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DARREN E. IRWIN
AND JESSICA H. IRWIN

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Siberian Migratory Divides

The Role of Seasonal Migration in Speciation

MIGRATORY BEHAVIOR MAY PLAY an important role in the evolution of new species. Differences in migratory behavior could promote reproductive isolation among related groups in several ways. First, they can lead directly to premating isolation, for example, if two groups have different arrival times on the breeding grounds. Second, postmating isolation may occur if hybrids have intermediate but suboptimal migratory behavior, for instance, if two groups migrate by different routes around a geographic barrier and hybrids migrate across the barrier. Third, selection against hybrids can promote premating isolating mechanisms. We did a survey of migratory routes of all passerine species breeding in Siberia, and the results suggest that the Tibetan Plateau is a major barrier to migration. Of 97 long-distance migrants in Siberia, most (85%) use only one route around Tibet (42 through Kazakhstan, 40 through eastern China). Of the 15 species that use both routes, seven of these are known to have migratory divides between western and eastern subspecies. In at least one group, the Greenish Warblers (*Phylloscopus trochiloides*), the western and eastern Siberian forms are reproductively isolated in Siberia, although there is a chain of populations connecting them around the Tibetan Plateau to the south. In four additional cases, migratory divides occur between western and eastern sister species. These patterns suggest that two very different migratory programs can seldom coexist in a single gene pool, and that migration may play a strong role in speciation in Siberia. The need to migrate can also hinder range expansion, thus preventing colonization of new regions and limiting opportunities for speciation.

INTRODUCTION

It is well known that migratory behavior can have strong influences on the evolution of ecological, behavioral, and physiological characteristics of individual species (Alerstam 1990; Dingle 1996). Less studied is the possibility that migratory behavior may influence the process by which one species splits into two or more species. In this chapter we explore how the process of speciation might be promoted or hindered by migratory behavior in different biogeographical situations. By influencing when and how new species originate, migratory behavior might influence the numbers, distributions, and relationships of birds around the world.

To explore the possible role that migration has in speciation in passerine birds, we focus on biogeographic patterns in central Siberia. By considering migratory routes one can gain much insight regarding biogeographic history, distributions of species and subspecies, and the possible role of divergent migratory behaviors in causing reproductive isolation. We conclude that the Tibetan Plateau, a high-altitude desert in central Asia, is a major barrier to migration and has had a major influence in shaping biogeographic patterns in northern Asia. Central Siberia contains many examples of "migratory divides" in which divergent but geographically adjacent groups of a single species use strongly differing routes to migrate to their winter grounds. Migration could be playing a significant role in generating reproductive isolation and hence promoting speciation in these cases.

The arguments made in this chapter rely on five basic assumptions, each of which has empirical and theoretical support. First, the routes used by migratory birds are genetically influenced. Second, birds are under selection to use optimal migration routes (which are influenced by various factors such as distance, opportunities for refueling, predation risk, winds, and elevation changes), and some of these routes include significant detours around regions that are difficult to migrate across. Third, when two groups with different migratory behaviors hybridize, the hybrids might instinctively choose a migratory route that is intermediate to the two parental routes. Fourth, hybrids may be selected against if their intermediate migratory behavior leads them across unsuitable regions. Fifth, selection against hybrids (i.e., post-zygotic isolation) can cause selection for behaviors that prevent the two parental groups from interbreeding (i.e., premating isolation). We review the evidence for these assumptions below.

Genetics of Migration

Successful migration is usually the result of a complex and finely tuned set of morphological, physiological, cognitive, and behavioral traits (Dingle 1991; Berthold 1999b). Although learning has a role, many of these migratory traits have been shown to have a genetic basis, and it appears that most are influenced by multiple genes (Berthold 1999b). Hybrids between two groups that differ in migratory traits often have intermediate characteristics. For example, instinctive migratory direction has been studied extensively in Blackcaps (*Sylvia atricapilla* [Helbig 1991, 1996; Berthold et al. 1992]). In central Europe during the autumn, Blackcaps from western populations orient toward the southwest, whereas those from eastern populations orient toward the southeast. Hybrids that were raised in the lab tended to orient directly south, in an intermediate direction with respect to the parental forms (Helbig 1991). Such intermediacy of hybrids has been shown with respect to the time of the onset of migration, the length of migration, rate of fat deposition, and wing shape (Berthold and Querner 1981; Berthold 1999a). The many traits involved in migration appear to be fine-tuned for each species, the result of many genes that have evolved together.

Ecological Barriers and Migratory Divides

One of the difficulties that migratory birds often face is that breeding and wintering ranges are usually separated by regions of unsuitable habitat (Alerstam 1990). The Gulf of Mexico and the deserts of northern Mexico and the southwestern United States separate many breeding ranges in North America from wintering ranges in Central and South America. European breeding ranges are separated from winter ranges in central Africa by the Mediterranean Sea and the Sahara Desert. And north Asian breeding ranges are separated from wintering areas in southern Asia by a variety of deserts and mountains in central Asia. These ecological barriers offer little opportunity for feeding or resting, presenting a major challenge because migrating birds need stopover sites to refuel (Moore et al., Chap. 20, this volume). In fact, the great majority of time during migration is spent refueling rather than flying (Hedenström and Alerstam 1997). In response to the challenge presented by ecologically poor areas between breeding and wintering areas, migratory birds have developed two basic strategies: they either can build up huge fat reserves for nonstop flights directly across the barrier or they can make a series of shorter flights around the barrier using the best available detour. Of course, birds may also use a combination of these approaches.

Some species that fly around the barriers have more than one optimal route, and this can contribute to the formation of migratory divides, in which two adjacent breeding populations take different routes to their wintering grounds. For example, several European species that migrate to sub-Saharan Africa, such as Blackcaps and Willow Warblers (*Phylloscopus trochilus*), have a migratory divide between two forms, one of which migrates across the western side of the Mediterranean and Sahara, the other of which migrates across the eastern side of these areas (fig. 3.1A) (Hedenström and Pettersson 1987; Helbig 1991; Bensch et al. 1999). By using these routes, the birds avoid the central Mediterranean and Sahara, where those areas are widest. In northwestern North America, Swainson's Thrushes (*Catharus ustulatus*) have a migratory divide between a form that migrates down the west coast to Central America and another form that migrates to eastern North America before flying

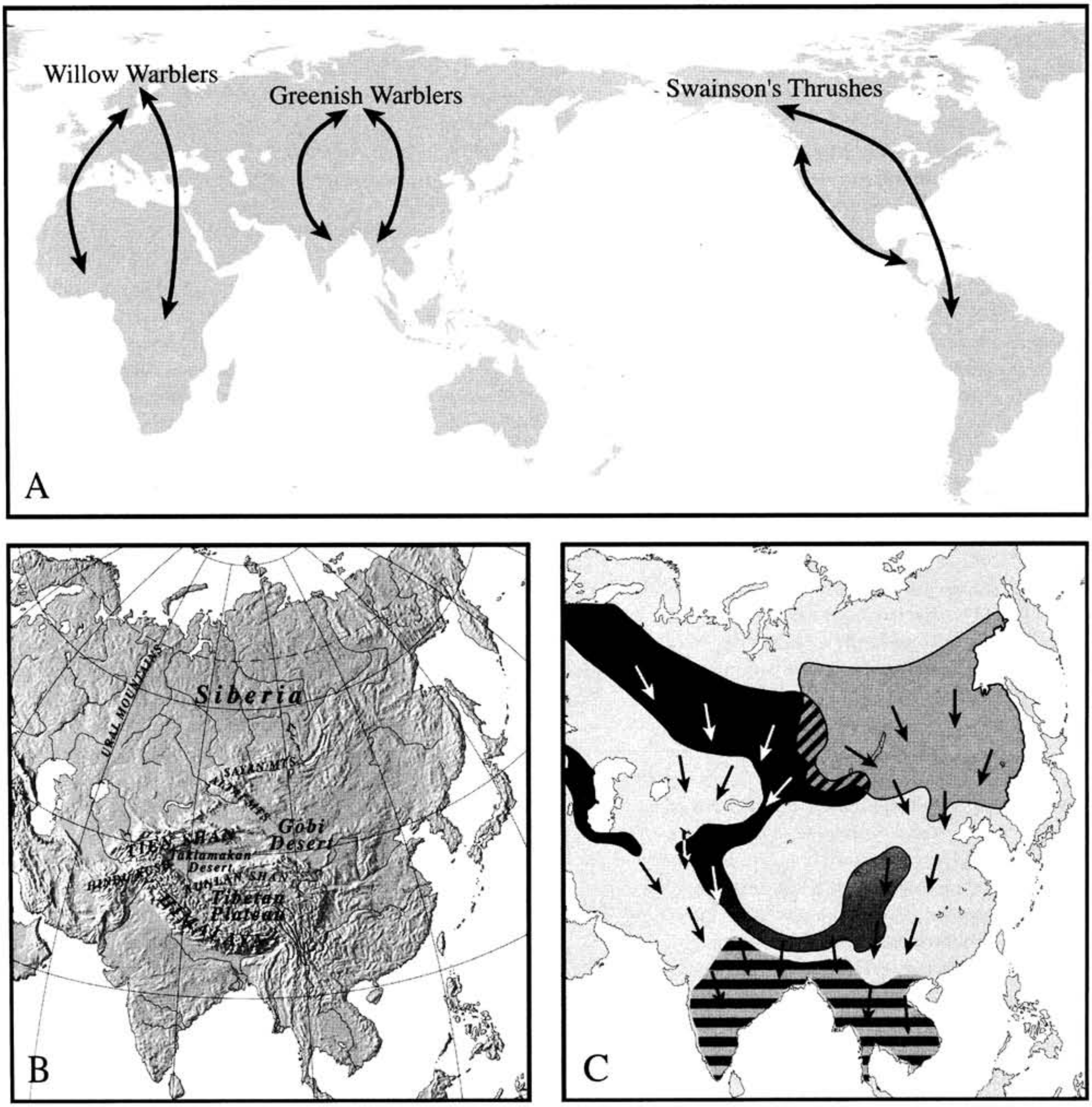

Fig. 3.1. Maps of the world and Asia, showing (A) migratory routes of three species with migratory divides, (B) geographical features of Asia, and (C) breeding range, migratory routes, and wintering range (horizontal gray stripes) of Greenish Warblers (*Phylloscopus trochiloides*). Greenish Warblers breed in forests that occur across middle and southern Siberia as well as in a ring of mountains encircling a region of deserts (the Tibetan Plateau and the Taklamakan and Gobi deserts). Two distinct forms of Greenish Warbler meet in central Siberia (*P. t. viridanus* in the west, *P. t. plumbeitarsus* in the east) but migrate along different western and eastern routes to their wintering ranges.

south across the Caribbean into South America (fig. 3.1A) (Ruegg and Smith 2002). It is possible that birds use these routes in part to avoid deserts and mountains in the southwestern United States and northern Mexico.

Another migratory divide is located in Asia, where two forms of Greenish Warblers (*Phylloscopus trochiloides*) coexist in the forests of central Siberia but migrate by different routes to their wintering areas (fig. 3.1A). The west Siberian form, *P. t. viridanus,* migrates through west-central Asia to winter in forests within India, whereas the east Siberian form, *P. t. plumbeitarsus,* migrates through eastern China to forests in Southeast Asia (fig. 3.1B,C) (Ticehurst 1938). By taking these routes, the birds travel either to the west or the east of a large region of deserts that includes the Tibetan Plateau as well as the low-altitude deserts of the Gobi and the Taklamakan. This region also contains some of the tallest mountain ranges in the world, including the Himalayas, the Tian Shan, and the Kunlun Shan (fig. 3.1B). It is likely that forest-dependent insectivorous birds such as warblers would have an extremely difficult time finding food in this area, especially during early spring and late fall. Populations of Greenish Warblers also occur to the west, south, and east of the Tibetan plateau, and all of these populations migrate roughly southward to their wintering areas (fig. 3.1C).

To fully understand patterns of migration, we must consider historical factors as well as current ecological and geographical ones. The migratory divides mentioned above appear to be, in part, the result of secondary contact of two expanding range fronts. The migratory divide in the Swainson's Thrushes coincides with sudden changes in genetics and morphology, suggesting secondary contact between forms that were isolated in western and eastern refugia during the last glacial maximum (Ruegg and Smith 2002). Populations of Swainson's Thrushes in western Canada and Alaska, on the northeastern side of the migratory divide, are thought to have originated from range expansion from a glacial refugium in southeastern North America. Their migration route seems to retrace this route of expansion, with birds migrating to eastern North America before turning south toward South America (Ruegg and Smith 2002). Likewise, the two forms of Greenish Warblers in Siberia resulted from two divergent groups expanding into the same area from populations to the west and east of Tibet (Irwin et al. 2001b). The different migratory routes reflect these ancestral origins.

Speciation and Migration

Speciation can be defined as the evolution of reproductive isolation between two groups (Mayr 1942; Price 1998). Differences in migratory behavior could promote reproductive isolation in three basic ways. First, migratory differences could directly lead to premating isolation, preventing mating between individuals from the two groups. Such premating isolation could result from different arrival times on the breeding grounds or from pairing on the wintering grounds or during migration. Second, migratory differences might cause postmating isolation due to selection against hybrids because of their inferior migratory traits. Third, selection against hybrids may lead to selection for premating isolation, in a process known as reinforcement (Dobzhansky 1940; Howard 1993; Liou and Price 1994). In this way differences in migratory behavior might have caused the evolution of greater differences in traits involved in mate choice, such as song.

Migratory divides could be maintained by each of these processes or a combination of them. Helbig (1991) argued that the migratory divide in Blackcaps is maintained by assortative mating (premating isolation), which could result from different arrival times on the breeding grounds, or by selection against hybrids (postmating isolation), which could result from inferior migratory behavior in hybrids, as suggested by orientation experiments in which hybrids oriented in an intermediate direction toward the south. Helbig (1991) suggested that hybrids in the wild would also orient southward, taking them directly across the Alps, the Mediterranean Sea, and the Sahara Desert where they are widest. In their analysis of variation in Willow Warblers, Bensch et al. (1999) concluded that the migratory divide in central Sweden must be maintained by assortative mating and/or selection against hybrids, perhaps due to intermediate instinctive migratory direction; the zone of contact between the two groups is too narrow to be explained by secondary contact alone.

The few migratory divides that have been studied in detail, most notably those of the Blackcaps and Willow Warblers, illustrate the possible importance of migratory behavior in maintaining or promoting reproductive isolation and speciation. But how often migration plays a role in speciation is not yet known. Are the Blackcaps, Willow Warblers, Swainson's Thrushes, and Greenish Warblers unusual cases? Or could migration play a major role in speciation in passerines, structuring the biogeographical patterns in an entire region? To address this question in a systematic way we examined migration routes in Asia, a region that has received relatively little attention from migration researchers compared with Europe and North America. Our research on Greenish Warblers (Irwin 2000; Irwin et al. 2001b; Irwin et al. 2001c) led us to postulate that many species that breed in Siberia and spend their winters in southern Asia might avoid flying across the Tibetan Plateau and the deserts to the north. If so, individual migrants must either migrate to the west or the east of Tibet. Because these routes differ so dramatically, and because migratory behavior is probably genetically based, we postulated that the use of both routes would rarely occur in a single gene pool (i.e., in a single species). If so, species that breed in Siberia should migrate only west of Tibet or only east of Tibet. Another possibility is that, as in the Greenish Warblers, a species has two or more distinct Siberian forms (i.e., subspecies) with a migratory divide between them. Such migratory divides indicate possible situations in which migratory behavior is promoting speciation.

MATERIALS AND METHODS

We surveyed the literature to uncover information on migratory routes of all long-distance passerine migrants breeding in north-central Eurasia. We focused on passerines because their juveniles usually migrate separately from adults, suggesting that genetic programs for migratory behavior play a dominant role; many non-passerines migrate in family groups, in which the offspring learn migratory routes from older individuals (Sutherland 1998). Because we were primarily interested in the role that the Tibetan Plateau and nearby deserts may have had in structuring patterns of migration and speciation, we limited our survey to those species that breed somewhere in western and central Siberia, an area that is roughly north of the Tibetan Plateau and Gobi Desert. We defined this area as being north of Russia's southern border (49–56° N latitude), east of the Ural Mountains (60° E longitude), west of 120° E longitude,

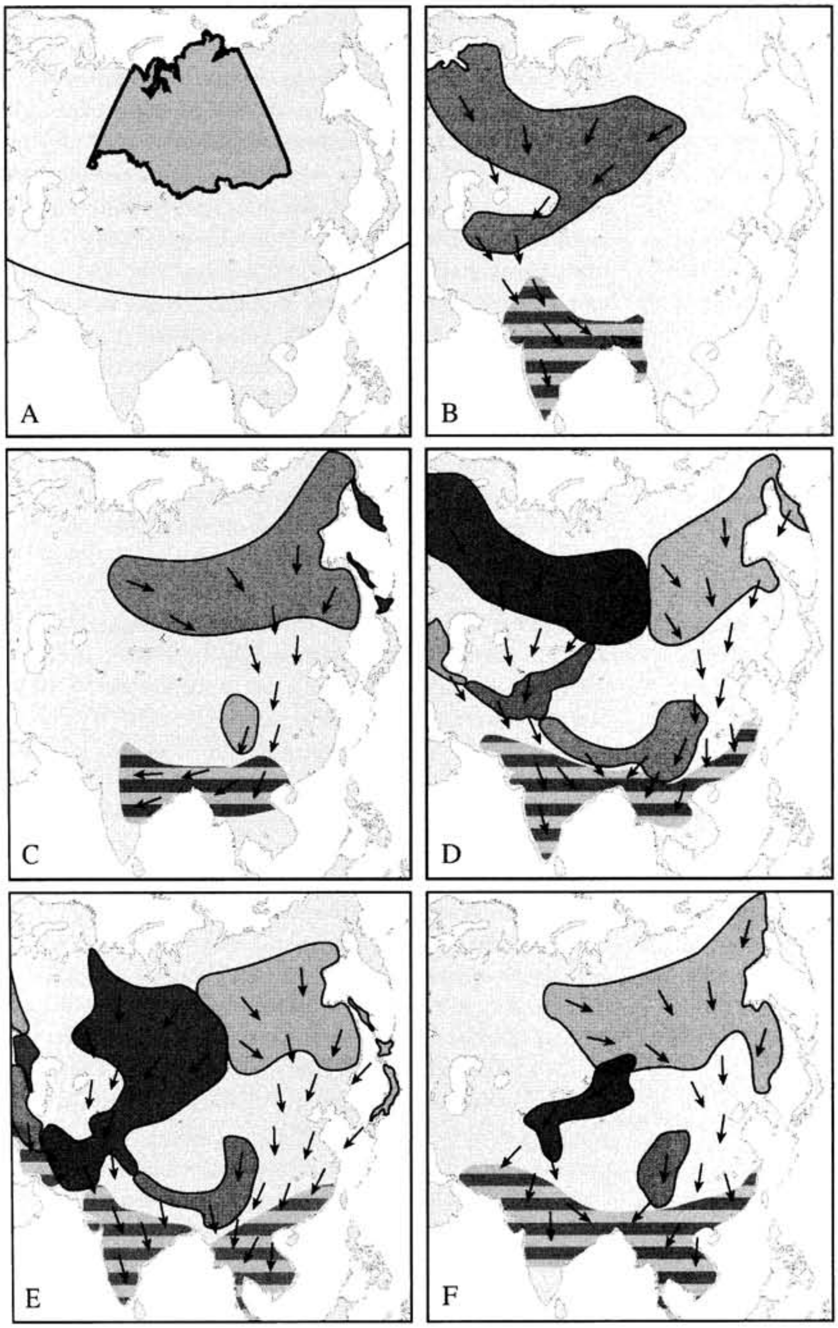

Fig. 3.2. Maps of Asia showing (A) the area in which species must breed to be included in our survey (western and central Siberia) and the 30° N latitude south of which a species must winter to be classified as a long-distance migrant; and (B–F) ranges and migratory routes for five groups of taxa. Breeding ranges are shown by gray regions, and wintering areas are shown by horizontal stripes. Different subspecies or species are indicated by different shades of gray. (B) Blyth's Reed Warbler; (C) Siberian Rubythroat; (D) Common Rosefinch; (E) Siberian Stonechat; (F) Hume's Leaf Warbler and Yellow-browed Warbler.

and south of the Arctic Ocean (fig. 3.2A). We chose the eastern boundary to deliberately exclude many species that breed in the Russian Far East but not farther west. We also excluded several central Asian species with ranges that extend only slightly into steppe or mountain habitats of extreme southern Russia (e.g., Red-headed Bunting, *Emberiza bruniceps*).

To determine which species of passerines breed in this area, we consulted Dementev and Gladkov (1954), Flint et al. (1984), Sibley and Monroe (1990), and Rogacheva (1992). We then used those references and the following to compile information regarding wintering areas and migration routes: McClure (1974) provided broad information on migration in Asia; MacKinnon and Phillips (2000) described ranges in China, with some information on migration; Ali and Ripley (1987–1999), Grimmett et al. (1999), and Kazmierczak and van Perlo (2000) described ranges and migration routes in India and Pakistan; Robson (2000) detailed birds wintering in Southeast Asia; Keith et al. (1992) provided information on birds that winter in Africa; and Cramp (1988–1994) provided useful migration data on species that extend into the western Palearctic. We also consulted tables in two books (Dolnick 1985, 1987) that summarize the species identity of 12,994 passerine birds that were caught during spring and fall migration at a wide variety of research sites in central Asia (i.e., Kazakhstan, Kyrgyzstan, Uzbekistan, Tajikistan, and Turkmenistan). For more information on specific groups of passerines, we consulted specialty books on swallows and martins (Turner and Rose 1989), pipits and wagtails (Alström and Mild 2003), stonechats (Urquhart 2002), warblers (Baker 1997; Shirihai et al. 2001), thrushes (Clement and Hathway 2000), finches and sparrows (Clement et al. 1993), buntings (Byers et al. 1995), and crows and jays (Madge and Burn 1994). Using these sources, we were able to gain a good understanding of migration routes and wintering ranges of the large majority of species breeding in western and central Siberia.

The Tibetan Plateau would be expected to play a role in shaping migration routes primarily in those species that actually migrate far enough south to potentially encounter it during migration. We therefore focused our survey on long-distance migrants, which we defined as those with a winter range that is primarily south of 30° N latitude (fig. 3.2A). This is approximately the latitude of Lhasa, in south-central Tibet. Thus our list of long-distance migrants includes those wintering in India, Southeast Asia, and Africa, but not those that winter primarily in central Asia or northern China. We examined all available range maps and used the consensus to determine whether the majority of the wintering range of each species was south of 30° N latitude. We then recorded whether each species migrated to the west of Tibet, to the east of Tibet, or over Tibet. Whenever a species consisted of multiple subspecies, we recorded information specific to each subspecies, when available. Our goal was to determine whether different subspecies had different migratory behaviors. Some of the species or subspecies are given different names and taxonomic treatments by different authors; we generally followed Beaman's (1994) list of Palearctic birds or a more recent authority.

RESULTS

We counted 171 species of passerine birds breeding in western and central Siberia. Of these, 97 are long-distance migrants, with their wintering range primarily south of 30° N latitude (fig. 3.2A). Roughly one-third of these winter in Africa, one-third in India, and one-third in Southeast Asia, although some species winter in more than one of those regions.

Most of the long-distance migrants appear to avoid migrating across the Tibetan Plateau and the deserts of northwest China. Rather, all of the species have been found in large numbers during migration in at least one of two major flyways: on the west through the central Asian countries of Kazakhstan, Uzbekistan, Kyrgyzstan, Tajikistan, and Turkmenistan (Dolnik 1990) and on the east through eastern China (McClure 1974; MacKinnon and Phillips 2000).

Most species use only one of these migration routes. Of the 97 species of long-distance migrants (see the Appendix to this chapter), 42 apparently migrate only to the west of Tibet and 40 migrate only to the east of Tibet. Of the western migrants, about half spend the winter in India. An example is the Blyth's Reed Warbler (*Acrocephalus dumetorum*) (fig. 3.2B), which apparently migrates only west of Tibet even though its breeding range extends to eastern Siberia and its wintering range extends east to Bangladesh and Myanmar. Many of the western migrants winter in Africa, for example, the Willow Warbler (*Phylloscopus trochilus acredula* and *P. t. yakutensis*), which has a breeding range extending to far-eastern Siberia. The eastern migrants, on the other hand, winter primarily in southern China and Southeast Asia, although some have wintering ranges that extend west into India. For example, the Siberian Rubythroat (*Luscinia calliope*) (fig. 3.2C) breeds as far west as the Ural Mountains and winters as far west as central India, but does not migrate through central Asia in large numbers, instead flying during autumn migration to east Siberia, turning south across eastern China, and finally turning west.

This leaves 15 species that use both the western and the eastern migratory routes (table 3.1). However, seven of these species have a migratory divide between recognized subspecies. In most of these cases, two subspecies breed in adjacent western and eastern ranges in Siberia, with the western form migrating along the western route to India and the eastern form migrating along the eastern route to Southeast Asia. Examples include the Greenish Warbler (fig. 3.1C), the Common Rosefinch (*Carpodacus erythrinus*) (fig. 3.2D), and the Siberian Stonechat (*Saxicola maura*) (fig. 3.2E). Such migratory divides between subspecies are found in a diverse group of passerine species (table 3.1). Migratory divides also sometimes occur between taxa that are classified as separate species; there are at least four cases in which two closely related species migrate along different sides of Tibet and have breeding ranges that meet in a narrow region of Siberia (table 3.1). One example consists of the Hume's Leaf Warbler (*Phylloscopus humei humei*), which migrates through central Asia and winters in India, and the Yellow-browed Warbler (*Phylloscopus inornatus*), which migrates through eastern China and winters in Southeast Asia (fig. 3.2F). Because of their morphological similarity, only recently have these two taxa been recognized as separate species (Svensson 1987; Formozov and Marova 1991; Irwin et al. 2001a).

Out of the 97 long-distance migrants breeding in western and central Siberia, eight have at least one subspecies that apparently uses both the western and eastern migratory routes (table 3.1). Six of these taxa are pipits and wagtails, which are known to migrate in mixed subspecies flocks, suggesting an important role for cultural, rather than genetic, transmission of migratory behavior (Rogacheva 1992). Wagtails also commonly inhabit open areas, suggesting that Tibet and nearby areas may not serve as a strong migratory barrier in these taxa. Two of the taxa, the Red-throated Pipit (*Anthus cervinus*) and the Citrine Wagtail (*Motacilla citreola*), have been described by some authors as having a migratory divide between two subspecies, but later treatments have classified them as monotypic across Siberia, where there is clinal west-to-east variation (see footnotes in table 3.1). One of the remaining species, the Dark-

Table 3.1 Long-distance migrating passerine taxa (species or pairs of sister species) that breed in central Siberia and migrate along both sides of Tibet to their wintering areas

Taxa	West of Tibet	East of Tibet
Sand Martin		
Riparia riparia riparia	X	
R. r. ijimae		X
Barn Swallow		
Hirundo rustica rustica	X	
H. r. tytleri		X
Common House Martin		
Delichon urbica urbica	X	
D. u. lagopoda		X
Red-throated Pipit[1]		
Anthus cervinus	X	X
Tree Pipit / Olive-backed Pipit[2]		
Anthus trivialis trivialis	X	
A. hodgsoni yunnanensis		X
Water Pipit		
Anthus spinoletta blakistoni	X	X
Yellow Wagtail		
Motacilla flava thunbergi	X	X
M. f. beema	X	
M. f. tschutschensis		X
Citrine Wagtail[3]		
Motacilla citreola citreola	X	X
Grey Wagtail		
Motacilla cinerea cinerea	X	X
White Wagtail		
Motacilla alba alba	X	
M. a. personata	X	
M. a. baicalensis	X	X
M. a. ocularis		X
Bluethroat		
Luscinia svecica svecica	X	X
L. s. pallidogularis	X	
Siberian Stonechat		
Saxicola maura maura	X	
S. m. stejnegeri		X
Dark-throated Thrush		
Turdus ruficollis ruficollis	X	X
T. r. atrogularis	X	X
Great Reed Warbler / Oriental Great Reed Warbler		
Acrocephalus arundinaceus zarudnyi	X	
A. orientalis		X
Hume's Leaf Warbler / Yellow-browed Warbler		
Phylloscopus humei	X	
P. inornatus		X
Greenish Warbler		
Phylloscopus trochiloides viridanus	X	
P. t. plumbeitarsus		X
Red-breasted Flycatcher		
Ficedula parva parva	X	
F. p. albicilla	Few	X
Red-backed Shrike / Brown Shrike		
Lanius collario	X	
L. cristatus		X
Common Rosefinch		
Carpodacus erythrinus erythrinus	X	
C. e. grebnitzkii		X

Note: In each case, we list subspecies or species that breed in central Siberia and indicate whether they migrate on the western or eastern side of Tibet. Migratory divides between subspecies or sister species occur in 11 cases.

[1] Although recent authors have treated the Red-throated Pipit as monotypic (Cramp 1988-1994; Alström and Mild 2003), Dementev and Gladkov (1954) described two subspecies, *A. c. rufogularis* in the west and *A. c. cervinus* in the east, with a migratory divide between them.

[2] These species overlap substantially over a broad region of Siberia, yet they take different routes to their wintering areas.

[3] Most authors (e.g., Dementev and Gladkov 1954; Cramp 1988–1994) have treated Citrine Wagtails in western Siberia as two subspecies, *M. c. werae* in the west and *A. c. citreola* in the east, with a migratory divide between them. Here we follow the latest authority, Alström and Mild (2003), in treating the Siberian populations as a single subspecies.

throated Thrush (*Turdus ruficollis*), is apparently not an obligate migrant; in most years birds winter in southern Asia, but in years with a good berry crop many birds spend the winter in Siberia (Cramp 1988:vol. 5). The last remaining case, the Bluethroat (*Luscinia svecica*), is an obligate migrant, but little is known about its migratory behaviors in Siberia. It is possible in all of these cases that there are narrow migratory divides and that the morphology across these divides is so similar that different subspecies have not been recognized.

DISCUSSION

One caveat regarding these results is that relatively little ornithological work has been done in Tibet and northwest China, so we cannot presently rule out the possibility that some species do migrate across those regions. In fact, a few passerine species breed on the Tibetan Plateau and necessarily migrate across it, but most of these are alpine, desert, or steppe specialists that do not have ranges that extend far into Siberia. For example, Black Redstarts (*Phoenicurus ochruros*), which breed in Tibet and the Altai Mountains of southern Siberia, migrate both across Tibet and around it on the west side (MacKinnon and Phillips 2000). However, several lines of evidence suggest that the great majority of passerine species breeding in Siberia avoid Tibet. First, studies on the west side (Dolnik 1990) have documented that many birds take a circuitous route through that region; during spring migration, birds tend to fly toward the northwest first and then turn to the northeast, staying in the lowland deserts rather than crossing the snow-covered mountain ranges. Second, most taxa have been observed migrating in large numbers to either the west or east of Tibet, suggesting that crossing Tibet is not the predominant strategy for any of them. Third, Dolnick (1990), who summarized decades of research on birds migrating across central Asia (i.e., the western route around Tibet), concluded that most species stop to refuel often while crossing that region; birds usually leave stopover sites with only a small amount of fat, enough to fly for less than 4.5 h. Such a strategy would probably be deadly if used during migration across Tibet or the Gobi Desert, which offer little opportunity for feeding compared with the milder deserts along the western fly route.

Migratory behavior is closely associated with subspecific variation in a variety of passerine species. This pattern is consistent with a role for different migratory behaviors in preventing gene flow between subspecies and promoting speciation. However, differences between western and eastern subspecies in Siberia, both in migration routes and in other traits, are also the result of biogeographic history. During Pleistocene glaciations, most of Siberia was unsuitable for many of the species that are there now, especially for the species that inhabit forests (Grichuk 1984; Ukraintseva 1993; Adams and Faure 1997; Price et al. 1997). According to Adams and Faure (1997), who reconstructed vegetation cover from many types of evidence, just after the last glacial maximum at about 17,000 to 15,000 years ago (^{14}C years) "conditions all across northern Eurasia appear to have been dry and treeless, dominated by polar desert or semi-desertic steppe-tundra." Glaciers were covering northwest Siberia, and all of central and eastern Siberia consisted of polar desert, steppe-tundra, or extreme desert. Forests were confined to central China, Japan, the Himalayas, southern India, and Southeast Asia. It is also likely that some of the mountains of central Asia, such as the Tian Shan range, harbored forests (Grichuk 1984). Following a warming and moistening of the climate at about 13,000 ^{14}C years ago, open woodlands of birch and boreal conifers gradually expanded into Siberia, but strong cooling between 11,200 and 10,200 ^{14}C years ago then caused the trees to recede. Tree cover again expanded into Siberia following a rapid warming of the climate about 10,000 ^{14}C years ago, and by about 8,000 ^{14}C years ago most areas of northern Eurasia were even more forested than they would be today under natural conditions (Ukraintseva 1993; Adams and Faure 1997). Although the amount of forest in Siberia has fluctuated some since then, it has never fully receded (Khotinsky 1984). Given this inferred history, contact zones between divergent forest-dependent taxa in central Siberia must have formed within the last 10,000 years or so.

During the last glaciation, extreme desert conditions prevailed over the Tibetan, Taklamakan, and Gobi desert region (Grichuk 1984; Ukraintseva 1993; Adams and Faure 1997), forming a large ecological barrier in the center of Asia. When forest moved into Siberia, many species may have expanded into Siberia along two pathways on either side of this ecological barrier. For example, in the case of the Greenish Warblers, molecular evidence has supported the hypothesis (Ticehurst 1938) that an ancestral species in southern Asia expanded northward along two pathways on either side of Tibet, resulting in distinct forms with differing migration routes when the two expanding fronts met in central Siberia (Irwin et al. 2001b). The many subspecies and species boundaries in central Siberia suggest that many taxa have similar histories of expansion into Siberia along two pathways. Ancestral migration routes appear to have been conserved during these expansions, such that species or subspecies that expanded from central Asia into Siberia still migrate through central Asia to India, whereas those that expanded from eastern China into Siberia still migrate through eastern China to Southeast Asia.

Although the different migratory behaviors are partly a result of history, the future of a species may be influenced by migratory behavior. When two divergent forms meet, at least two outcomes are possible. First, they may interbreed freely, exchanging genes and blending the differences between the forms. Second, they may have some amount of reproductive isolation, perhaps allowing or causing them to diverge further into separate species. In central Siberia, migratory behavior may make the second scenario much more likely to occur. As discussed in the Introduction, migratory differences can cause premating or postmating reproductive isolation, and postmating isolation due to migratory behavior might lead to reinforcement (i.e., selection for premating isolation).

Some of the pairs of subspecies that have a migratory divide between them are sometimes treated as separate species. Four other migratory divides (see Results) consist of taxa that are generally considered separate species. In all of these cases, speciation has been completed or has proceeded almost to completion. These may be cases in which divergent forms met in Siberia, and different migratory behavior, along with differences in other traits, promoted the development of stronger reproductive isolation. For example, the two Siberian forms of the Greenish Warbler appear to be separate species, differing distinctly in molecular markers, songs, song recognition, plumage patterns, and migration routes. These traits change gradually through the chain of populations that encircle the Tibetan Plateau to the south (Ticehurst 1938; Irwin 2000; Irwin et al. 2001b), making the Greenish Warblers an example of a "ring species," in which a ring of populations has only a single species boundary (Mayr 1942; Irwin et al. 2001c). Geographical variation within a ring species can illustrate the evolutionary changes that can occur during divergence of two species from their common ancestor. Irwin (2000) and Irwin et al. (2001b) emphasized the likely role of divergence in male song in causing premating reproductive isolation between the Siberian forms. But speciation is most likely to occur when both premating and postmating reproductive isolation are present, and migratory behavior could have caused both. If *viridanus* and *plumbeitarsus* did ever hybridize, the hybrids probably had inferior migratory behavior. By causing selection against hybrids in this way, migratory behavior may have reduced gene flow between *viridanus* and *plumbeitarsus*, promoting speciation (Irwin et al. 2001c). The overall patterns of reproductive isolation in the Greenish Warblers are consistent with the hypothesized role of migratory divides in speciation: in central Siberia, on the northern side of the migratory barrier (where there is a migratory divide), there is a species boundary, whereas in the Himalayas, along the southern side of the migratory barrier (i.e., presumably where migratory divides are not an important factor), there are no known species boundaries (Irwin et al. 2001b, 2001c).

Two other species in Asia have distributions and migratory patterns that are strikingly similar to those of the Greenish Warblers. These are the Common Rosefinch (fig. 3.2D) and Siberian Stonechat (fig. 3.2E). Both consist of a ring of populations encircling the Tibetan Plateau, and both have a migratory divide between distinct subspecies in Siberia. Perhaps the biogeographic histories of these species are similar to that of the Greenish Warblers, and perhaps they are ring species as well.

Although we have emphasized how migratory behavior might directly cause reproductive isolation, migration might also promote speciation indirectly by promoting the divergence of sexually selected traits. Researchers have proposed that migrants experience more intersexual selection on song than nonmigrants (Catchpole 1980, 1982; Morton 1996) because females must choose mates quickly after arriving on the breeding grounds, and song is a signal that can be assessed quickly. In resident species, songs may be more important in male-male territorial interactions. This hypothesis was supported by Read and Weary (1992), who conducted a broad survey of passerine species and found that migrants on average had larger song repertoires, something that females usually prefer (Catchpole and Slater 1995; Searcy and Yasukawa 1996). Researchers have also proposed that intersexual selection can lead to rapid divergence of mating signals (West-Eberhard 1983; Iwasa and Pomiankowski 1995; Price 1998). By combining these ideas, we postulate that increased migratory behavior may lead to increased divergence in songs and song preferences between geographically distant populations, thereby promoting the evolution of reproductive isolation and speciation. The patterns of variation in the Greenish Warblers are consistent with this hypothesis: songs in the north, where birds migrate farther and spend less time on the breeding grounds, are much longer and complex than those in the south (Irwin 2000). Apparently, complex songs have evolved from simple ones during both northward expansions, but the form of complexity differs between the two Siberian forms, probably contributing to premating reproductive isolation between them (Irwin et al. 2001b, 2001c).

In addition to revealing a number of migratory divides in Siberia, our survey revealed that migratory routes in Siberia appear to be highly conserved. Few species migrate along both western and eastern sides of Tibet without having a migratory divide between subspecies, and some populations of many species seem to have suboptimal migratory routes. Clearly, both the western route through central Asia and the eastern route through eastern China are suitable routes for a wide variety of species. Why, then, do some species, such as the Blyth's Reed Warbler (fig. 3.2B), only use the western route, although the eastern one would be shorter for birds breeding in the eastern side of the range? Likewise, why do some species, such as the Siberian Rubythroat (fig. 3.2C), use only the eastern route, although the western one would be shorter for some birds? We conclude from these patterns that large and sudden changes in migration routes seldom occur during evolution and that two strongly divergent migratory routes are seldom used by a single subspecies.

The concept of fitness landscapes (Fear and Price 1998) is a useful aid in understanding both the formation of migratory divides and the conservation of ancestral migratory routes. A fitness landscape illustrates graphically how fitness depends on the traits of an individual (note that we are referring to individual fitness landscapes, not "adaptive surfaces," which show the mean fitness of a population). In fig. 3.3, we show how fitness landscapes might change during northward expansion of a species along two pathways around a barrier such as Tibet. Each graph shows how the fitness of a bird breeding in a certain location depends on two traits, in this case two instinctive migratory directions. In this hypothetical example, the birds migrate according to a simple rule; they have an initial instinctive migratory direction, and after some time change to a second instinctive direction. Orientation experiments have demonstrated that Garden Warblers (*Sylvia borin*) migrate in this way, enabling them to avoid crossing the widest parts of the Mediterranean and Sahara (Gwinner and Wiltschko 1978). In our example (fig. 3.3), birds in the south have optimal behavior if they migrate directly south to their wintering area. As the species expands north, the optimal behavior gradually changes, such that birds on the northwest side of Tibet should first migrate southwest and then turn southeast, and birds on the northeast side of Tibet should first migrate southeast and then turn southwest. When the two populations meet directly north of Tibet, there are two optimal migratory behaviors (i.e., two peaks on the fitness landscape), but hybrids with intermediate migratory behaviors are at a fitness disadvantage (i.e., a valley on the fitness landscape). Speciation can be thought of as the evolution of a species from a single fitness peak onto two fitness peaks separated by a valley. Gradual change in migratory behavior during expansion around a barrier provides a way for a species to evolve onto two peaks gradually without ever crossing a fitness valley. Although we have illustrated this concept by using traits for migratory direction, many other traits (e.g., migratory distance, refueling frequency, physiology, molt) might evolve along similar fitness landscapes and thus promote speciation.

The fitness landscapes in fig. 3.3 also illustrate how suboptimal migratory routes may be conserved. A species that expands into Siberia from only a single refugium, on either the west or east side of Tibet, might be "trapped" on a single adaptive peak in Siberia. Another, higher fitness peak may exist somewhere in genotypic and phenotypic space, but if the two peaks are far enough apart with a deep enough valley between them, the necessary mutations may not occur in a single individual. Furthermore, even if one individ-

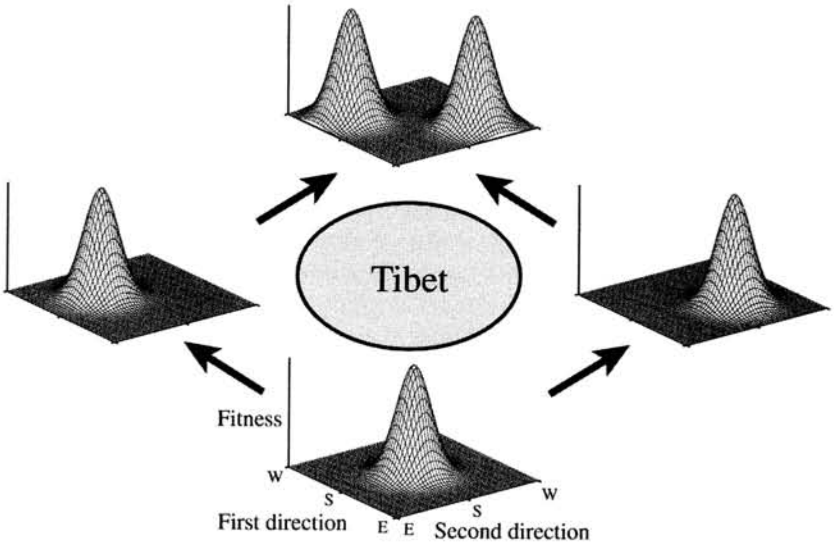

Fig. 3.3. A depiction of hypothetical fitness landscapes at four locations around a barrier to migration such as Tibet. Each graph shows how fitness depends on two traits, in this case a first and second instinctive migratory direction. In the south, there is a single optimal behavior (i.e., a single fitness peak), but these diverge to the north, on the west and east sides of the barrier. On the north side of the barrier, there are two optimal migratory behaviors (i.e., two fitness peaks), but intermediate behaviors are selected against (i.e., a valley on the fitness surface). Starting on the southern side of the barrier, a species could expand northward along two pathways, diverging and eventually ending up on different fitness peaks (i.e., speciating), without ever crossing a fitness valley.

ual did somehow "jump" to the other peak (i.e., the other migratory behavior), it might then breed with an individual on the first peak, perhaps leaving their offspring in the fitness valley. This may explain why populations of some species, such as the Blyth's Reed Warbler (fig. 3.2B) and Siberian Rubythroat (fig. 3.2C) have not evolved more direct migratory routes to their wintering ranges. Furthermore, the conserved migratory routes of these species may be constraining their ability to expand their breeding ranges farther west or east. As a species spreads farther and farther from its wintering range, the height of the fitness peak that it is on may decrease because of the challenge of migrating farther.

Although we have emphasized constraints on evolving new migratory programs, there is abundant evidence for rapid evolutionary change in migratory behavior in many species. Phylogenetic reconstructions of both Old World Warblers (Helbig 2003) and New World Warblers (I. J. Lovette and T. B. Smith, unpubl. data) show that migratory species often evolve from resident species and vice versa. Sutherland (1998) listed 43 cases in which birds have changed migration routes in historical times. A particularly well-studied example is the Blackcap: before 1960, Blackcaps breeding in Germany generally wintered in Spain or southwest France, but now many use a migration route that brings them to Britain for the winter (Berthold et al. 1992). However, this west-northwest migratory direction probably falls within the normal range of genetic variation (Berthold et al. 1992), and Blackcaps often winter along the west coast of France. Sutherland (1998) observed that changes in migration routes tend to be rather small, and thus concluded that migratory behaviors can change rapidly in some situations but are highly constrained in others, leading to many cases of suboptimal migratory routes. Interestingly, Sutherland (1998) noted that all species with seemingly suboptimal migratory routes (14 cases) have short periods of parental care, suggesting that genetically determined migratory behaviors are more constrained than culturally determined migratory behaviors. A change between a migratory route along the west of Tibet to one along the east of Tibet, or vice versa, would be a much larger change than those that have been observed to date. Furthermore, many of the observed changes can occur by a series of small steps; intermediate forms might not suffer a loss in fitness. Both flexibility and constraints in the evolution of migratory behavior (Sutherland 1998) can be understood by thinking in terms of fitness surfaces (e.g., fig. 3.3). If there is no fitness valley between the presently used route and the optimal route, gradual evolution can lead to the population's using the new route. But if there is a deep valley between the present route and the optimal route, the population may not be able to evolve to use the optimal route.

In this chapter we have emphasized the role that migratory behavior may have in promoting speciation. However, the possibility that migratory behavior constrains the ability of a species to expand into uninhabited regions brings up the possibility that migratory behavior can also hinder speciation. If a species is prevented from colonizing new regions, it may be prevented from differentiating in response to novel selection pressures or genetic drift in combination with geographic isolation. It has often been observed that migratory species usually have smaller range sizes than nonmigratory species (e.g., Edward Blyth quoted by Darwin 1838, Notebook C [in Barrett et al. 1987:p. 36]; Mayr 1976; Böhning-Gaese et al. 1998; Bensch 1999). For example, Böhning-Gaese et al. (1998) showed that migratory species are less likely to occur in both North America and Europe, and Bensch (1999) showed that migratory species are less likely to have a range that includes both Scandinavia and eastern Siberia. These results are notable given the intuitive prediction that migratory species should have more potential than resident species to disperse and colonize new regions. Both Böhning-Gaese et al. (1998) and Bensch (1999) argued that migrants are more constrained than residents by the need to migrate to distant wintering grounds and to evolve a new migratory program as they expand into new regions. Many of the remarkable differences in the avian fauna of Asia and North America (e.g., the Old World warblers [Silviidae] vs. the New World warblers [Parulidae], the Old World flycatchers [Muscicapidae] vs. the New World flycatchers [Tyrannidae]) may be a result of the inability of these highly migratory groups to expand from one continent to the other because of their inability to evolve new migratory programs. In contrast, families dominated by resident species (e.g., Corvidae, Paridae, Emberizidae) are usually widespread on both continents.

The few migratory species that have successfully colonized North America from Asia or vice versa illustrate the constraints imposed by migration. The Bluethroat (*Luscinia svecica svecica*), the Arctic Warbler (*Phylloscopus borealis kennicotti*), and the Yellow Wagtail (*Motacilla flava tschutschensis*) have colonized Alaska from Siberia, but each continues to winter in Southeast Asia. The Grey-cheeked Thrush (*Catharus minimus*) has gone in the opposite direction, expanding from Alaska into eastern Siberia, while still wintering in South America. The most dramatic example is the Northern Wheatear (*Oenanthe oenanthe*), which has colonized far into North America along two fronts, one from eastern Siberia into Alaska and the other from Europe into Greenland and northeast Canada. All of these populations continue to migrate back to sub-Saharan Africa for the winter. An intriguing question is, what would happen if these expanding fronts meet in central Canada? The two populations would have different instinctive migratory directions, the western one orienting westward and the eastern one orienting eastward, creating a dramatic migratory divide. Hybrids would almost certainly have inferior migratory behavior, perhaps leading to a species boundary forming in Canada. If so, the Wheatear would become a circumpolar ring species.

In this chapter we have documented strong associations between migratory routes and subspecific and specific variation in northern Asia. Although these patterns are consistent with a role for migration in causing reproductive isolation and speciation, they are certainly not proof. Generally, migratory divides correspond to places where two groups have come into secondary contact after diverging in allopatry. The two groups may differ in many traits, some of which could play an important role in generating reproductive isolation (e.g., song, plumage, habitat preferences). We have argued that differences in instinctive migratory routes may be particularly powerful in causing selection against hybrids, but it is also possible that other factors play more important roles in speciation of central Siberian migratory birds. In the Greenish Warblers, for instance, song differences between the two expanding fronts may have been sufficient to cause complete reproductive isolation when the two fronts met (Irwin et al. 2001b).

FUTURE DIRECTIONS

We suggest several approaches that researchers could take to more directly examine whether reproductive isolation in migratory divides is in fact caused by divergent migratory behaviors. One approach is to compare contact zones of migratory and resident taxa that have otherwise similar biogeographic histories. If migration has played an important role in generating reproductive isolation, we would expect reproductive isolation to be greater in contact zones between migratory taxa than in contact zones between resident taxa. We are aware of only three contact zones in passerine birds of central Siberia that have been studied in detail. Of these three, the two migratory cases (the Greenish Warblers, and the Hume's Leaf / Yellow-browed Warblers) show complete reproductive isolation (Ticehurst 1938; Irwin et al. 2001a, 2001b), whereas the one resident case (Yellowhammer [*Emberiza citrinella*] / Pine Bunting [*Emberiza leucocephalos*]) shows extensive interbreeding between the taxa (Panov et al. 2003). This sort of comparison could extend beyond birds; it is interesting to note that the Siberian Larch (*Larix sibirica*), in west Siberia, and the Daurian Larch (*Larix dahurica*), in east Siberia, hybridize across a contact zone in central Siberia (Knystautus 1987). A difficulty with this approach is that migratory and resident taxa differ in many ways aside from migratory behavior itself; some other factor that is correlated with migratory behavior might influence reproductive isolation. A more direct approach is to conduct intensive population studies of the divergent taxa that meet at migratory divides. Most informative would be a study in the contact zone between taxa that hybridize occasionally. Orientation experiments might reveal that the two taxa have different instinctive migratory orientation (e.g., to the southwest and to the southeast) and that hybrids have an intermediate orientation (e.g., to the south). By banding nestlings and recording their return to the study area the following year, researchers might observe that hybrid offspring have a lower rate of return than pure offspring. These results would strongly indicate that differences in migratory orientation are causing post-zygotic isolation. By studying patterns of variation in traits used in mate choice along with the fitness consequences of mating decisions (i.e., offspring return rates), researchers might be able to determine the strength of selection for premating isolation due to differences in migratory behavior. Eventually, researchers may even be able to affix passerine birds with satellite-tracking devices, perhaps revealing in detail how the two parental groups avoid a barrier to migration, while the hybrids attempt, unsuccessfully, to fly directly across.

APPENDIX

Long-Distance Migrants That Breed in Western or Central Siberia and Migrate Only West of Tibet

Tree Pipit (*Anthus trivialis*)
Tawny Pipit (*Anthus campestris*)
Black-throated Accentor (*Prunella atrogularis*)
Altai Accentor (*Prunella himalayana*)
European Robin (*Erithacus rubecula*)

Thrush Nightingale (*Luscinia luscinia*)
Eversmann's Redstart (*Phoenicurus erythronota*)
Black Redstart (*Phoenicurus ochruros*) (also goes over Tibet)
Common Redstart (*Phoenicurus phoenicurus*)
Whinchat (*Saxicola rubetra*)
Isabelline Wheatear (*Oenanthe isabellina*)
Northern Wheatear (*Oenanthe oenanthe*)
Pied Wheatear (*Oenanthe pleschanka*)
Rufous-tailed Rock Thrush (*Monticola saxatilis*)
Song Thrush (*Turdus philomelos*)
Redwing (*Turdus iliacus*)
Common Grasshopper Warbler (*Locustella naevia*)
River Warbler (*Locustella fluviatilis*)
Savi's Warbler (*Locustella luscinioides*)
Aquatic Warbler (*Acrocephalus paludicola*)
Sedge Warbler (*Acrocephalus schoenobaenus*)
Paddyfield Warbler (*Acrocephalus agricola*)
Blyth's Reed Warbler (*Acrocephalus dumetorum*)
Great Reed Warbler (*Acrocephalus arundinaceus*)
Marsh Warbler (*Acrocephalus palustris*)
Booted Warbler (*Hippolais caligata*)
Icterine Warbler (*Hippolais icterina*)
Barred Warbler (*Sylvia nisoria*)
Lesser Whitethroat (*Sylvia curruca*)
Common Whitethroat (*Sylvia communis*)
Garden Warbler (*Sylvia borin*)
Blackcap (*Sylvia atricapilla*)
Hume's Leaf Warbler (*Phylloscopus humei*)
Chiffchaff (*Phylloscopus collybita*)
Willow Warbler (*Phylloscopus trochilus*)
Spotted Flycatcher (*Muscicapa striata*)
European Pied Flycatcher (*Ficedula hypoleuca*)
Eurasian Golden Oriole (*Oriolus oriolus*)
Red-backed Shrike (*Lanius collurio*)
Lesser Grey Shrike (*Lanius minor*)
Rose-coloured Starling (*Sturnus roseus*)
Ortolan Bunting (*Emberiza hortulana*)

Long-Distance Migrants That Breed in Western or Central Siberia and Migrate Only East of Tibet

Red-rumped Swallow (*Hirundo daurica*)
Olive-backed Pipit (*Anthus hodgsoni*)
Pechora Pipit (*Anthus gustavi*)
Buff-bellied Pipit (*Anthus rubescens*)
Richard's Pipit (*Anthus richardi*)
Blyth's Pipit (*Anthus godlewskii*)
Rufous-tailed Robin (*Luscinia sibilans*)
Siberian Rubythroat (*Luscinia calliope*)
Siberian Blue Robin (*Luscinia cyane*)
Red-flanked Bluetail (*Tarsiger cyanurus*)
Daurian Redstart (*Phoenicurus auroreus*)
White-throated Rock Thrush (*Monticola gularis*)
Scaly Thrush (*Zoothera dauma*)
Siberian Thrush (*Zoothera sibirica*)
Grey-backed Thrush (*Turdus hortulorum*)
Eyebrowed Thrush (*Turdus obscurus*)
Dusky Thrush (*Turdus naumanni*)
Spotted Bush Warbler (*Bradypterus thoracicus*)
Chinese Bush Warbler (*Bradypterus tacsanowskius*)
Pallas's Grasshopper Warbler (*Locustella certhiola*)
Lanceolated Warbler (*Locustella lanceolata*)
Gray's Grasshopper Warbler (*Locustella fasciolata*)
Oriental Great Reed Warbler (*Acrocephalus orientalis*)
Thick-billed Warbler (*Acrocephalus aedon*)
Arctic Warbler (*Phylloscopus borealis*)
Pallas's Leaf Warbler (*Phylloscopus proregulus*)
Yellow-browed Warbler (*Phylloscopus inornatus*)
Radde's Warbler (*Phylloscopus schwarzi*)
Dusky Warbler (*Phylloscopus fuscatus*)
Dark-sided Flycatcher (*Muscicapa sibirica*)
Asian Brown Flycatcher (*Muscicapa daurica*)
Mugimaki Flycatcher (*Ficedula mugimaki*)
Brown Shrike (*Lanius cristatus*)
Purple-backed Starling (*Sturnus sturninus*)
White-cheeked Starling (*Sturnus cineraceus*)
Black-faced Bunting (*Emberiza spodocephala*)
Yellow-browed Bunting (*Emberiza chrysophrys*)
Little Bunting (*Emberiza pusilla*)
Chestnut Bunting (*Emberiza rutila*)
Yellow-breasted Bunting (*Emberiza aureola*)

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