

Not as the crow flies: a historical explanation for circuitous migration in Swainson's thrush (*Catharus ustulatus*)

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Many migratory songbirds follow circuitous migratory routes instead of taking the shortest path between overwintering and breeding areas. Here, we study the migration patterns in Swainson's thrush (*Catharus ustulatus*), a nearctic–neotropical migrant songbird, using molecular genetic approaches. This species is presently separated into genetically distinct coastal and continental populations that diverged during the Late Pleistocene (as indicated by molecular dating), yet appear to have retained ancestral patterns of migration. Low nucleotide diversity, a star-like haplotype phylogeny and unimodal mismatch distributions all support the hypothesis that both the coastal and the continental populations have undergone recent demographic expansions. Nearctic–neotropical banding and genetic data show nearly complete segregation of migratory routes and of overwintering locations: coastal populations migrate along the Pacific Coast to overwintering sites in Central America and Mexico, whereas continental populations migrate along an eastern route to overwintering sites in Panama and South America. Nearctic–neotropical banding data also show that continental birds north, northwest and east of this migratory divide fly thousands of miles east before turning south. We conclude that circuitous migration in the Swainson's thrush is an artefact of a Late Pleistocene range expansion.

Keywords: indirect migration; migratory divide; Late Pleistocene range expansion

1. INTRODUCTION

Migrating birds often follow circuitous routes instead of taking the shortest path between overwintering and breeding areas, but for most such species, the factors responsible for indirect routes remain unclear. Two major classes of explanation have been invoked to explain this phenomenon. One possibility is that indirect migration routes allow migrating individuals to avoid potentially dangerous geographical features such as large bodies of water, deserts or mountain ranges (Rappole 1995), or are otherwise adaptive (Alerstam 2001). However, this explanation seems insufficient given the many contrary examples of birds migrating across seemingly hostile geographical regions or barriers (e.g. Wolfson 1948; Nisbet 1970). An alternative explanation is that present day migration routes are an artefact of historic range shifts (Wolfson 1948). Under this scenario, migratory direction is a heritable trait (Berthold & Querner 1981; Berthold 1988; Berthold *et al.* 1992) that has not yet been modified by selection. Given the complexities of migratory behaviour, it is probable that both historical and ecological factors have influenced the evolution of present day migratory routes.

It is possible that a number of migratory songbirds undertake indirect migrations as a result of shifts in Late Pleistocene habitat distributions. This explanation may

also account for the presence of the migratory divides described by Bensch *et al.* (1999) as 'the zone of contact between parapatric populations with disparate migratory directions'. Such divides are found in several species of Old World migrants (e.g. Helbig 1992; Bensch *et al.* 1999). In North America, palaeoecological evidence indicates that glacial advances during the Late Pleistocene split transcontinental populations of plants and animals into isolated eastern and western refugia (Pielou 1991). Phylogenetic analysis of some nearctic–neotropical migrants has revealed intraspecific phylogenetic splits between eastern and western groups that is probably a result of geographical isolation during this period (Avisé & Walker 1998; Milot *et al.* 2000). As glaciers receded, eastern populations of forest dwelling organisms spread northwest along with the expansion of boreal forest (Pielou 1991; Webb & Bartlein 1992). Present day indirect migration routes in these species may be the result of populations once isolated in eastern refugia that now retrace their postglacial expansion routes while migrating to overwintering locations.

Molecular techniques allow one to study some of the historical processes important to migration. Historic population increases are likely to have resulted in range expansions, and such increases can be inferred from molecular data in two ways. First, a past population increase results in a signature star-like haplotype phylogeny, with most high frequency haplotypes separated from low frequency haplotypes by one or two mutational steps (Avisé *et al.* 1987; Zink 1997). Second, analysis of the average number of pairwise differences between mtDNA sequences, referred to as mismatch distribution, provides

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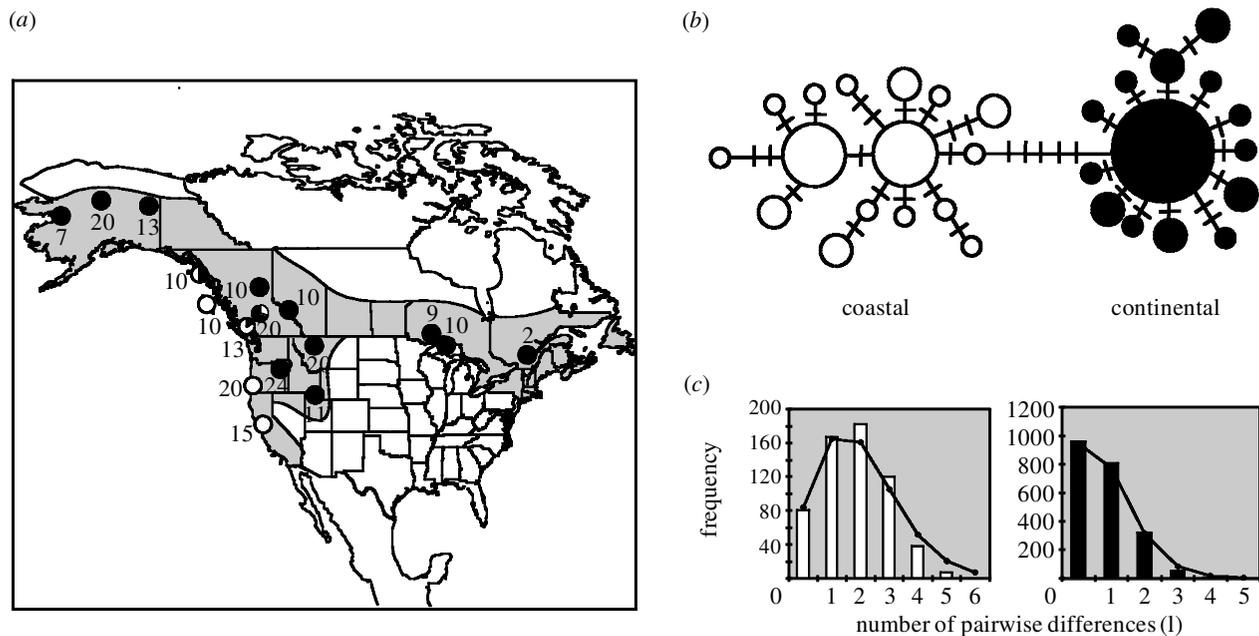


Figure 1. Summary of genetic analyses based on mtDNA control region haplotypes. (a) Frequency of coastal (white circles) and continental (black circles) haplotypes in 17 intensively sampled breeding populations. (b) Minimum-spanning network with bars across branches indicating single nucleotide changes. 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). (c) Mismatch distributions indicate recent demographic expansions in both the coastal and continental clades.

a way to estimate statistically both magnitude and approximate timing of population growth (Rogers & Harpending 1992; Rogers 1995; Schneider & Excoffier 1999). These approaches have demonstrated that low genetic diversity in a few species of Old and New World songbirds is probably the result of rapid, postglacial demographic expansion (Merilä *et al.* 1997; Bensch *et al.* 1999; Milá *et al.* 2000). A combination of these molecular analyses provides the information necessary to assess the influence of Late Pleistocene demographic and range expansions on present day indirect migration routes.

Molecular techniques may also be used in combination with field methods to trace migratory pathways and explore the demographic connectivity between overwintering and breeding areas (e.g. Wennerberg 2001). Efforts to document migratory routes using field techniques have relied primarily on banding recapture data and identification of subspecies (Ramos & Warner 1980). Banding efforts alone, however, have generally met with limited success because band returns are extremely low, particularly for passerine migrants. In addition, subspecies designations may be unreliable, as accurate identification requires a rare degree of expertise. Molecular techniques are now being used to find genetic tags to identify breeding population units and then screen for these tags in individuals caught on the overwintering grounds (e.g. Wenink & Baker 1996; Haig *et al.* 1997; Wennerberg 2001). Here, we show the utility of using a combination of field and laboratory techniques to define current migration routes and overwintering locations of migrant songbirds.

We use the Swainson's thrush (*Catharus ustulatus*), a neotropical migrant songbird with a widespread New World distribution, to examine the evolution of indirect migration routes. This long-distance migrant breeds across Canada, along the Pacific Coast of North America

and in parts of the Rocky Mountains (figure 1a), and overwinters in southern Mexico, Central America and northern South America. Swainson's thrush is an appropriate model organism with which to address the evolution of indirect migration because it breeds in the band of boreal forest that has recently expanded into northern North America, and a summary of banding recaptures in Canada indicates that this species may be following indirect migration routes (Brewer *et al.* 2000). Additionally, the existence of morphological subspecies (western subspecies, *C. ustulatus* and *C. oedicus*; eastern subspecies, *C. u. alame* and *C. u. swainsoni*) (Bond 1963) indicates that historical biogeographical processes may have influenced differentiation in this species.

Here we use molecular analyses to reconstruct the phylogeographic history and past demographic events of Swainson's thrush, and use molecular tags in combination with all available nearctic–neotropical banding data to define current migratory pathways and establish demographic connectivity between breeding and overwintering areas. We use this information to support the hypothesis that circuitous migration in Swainson's thrush is an artefact of a Late Pleistocene range expansion.

2. MATERIAL AND METHODS

(a) Genetic sampling and laboratory methods

We analysed genetic material from 420 Swainson's thrushes from across the species' breeding and overwintering range, as well as from migratory stopover points. Breeding ground samples comprised representatives of all four morphologically diagnosed subspecies (*sensu* Bond 1963; Ramos & Warner 1980). Birds were captured using mist nets and the two outer rectrices were collected. Small blood samples were collected

from the sub-brachial wing vein of 74 individuals and blood was preserved in lysis buffer (Seutin *et al.* 1991).

To reconstruct the phylogenetic history of Swainson's thrush we initially examined mtDNA sequence variation in 105 samples from 10 populations. DNA was extracted from blood and feathers following Milá *et al.* (2000). We used a species-specific primer (LITH 5' TGTTTTCTCATGCTTTACAGG 3') in combination with primers L437 and H1248 (Tarr 1995) to amplify a 1100 bp fragment of the mitochondrial control region. All samples were sequenced using these primers in an ABI Prism 377 automated sequencer (Applied Biosystems, Inc.). The resulting sequence consisted of *ca.* 800 bp of double-stranded sequence and 300 bp of single-stranded sequence per individual.

We examined the remaining 315 Swainson's thrush samples from breeding, overwintering and stopover sites using a restriction site analysis. Phylogenetic analysis of the 105 control region sequences identified two reciprocally monophyletic haplotype groups (see § 3). To survey the distribution of these clades in migrating and overwintering birds, we amplified the 800 bp fragment of control region using the primers described above and used restriction enzyme Sfc I to assay a variable site in which cleavage is diagnostic of the coastal clade. Five microlitres of the digest reaction were electrophoresed on a 6% polyacrylamide gel and restriction fragments were stained with ethidium bromide and visualized under ultraviolet light.

(b) Analysis of molecular data

We estimated evolutionary relationships among haplotypes via a minimum-spanning tree generated using the program ARLEQUIN (Schneider *et al.* 1999). The net sequence divergence between clades was estimated using the program MEGA2 (Kumar *et al.* 2002) and corrected for polymorphisms within each clade by subtracting the within-clade divergence from the total divergence. We used ARLEQUIN to calculate nucleotide diversity (π), haplotype diversity (h), and estimated population structure via F_{ST} and AMOVA. We performed the analysis of molecular variance (AMOVA) (Excoffier *et al.* 1992) by grouping sampling sites into coastal and continental morphologically defined subspecies groups.

Mismatch analysis was also performed in ARLEQUIN. We quantified the estimators τ , θ_0 , θ_1 (τ , the age of expansion in generations and θ_0 , θ_1 , population sizes before and following expansion, each expressed in units of mutational time) and used them to generate the mismatch distribution expected under the sudden-expansion model (Schneider *et al.* 1999). We generated 95% confidence intervals (CI) around the demographic parameters τ , θ_0 , θ_1 using 1000 bootstrap replications (Schneider & Excoffier 1999). The fit of the simulated mismatch distribution to the observed distribution was tested by comparison of the sums of squared deviations (Schneider & Excoffier 1999).

(c) Analysis of banding recapture data

We used all available nearctic–neotropical banding data to trace the current migration routes and overwintering locations used by Swainson's thrush. Banding encounter records were requested from the USGS Patuxent Wildlife Research Center (Laurel, Maryland 20708-4039, USA). Because we were concerned with broad scale movements only, records under 800 km from the site of banding to the site of recapture were not included in our analysis. We considered encounters between the months of November through to March to be overwintering individuals and we excluded all other Latin American encounters. In total, 71 of the 251 recorded encounters were included

in our encounter summary map. Banding data, consisting of the banding site and the point of recapture, were plotted onto a map within 10 min latitude and longitude blocks.

3. RESULTS

(a) Phylogeographic variation and evidence for Late Pleistocene, postglacial range expansion

Phylogenetic reconstructions demonstrated that Swainson's thrush is separated into two mitochondrially differentiated clades: (i) a coastal clade that occurs west of the Coast, Cascade and Sierra Nevada mountain ranges from Juneau, Alaska to Big Sur, California; and (ii) a continental clade that occurs throughout the remainder of the breeding range (figure 1*a,b*). Populations containing a mixture of individuals from the coastal and continental clades at the same site were found in a valley that bisects the Coast Mountains in British Columbia and at sites near Juneau, Alaska (figure 1*a*). Restriction-site analysis of seven additional populations provided further support for the separation of coastal and continental clades across North America (figure 1*a*). The distribution of coastal populations is concordant with the combined distribution of western subspecies *C. u. ustulatus* and *C. u. oedicus*; the distribution of the continental populations is concordant with the distribution of eastern subspecies, *C. u. alame* and *C. u. swainsoni* (Bond 1963).

The net sequence divergence between clades is 0.69%; five apomorphic nucleotide differences separate the clades. A rate of 14.8% divergence per million years (Quinn 1992; Wenink *et al.* 1993) is the calibration most widely used for control region I sequence in passerines. However, no calibrations are available for taxa closely allied to Swainson's thrush, and both the calibration itself and our estimates of sequence divergence have errors that are difficult to assess quantitatively. We are therefore cautious about assigning an absolute date to the time of divergence based on our molecular information. Nonetheless, the simple application of this calibration to our system indicates that coastal and continental populations diverged roughly 10 000 years ago. Even if this calibration overestimates the rate of sequence divergence by an order of magnitude, the split occurred during the Late Pleistocene. It therefore seems likely that the split between coastal and continental populations was associated with geographical changes in habitat distribution that occurred during this period.

On average, coastal populations have higher estimates of genetic diversity than continental populations (table 1). However, there is no apparent pattern associated with latitude and genetic diversity as documented in other studies (Merilá *et al.* 1997). Analysis of the geographical distribution of genetic diversity on the breeding grounds reveal significant population subdivision, with an overall F_{ST} of 0.64 ($p < 0.001$). A hierarchical analysis of molecular variance also reveals significant population subdivision on the breeding grounds (table 2). Most of this significant geographical structure stems from the relatively deep divergence between the coastal and continental clades. When populations are grouped on the basis of morphologically defined subspecies designations into coastal and continental groups, 65.15% of the overall genetic variation is explained by differences between groups (table 2).

Table 1. Haplotype (h) and nucleotide diversity (π) for 10 sampling sites. (n , number of individuals; n_H number of distinct haplotypes.)

| locality | n | n_H | h (\pm s.d.) | π (\pm s.d.) |
|----------------------------|-----|-------|-------------------|-------------------------|
| <i>coastal</i> | | | | |
| Queen Charlotte Island, BC | 10 | 7 | 0.80 \pm 0.10 | 0.0022 \pm 0.0015 |
| Bolinas, CA | 12 | 5 | 0.67 \pm 0.14 | 0.0011 \pm 0.000 89 |
| <i>mixed</i> | | | | |
| Squamish, BC | 11 | 8 | 0.93 \pm 0.07 | 0.0041 \pm 0.0025 |
| Juneau, AK | 5 | 4 | 0.90 \pm 0.16 | 0.0062 \pm 0.0041 |
| Pemberton, BC | 19 | 8 | 0.77 \pm 0.09 | 0.0043 \pm 0.0025 |
| <i>continental</i> | | | | |
| Thunder Bay, ON | 9 | 5 | 0.72 \pm 0.15 | 0.000 99 \pm 0.000 83 |
| Kakabeka Falls, ON | 10 | 5 | 0.67 \pm 0.16 | 0.000 89 \pm 0.000 77 |
| Revelstoke, BC | 11 | 6 | 0.73 \pm 0.14 | 0.0011 \pm 0.000 85 |
| Grantsville, UT | 9 | 3 | 0.42 \pm 0.19 | 0.000 44 \pm 0.000 49 |
| Quesnel, BC | 11 | 2 | 0.18 \pm 0.14 | 0.000 36 \pm 0.000 42 |

Table 2. Analysis of molecular variance. Swainson's thrush populations divided into coastal and continental groups.

| source of variation | degrees of freedom | variance components | p | percentage of variation |
|---------------------------------|--------------------|---------------------|---------|-------------------------|
| among groups | 1 | 2.33 | < 0.001 | 65.15% |
| among populations within groups | 8 | 0.08 | < 0.001 | 6.56% |
| within populations | 97 | 1.23 | < 0.001 | 28.29% |

Table 3. The demographic parameters (95%) and $p(\text{SSD}_{\text{obs}})$, the probability of observing a less than good fit between the generated mismatch distribution and the observed mismatch.

(τ , θ_0 , θ_1 are the age of expansion and the population size before and following expansion, expressed in units of mutational time.)

| lineage | τ | θ_0 | θ_1 | $p(\text{SSD}_{\text{obs}})$ |
|-------------|------------------|------------------|-------------------------|------------------------------|
| coastal | 2.00 (0.64–2.72) | 0.00 (0.00–1.59) | 3402.50 (17.34–7800.00) | 0.32 |
| continental | 1.66 (0.14–4.76) | 0.00 (0.00–0.64) | 1.15 (0.42–3311.15) | 0.68 |

The minimum-spanning tree and the mismatch distributions indicate that coastal and continental populations of Swainson's thrush have both undergone recent demographic expansions (figure 1*b,c*). Both clades display a star-like phylogeny of haplotypes indicative of a recent population increase (Avice *et al.* 1987; Zink 1997), with high-frequency haplotypes separated by one or two base pairs from low-frequency haplotypes (figure 1*b*). The mismatch distributions for both coastal and continental populations show the unimodal shape predicted for populations that have undergone sudden demographic expansions (Rogers & Harpending 1992; Zink *et al.* 2001; figure 1*c*). Although the age expansion parameter (τ) of the continental clade suggests that continental expansion was more recent, the difference was not significant due to the wide CIs (table 3). Estimation of the magnitude of expansions is not possible due to the large CIs surrounding θ_1 (table 3). The probability of observing a less-than-good fit between the observed mismatch and the mismatch generated under the hypothesis of population expansion is non-significant for both coastal and continental clades (table 3).

(b) *Combining molecular and field data to establish demographic connectivity*

Restriction site analysis of migrant and overwintering individuals demonstrated that coastal and continental populations are following distinct migratory routes and overwinter almost exclusively in different locations (figure 2*b*). Coastal populations migrate down the Pacific Coast and overwinter from Mexico to Costa Rica, whereas continental populations follow a more eastern route within North America and overwinter from Panama to Bolivia (figure 2*a,b*).

The plot of nearctic-neotropical banding data highlights three important patterns. First, it provides independent support that coastal and continental populations follow distinct migratory routes and overwinter in different locations. Second, it indicates that the westernmost continental populations, such as those in central Alaska, fly thousands of kilometres east across northern and middle North America before turning south towards overwintering grounds in northern South America. Third, it indicates the presence of a migratory divide that corresponds to the

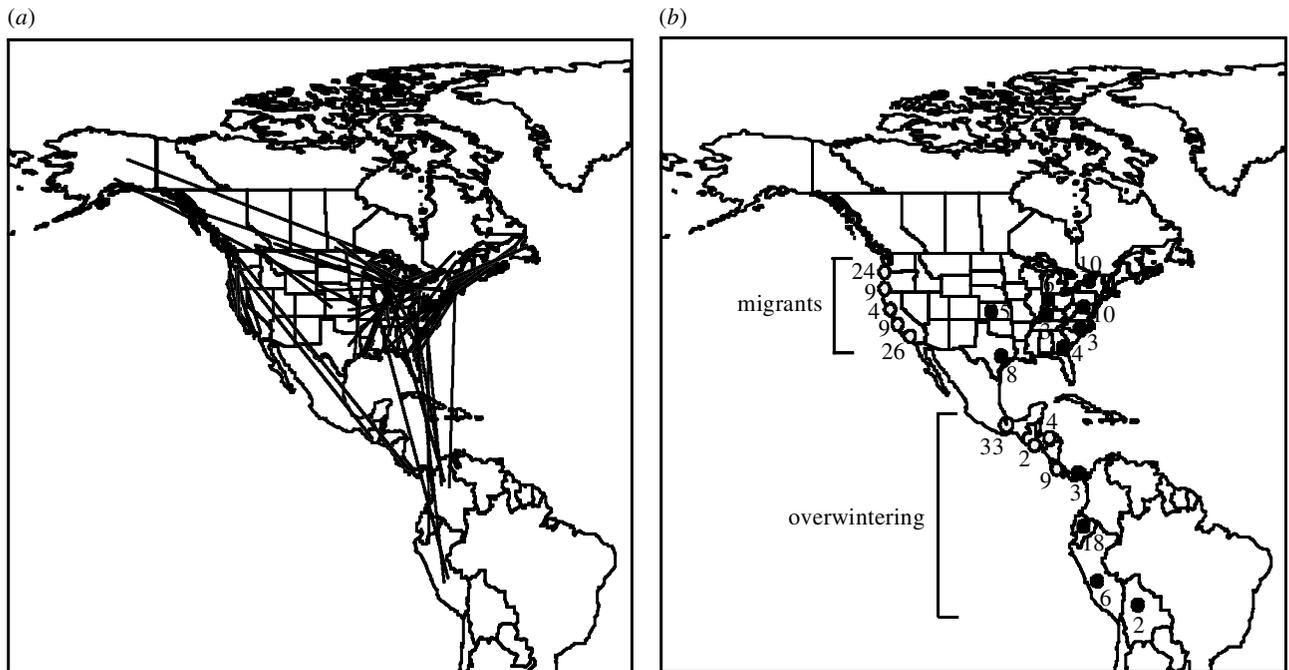


Figure 2. Migration routes and overwintering locations. (a) Nearctic–neotropical banding summary. (b) Frequencies of coastal (white circles) and continental (black circles) haplotypes captured at their overwintering locations and during migration in North America.

contact zone between the two mitochondrial clades that meet along the Coast Mountains in British Columbia, possibly continuing along the Cascades through Washington and Oregon.

4. DISCUSSION

(a) Evidence for Late Pleistocene, postglacial range expansions

Our results indicate that phylogenetic variation in Swainson's thrush was affected by the geological events of the Late Pleistocene. Phylogenetic analysis reveals that the species is separated into two monophyletic groups on the breeding grounds, a coastal clade that occurs along the west coast of North America from central California to central southeast Alaska and a continental clade present throughout the remainder of the breeding range (figure 1a). Coastal and continental mtDNA haplotypes are geographically concordant with combined Pacific Coast (*C. u. ustulatus* and *C. u. oedicus*) and continental subspecies (*C. u. alame* and *C. u. swainsoni*) described by Bond (1963). The banding data indicate that these morphologically and genetically differentiated groups are further separated by a migratory divide (figure 2a). The magnitude of genetic differentiation between the clades suggests coastal and continental lineages diverged during the Late Pleistocene. Palaeoecological data indicate that during the last glacial maximum (18 000 years ago), eastern and western refugia south of the glaciers' edge were separated by desert (Pielou 1991). Geographically concordant splits in genetics, morphology and migratory behaviour strongly support the hypothesis that coastal and continental groups diverged during the Late Pleistocene while isolated in glacial refugia and have met following postglacial range expansions.

Low levels of nucleotide diversity, star-like haplotype

phylogenies and the unimodal shape of the mismatch distributions provide additional evidence of recent and rapid population growth in these two groups. Population growth probably resulted in range expansions, as ice sheets melted and suitable habitats became available. Boreal forest tree species vastly increased their range from refugia in the southeast, to a band of forest that currently spans from the eastern Canadian coast to the western Alaskan coast (Webb & Bartlein 1992). The circuitous migration route of western continental populations of Swainson's thrush mirrors the expansion route of the boreal forest.

In comparison with coastal populations, the continental populations of the Swainson's thrush have lower genetic diversity, a strongly L-shaped mismatch distribution and a younger estimate of the time since the most important demographic expansion (figure 1b; tables 1 and 3). In populations that have undergone recent population growth, the shape of the mismatch distribution is wave-like (Rogers & Harpending 1992), as seen in the mismatch distribution of the coastal lineage (figure 1c). The L-shaped mismatch distribution in the continental lineage may be explained by lack of sufficient time to differentiate following bottlenecking (Merilä *et al.* 1997) and may therefore indicate a very recent expansion. These data are congruent with geological evidence that the geographical region currently occupied by the continental lineage was more dramatically affected by the last glaciation than the geographical region currently occupied by the coastal lineage (Pielou 1991).

(b) Establishing demographic connectivity

Our study provides, to our knowledge, the first attempt to define migration routes and overwintering locations of a New World migrant songbird using a combination of banding and genetic data. Our results show conclusively that coastal and continental phylogenetic groups follow

different migratory pathways and overwinter in different locations. Coastal populations migrate down the Pacific coast and overwinter from Mexico to Costa Rica and continental populations migrate along an eastern route and overwinter primarily in Panama and South America. Our results provide independent support for the assertion that western coastal and continental subspecies overwinter in separate locations (Ramos & Warner 1980; Phillips 1991). Further studies are needed to determine if selection at migratory stopover and overwintering locations may augment diversification in these two groups.

Using Swainson's thrush as a model, our results have significant implications for future studies of migration and conservation of nearctic–neotropical migrant birds. Some populations of nearctic–neotropical migrant species have been declining at precipitous rates (Robbins *et al.* 1989). However, research into the potential cause of population declines has been hindered because of the inability to trace migratory pathways and establish demographic connectivity between overwintering and breeding areas. Following the methods described by Wennerberg (2001), we were able to design a fast, inexpensive and reliable genetic tag to identify, on a broad geographical scale, the breeding origin of individuals captured at migratory stopover points and overwintering locations. This method may be improved by the use of a molecular marker with the ability to detect finer-scale population genetic structure.

(c) Circuitous migration and migratory divides as an artefact of Late Pleistocene range expansions

This study suggests that Swainson's thrush follows circuitous migration routes as a result of shifts in habitat during the Late Pleistocene. Our results show that western continental populations migrate thousands of miles towards their ancestral breeding range in southeastern North America, before heading south to their ultimate overwintering locations. This migration pattern strongly supports the idea that continental populations are retracing their historical expansion routes rather than following the most direct and presumably most efficient route to their overwintering grounds. Furthermore, continental populations in British Columbia and Alaska appear to migrate over major mountain ranges on their way east. This pattern is congruent with that seen in some other migrant species that follow indirect routes (Wolfson 1948; Nisbet 1970) and is contrary to the expectation that indirect migration routes circumvent major geographical barriers. The hermit thrush (*Catharus guttatus*) and the gray-cheeked thrush (*C. minimus*) are two examples of species with similar distributions that may also be following indirect migration routes (Brewer *et al.* 2000). We conclude that circuitous migration in Swainson's thrush is an artefact of a Late Pleistocene range expansion and that analogous migratory patterns may be found in other Neotropical migrants with similar breeding distributions.

The banding map identifies the first North American example of a possible migratory divide coincident with a contact zone between mtDNA haplotypes and morphologically distinguishable subspecies. Studies of the migratory divides in European blackcaps (*Sylvia atricapilla*) provide strong evidence for the genetic basis of migratory behaviour (Berthold & Querner 1981; Berthold

1988). Pedigree studies of blackcaps have shown that hybrid offspring of parents from either side of a migratory divide exhibit intermediate migratory behaviour (Helbig 1991). To our knowledge, in the only other detailed study of a migratory divide, Bensch *et al.* (1999) demonstrate coincidental character clines in morphology, plumage coloration and migratory direction of the European willow warbler (*Phylloscopus trochilus*), without divergence in mtDNA and microsatellite loci. In this context, the Swainson's thrush contact zone in British Columbia holds potential for understanding the role of migratory divides in divergence and potentially speciation.

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