection to riparian habitat is so close that, in California, it has been suggested that the loss of this habitat type may restrict dispersal (Johnson and Geupel 1996). By contrast, eastern and northern *swainsoni* populations occupy mixed-hardwood and Boreal spruce–fir forests, respectively; and, as Bent (1949) pointed out, these forest types are distinct from those of their *ustulatus* relatives. However, western interior *swainsoni* populations are associated with both *ustulatus*-like riparian habitat and mixed-conifer forests in interior British Columbia (Campbell et al. 1997) and the Rocky Mountains (Evans Mack and Yong 2000). The overlap in habitat types occupied by coastal *ustulatus* and western interior *swainsoni* populations suggests that habitat specialization is most likely not an important isolating barrier and that differences in habitat use across the range of *swainsoni* populations reflects plasticity rather than specificity.

The most striking difference between the two groups is not in habitat specialization, but in the occupation of distinctive coastal and interior climate-vegetation zones that likely reflect their unique evolutionary histories. The shift between coastal and interior climates is correlated with hypothesized regions of secondary contact between numerous sister species and subspecies of birds that likely were isolated in separate refugia during the LGM (Johnson 1978, Cicero 2004). The crest of the Cascade and Coastal mountains and the Sierra Nevada impose a significant precipitation shadow that produces a continent-wide shift from moist, coastal coniferous forest to the cool, dry forests of interior western North America. A recent study of climatic space occupied by the *ustulatus* and *swainsoni* groups supports the idea that regions of secondary contact fall on the boundary between coastal and interior climatic zones (Ruegg et al. 2006a). Interior *swainsoni* populations occupy breeding habitat characterized by lower annual mean temperature, greater extremes in temperature, and less fluctuation in precipitation across the year compared with the coastal *ustulatus* group's breeding habitat (Ruegg et al. 2006a). The question that remains unanswered is whether adaptations to distinctive climatic regions play a role in limiting gene flow between the subspecies. For example, do the *ustulatus* and *swainsoni* groups differ in the timing of migration, molt, and reproduction, and do these differences influence mate choice and the fitness of hybrids? I revisit this topic below.

## Acoustic Divergence

Throughout its range, the Swainson's Thrush is recognizable by its upward-spiraling flutelike song. The flutelike quality of the advertising song results from a string of syllables that increase in frequency and decrease in amplitude towards the end of the vocalization (Dobson and Lemon 1977). Each individual has multiple song types with significant individual variation in syllable type and order (Dobson and Lemon 1977, Ruegg et al. 2006b; Fig. 4). Despite significant individual variation, recognizable song types are often consistent within populations (Ruegg et al. 2006b). The high degree of individual variation suggests a strong capacity for vocal learning, consistent with data from other oscines in which song learning has been demonstrated (reviewed in

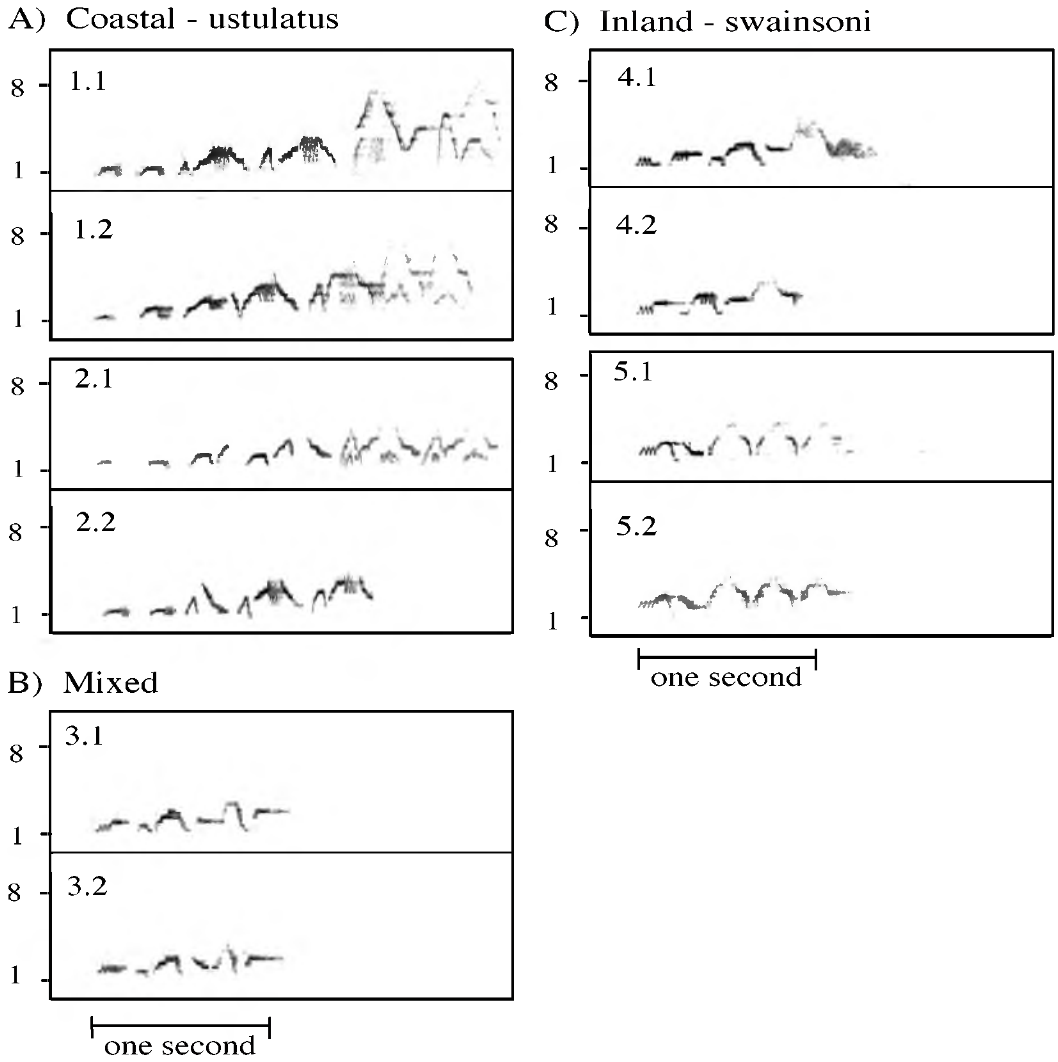

Fig. 4. Sonograms from two individuals from coastal *ustulatus* and inland *swainsoni* subspecies groups, as well as two individuals from a mixed population. The numbers in the upper left are the population number followed by the individual number. Although each individual has multiple song types, the figure illustrates the most common song type in the population (from Ruegg et al. 2006b).

Marler and Slabbekoorn 2004). Some geographic variation in the frequency of certain vocalizations, such as migration and nest-begging calls, has been reported (Evans Mack and Yong 2000), but a comprehensive survey of geographic variation in acoustic characteristics across the species' range is lacking. In addition, all work to date on the song of the Swainson's Thrush has focused on the advertising song (Dobson and Lemon 1977, Ruegg et al. 2006b). An especially useful future analysis would be to assess geographic variation in the frequency of call notes, which has been used previously to determine species status between Bicknell's and Gray-cheeked thrushes (Ouellet 1993).

In a study of genetic, ecological, and acoustic divergence in five populations of Swainson's Thrush—two from coastal temperate rainforest representing the *ustulatus* subspecies group, two from montane coniferous forest representing the *swainsoni* subspecies group, and one mixed population—Ruegg et al. (2006b) found a potential role for ecological selection in the evolution of vocal divergence. Overall, coastal songs were longer in duration and had lower initial frequencies than inland songs, whereas songs of the genetically more coastal, but ecologically more inland, mixed population were more similar to inland songs (Ruegg et al. 2006b). Ruegg et al. (2006b) hypothesized that the lower frequency and longer duration of coastal songs may result from the fact that sound transmission is more difficult in moist coastal forests, where background noise generated by rainfall is loud and mild winters allow for year-round growth of vegetation. Alternatively, shorter, higher-frequency inland songs may result from sound traveling more easily in drier mixed-coniferous forests, where understory vegetation is sparser. Further research is necessary to determine the extent to which habitat variables such as vegetation density and rainfall may influence sound transmission in the Swainson's Thrush.

The degree to which differences in song help maintain or promote further divergence between the *ustulatus* and *swainsoni* subspecies groups remains an open question and depends partly on the mechanism of song learning in this species. If song learning is restricted to the period before individuals disperse from their natal region, and if females prefer local song types, then song differences may present a barrier to gene flow (Ellers and Slabbekoorn 2003). However, if song learning occurs throughout life, individuals dispersing into new environments would have the capacity to adjust their song to the given ecological conditions and song would not present a barrier to gene flow (Ellers and Slabbekoorn 2003). Future research focused on the timing of song learning in the Swainson's Thrush will reveal the potential for acoustic variation to maintain or promote further divergence in this species.

## Hybrid Zone Dynamics

A detailed analysis of a hybrid zone between the *ustulatus* and *swainsoni* groups in the Coast Mountains of British Columbia revealed that the transition from *ustulatus* to *swainsoni* phenotypes and genotypes occurs over an 80-km region, which is concordant with the transition between coastal and interior climatic zones (Ruegg 2007). Using 15 amplified-fragment-length polymorphism (AFLP) markers and a Bayesian method for assigning individuals to hybrid classes (Anderson and Thompson 2002), Ruegg (2007) was able to distinguish between *ustulatus*, *swainsoni*, and hybrid individuals with >90% posterior probability. Morphological and plumage color analyses revealed that coastal *ustulatus* populations were larger, had relatively longer wings, and were more russet colored than inland *swainsoni* populations (Ruegg 2007). Clines in plumage color, body size, wing length, and nuclear genetic assignment (based on the AFLP markers) were coincident in position, whereas the mtDNA cline was shifted slightly southwest (Fig. 5). The width of the contact zone is approximately half the estimated dispersal distance of the Swainson's Thrush, which implies that there is a strong barrier to gene flow preventing the zone from becoming wider (Barton and Hewitt 1985, Barton and Gale 1993). The center of the hybrid zone was also characterized by low population density and the existence of pure *ustulatus* and *swainsoni* individuals as well as recent hybrids and backcrosses (Ruegg 2007). Ruegg (2007) evaluated a variety of models proposed to explain the maintenance of narrow hybrid zones in birds and concluded that the Swainson's Thrush hybrid zone had the characteristics of a tension zone in which dispersal into the zone was balanced by ecologically mediated selection against hybrids or premating barriers to gene flow, or both.

The correlation of the hybrid zone with the transition from coastal to interior climatic regions suggests that hybrid fitness and premating isolation in the Swainson's Thrush may be influenced by adaptations to distinctive climatic regions. For example, annual fluctuations in temperature and seasonality may result in differences in the timing of molt, migration, and reproduction. Similar scenarios have been proposed to help explain the maintenance of hybrid zones for the Baltimore Oriole (*Icterus galbula*) and Bullock's Oriole (*I. bullockii*) and for yellow-shafted and red-shafted Northern Flickers (*Colaptes auratus auratus* and *C. a. cafer*, respectively) (Moore and Price 1993). Rohwer and Manning (1990) hypothesized that differences between Baltimore and Bullock's orioles in timing of molt is an adaptation to mesic and xeric climates and that hybrids with intermediate timing of molt may be less fit. Alternatively, the situation in the Swainson's Thrush may be more similar to the situation in Black-capped Warblers (*Sylvia atricapilla*), in which populations

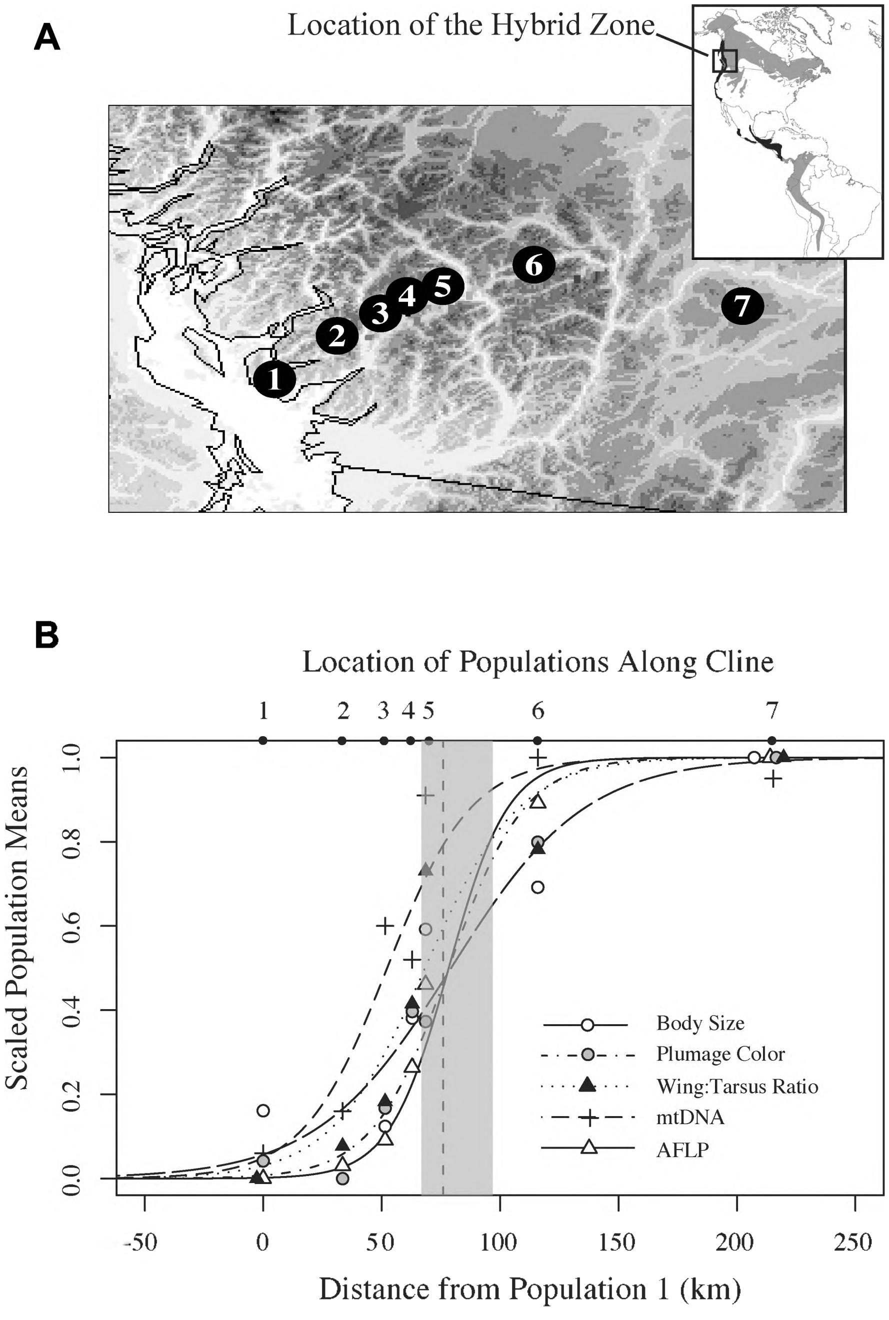

FIG. 5. Results from the hybrid-zone analysis. (A) Map of sampling locations in southwestern British Columbia. The smaller map in the upper right corner is the distribution of both forms, and the black rectangle represents the approximate region of the hybrid zone. (B) Shape and width of multiple character clines demonstrating concordant shifts from *ustulatus* to *swainsoni* phenotypes and genotypes across the hybrid zone.

with different wintering locations mate assortatively on the basis of arrival time (Bearhop et al. 2005). However, given evidence of hybridization between *ustulatus* and *swainsoni* populations in regions of overlap, premating isolation alone cannot explain the strong barrier to gene flow. To investigate the role of climate in hybrid-zone maintenance, future research should focus on how differences in the timing of migration, molt, and reproduction affect premating isolation and hybrid fitness.

### Implications for Speciation

From a speciation standpoint, the *ustulatus* and *swainsoni* subspecies groups reside in the interesting gray area between well-differentiated subspecies and recently diverged sister species. On one hand, the two groups share many characteristics of well-differentiated subspecies: (1) genetic divergence estimates between the groups is, in many cases, lower than levels of genetic divergence between many known sister taxa, but similar to levels of genetic divergence between subspecies; (2) the subspecies groups occupy distinctive climatic regions, but given the available data there is little to suggest that they are ecologically isolated; and (3) the two groups have differences in their advertising song, but the song differences are similar to dialect differences found within other species where song learning is prevalent. On the other hand, the two groups share many characteristics of recently diverged sister species: (1) *ustulatus* and *swainsoni* populations are diagnosable as distinct genetic entities using both mitochondrial and nuclear (AFLP) markers; (2) climatic models and genetic data both support the idea that the two groups have distinct evolutionary histories; and (3) cline analysis suggests that one hybrid zone is approximately half the estimated dispersal distance of the Swainson's Thrush, implying that there is a strong barrier to gene flow preventing the zone from becoming wider.

The AOU has traditionally relied on the biological species concept (BSC) of Dobzhansky (1937), which states that "species are systems of populations: the gene exchange between these systems is limited or prevented by a reproductive isolating mechanism or perhaps by a combination of several mechanisms." As discussed by Johnson et al. (1999), the gray area in the interpretation of the BSC for avian taxonomy is the extent to which hybridization is allowed before the two groups are considered subspecies rather than sister taxa. The situation in the Swainson's Thrush is comparable to that in Yellow-shafted and Red-shafted flickers (Moore and Price 1993), Myrtle and Audubon's warblers (*Dendroica coronata*; Barrowclough 1980), and Hermit and Townsend's warblers (*D. occidentalis* and *D. townsendi*; Rohwer and Wood 1998, Rohwer et al. 2001), in which sister groups are clearly diagnosable according to many criteria but are also known to hybridize extensively in restricted hybrid zones. Although the BSC allows for hybridization, a key component of Dobzhansky's (1937) definition is that there must be some evidence for reproductive isolation. In the case of the flickers and the Myrtle × Audubon's warblers, there is little evidence for reproductive isolation, and the two groups have been treated as one species. However, in the case of Hermit × Townsend's warblers, the high number of parentals in the center of the hybrid zone and the narrow width of the hybrid zone in relation to estimates of dispersal distance provide evidence for reproductive isolation and, as a result, the groups are considered separate species (AOU 1983). Similar to the situation in Hermit and Townsend's warblers, the Swainson's Thrush hybrid zone is narrow in relation to estimates of dispersal and contains a significant number of parentals within the centermost populations—thus indicating a strong potential for reproductive isolation between *ustulatus* and *swainsoni* individuals (Ruegg 2007). In addition, the Swainson's Thrush hybrid zone is correlated with the transition from coastal to interior climatic regions, which suggests a role for ecologically mediated reproductive isolation. However, additional research is necessary to identify the mechanisms of reproductive isolation that may be occurring to keep the hybrid zone from widening. If Ruegg's (2007) analysis is correct and climatic differences are important in limiting gene flow between the subspecies, then *ustulatus* and *swainsoni* populations will remain on distinct evolutionary trajectories as long as the coastal and interior climatic regions remain stable. Future research would benefit from analysis of additional hybrid-zone transects as well as tests for hybrid fitness and assortative mating within the hybrid zone.

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