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LANDBIRD MIGRATION IN THE AMERICAN WEST: RECENT PROGRESS AND FUTURE RESEARCH DIRECTIONS

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Abstract. Our knowledge of avian behaviors during the non-breeding period still lags behind that of the breeding season, but the last decade has witnessed a proliferation in research that has yielded significant progress in understanding migration patterns of North American birds. And, although the great majority of migration research has historically been conducted in the eastern half of the continent, there has been much recent progress on aspects of avian migration in the West. In particular, expanded use of techniques such as radar, plasma metabolites, mist-netting, count surveys, stable isotopes, genetic data, and animal tracking, coupled with an increase in multi-investigator collaborations, have all contributed to this growth of knowledge. There is increasing recognition that migration is likely the most limiting time of year for migratory birds, and this places increasing importance on continuing to decipher patterns of stopover ecology, identifying critical stopover habitats, and documenting migration routes in the diverse and changing landscapes of the American West. Here, we review and briefly synthesize the latest avian migration findings and advances and consider research needs to guide future research on migration in the West.

Key words: landbird migration, stopover ecology, western United States

INTRODUCTION

Migration is likely the most dangerous time of the annual cycle for migratory birds, although only recently has mortality during migration been quantified. More than 85% of annual mortality in Black-throated Blue Warblers (*Dendroica caerulescens*) is estimated to occur during spring and fall migration, with mortality rates during migration 15 times higher than those during the stationary breeding and wintering periods (Sillett and Holmes 2002). Similarly, 64% of annual mortality in the southwestern subspecies of Willow Flycatcher (*Empidonax traillii extimus*) occurs during migration although this period comprises only a quarter of the annual cycle (Paxton et al. 2007a). Breeding and wintering birds may face less uncertainty than actively migrating birds, which must simultaneously cope with elevated nutritional demands, abiotic perturbations, navigation challenges, migration

barriers (including water and deserts), annual variation in environmental conditions along migration routes, unfamiliarity with novel habitats, increased intra- and inter-specific competition, and shifting predator assemblages. *En route* migrants face increasing uncertainty in habitat and resource availability as human-associated landscape changes continue through such activities as urbanization, agriculture, livestock grazing, and water management. In addition, projected changes in global climate will intensify the existing uncertainties faced by migrants as the resources upon which they depend are redistributed in space and time. Increasingly, migrants face changes in the quality and quantity of stopover sites, experience increasing numbers of collisions with wind turbines and artificially lit man-made structures, and are threatened by rapidly spreading new and re-emerging avian pathogens and increased abundance of domestic and other human-associated predators (Mehlman et al. 2005, Kuvlesky et al. 2007). To what degree these anthropogenic challenges during migration have contributed to population declines of many migratory species (Robbins et al. 1989, DeSante and George 1994, Wang and Finch 1997, Sauer et al. 2008) is difficult to quantify. However, the high mortality experienced by actively migrating birds (Sillett and Holmes 2002, Paxton et al. 2007a) suggests that human activities have ample potential to influence migrant population dynamics (Holmes 2007). Given that migration is a critical time period in the annual cycle of birds, that humans are rapidly altering the migration landscape, and that the quality of stopover habitats is strongly tied to biogeographical factors as well as habitat (Kelly et al. 2000), we urge that a high priority be placed on the development of a more quantitative view of future scenarios to be faced by western migrants (Petit 2000).

Our objective in this paper is to advance the study of migration in western North America by (1) reviewing and briefly synthesizing the latest information on landbird migration through this region and (2) identifying research needs to guide future research. We focus on the West because this is the geographic region encompassing our collective expertise, although certainly the issues we discuss apply to bird migration throughout the world. The ideas presented here are derived in part from a symposium on "Landbird migration across the diverse western landscape: recent progress, the importance of riparian and other habitats, and future directions" held at the annual meeting of the Cooper Ornithological Society in 2007.

Western North America is topographically diverse, which results in extreme contrasts among adjacent habitat types and distinctive patterns of land use. How migratory birds travel through and use this diverse landscape during spring and autumn migration depends on several aspects of their life history, including natal habitat, fledging date, molting patterns, wintering location, flight capacity, and migration timing (e.g., Kelly et al. 1999, DeLong et al. 2005). Location, food availability, and predation risk are some of the most important factors shaping stopover habitat choices by migrants (DeLong et al. 2005). For many woodland birds, much of the western landscape (especially deserts, xeric shrublands, and alpine areas) may provide adequate habitat only when birds occur at low densities, whereas other habitats (i.e., deciduous forests) may support extraordinary densities of migrants during some parts of the year (Moore 2000). Human modifications to the landscape (including agriculture, livestock grazing, development, and modification of riparian systems) have likely increased the proportion of the western landscape that is unsuitable for some species, whereas many human-created oases (e.g., golf courses, cemeteries, irrigation ditches) likely provide migrant stop-over habitat in novel areas. Thus, whereas western migrants (traveling between breeding grounds in western Canada and the western United States – including Alaska – and wintering areas that stretch from the southwestern United States through Mexico to northern Central America) are not faced with major overwater flights like many of their eastern counterparts (Kelly and Hutto 2005), the western landscape likely holds many 'natural' and 'anthropogenic' challenges for passage migrants.

We still do not know how birds negotiate the western landscape during migration. In particular, what routes do they follow, how far do they fly each night, and what habitat types do they prefer? Do migration routes and stopover habitats differ seasonally? Do migration strategies differ among species based on their wintering and breeding habitat affinities? How much flexibility exists in migration strategies? And, what carry-over relationships exist between periods of migration, breeding and wintering that affect the fitness of western birds? These questions highlight the need to decipher patterns of stopover ecology and identify critical stopover habitats and migration routes in the diverse and changing landscape of the American West.

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RECENT PROGRESS

Over the past two decades, the number of scientific papers published annually on avian migration ecology has increased more than ten-fold. In North America, the focus of migration research has evolved from early studies on orientation and navigation to a broad diversity of topics, most notably climate change, distribution and phenology, evolution and genetics, linkages in the annual cycle, and physiology (ISI Web of Knowledge[SM] 2008). Research on avian migration in western North America has increased greatly over the last 10-15 years (Moore 2000, George and Dobkin 2002), advancing our knowledge of the ecology of western migratory birds (Table 1). Below we discuss many important recent findings that are helping to reshape our thinking about future research needs and directions.

HABITAT ASSOCIATIONS OF MIGRANTS

Riparian habitats in the West have long been recognized for their disproportionate contribution, relative to area, to faunal richness, particularly for breeding populations of birds and other animals. Riparian habitats are also considered critical to migrants, both as routes for migratory movement and as stopover habitats for many migrants (Stevens et al. 1977, Skagen et al. 1998, 2005, Wang et al. 1998, Kelly et al. 2000, DeLong et al. 2005). In addition to the vegetation and food resources, part of the importance of riparian areas for passage migrants might simply be the availability of water (Sapir et al. 2004). Riparian obligates and non-obligates alike use this habitat during migration, expanding its importance to the annual cycles of birds beyond those that breed there. The majority of riparian habitats in the West has been greatly altered or destroyed (Webb et al. 2007); thus, the conservation and restoration of existing riparian systems is of critical importance. In particular, management of riparian-associated vegetation during the predicted future water shortage will be critical to maintaining these diverse habitats (IPCC 2007).

Whereas the spatial configuration of riparian habitat can influence the distribution of migrants over large geographic scales, less is known about stopover habitat selection at finer scales. Migrants can occur in high densities in small isolated riparian oases as well as along continuous riparian corridors in southeast Arizona (Skagen et al. 1998). Migrant habitat selection with regard to exotic vegetation has been examined recently by Walker (2008), who compared abundance and diversity of autumn migrants in native vegetation and tamarisk (*Tamarix ramosissima*)-invaded habitats that differed in floristics and physiognomy. Along the Rio Grande, bird abundance is related to floristic composition of the vegetation whereas species diversity is more strongly linked to habitat structure. Walker (2008) speculates that floristic composition influences food availability (e.g., fruits, seeds, arthropods), which is, in turn, a stronger determinant of migrant habitat selection than availability of diverse foraging sites in structurally complex habitats. Migrant abundance was higher in tamarisk-dominated than native-dominated sites in the study area, and potential differences between the two habitat types in the composition, quality, and timing of availability of their arthropod communities may explain their differential use by autumn migrants. Along the lower Colorado River, van Riper et al. (2008) found a similar situation with spring migrant use of tamarisk-dominated habitats. Wilson's Warbler (*Wilsonia pusilla*) use of native vegetation and tamarisk on the Colorado River during spring migration matched the plants' flowering phenology, corresponding to likely changes in associated resource availability (Paxton et al. 2008). Likewise, both Hudson (2000) and Carlisle (unpubl. data) have found that some migrant species can be abundant and gain mass during stopover in habitats composed at least partially of Russian Olive (*Elaeagnus angustifolia*). These results caution against assuming that exotic vegetation is universally of low value to migrants and encourage further investigations of migrant-vegetation associations. Studies of the mechanisms underlying such associations (i.e., food availability, concealment from predators, etc.) and their effects on body condition, length of stay, etc. will be especially useful to our ability to understand the relative value of different habitats to migrating landbirds. On a related note, given that natural (e.g., Skagen et al. 1998) and artificial oases attract passage migrants, it would be worthwhile to examine how the size, plant composition, and location of various oases affect migrant use.

In recent years, investigations of habitats used by western migrants have expanded to include habitats other than cottonwood- (*Populus* sp.) and willow- (*Salix* sp.) dominated riparian. In particular, recent studies have investigated migrants' use of mesquite woodlands, montane deciduous and coniferous habitats, xeric riparian scrub, desert shrublands, and other habitats (e.g., Puschock 1998, Carlisle et al. 2004, 2006, Hardy et al. 2004, DeLong et al.

2005, McGrath et al. 2008, van Riper et al. 2008). Spring migrants on the Colorado River in Arizona reach their greatest abundance as honey mesquite (*Prosopis glandulosa*) flowering peaks (McGrath et al. 2008). Within stopover habitats, migrating birds preferentially choose high flowering honey mesquite trees, which support the highest insect biomass. Similarly, Hardy et al. (2004) found that xeric riparian scrub is especially important to spring migrants in the Sonoran desert of southwestern Arizona, particularly that containing mesquite and paloverde (*Parkinsonia* sp.) trees and catclaw acacia (*Acacia greggii*), willow, and creosote-bursage (*Larrea tridentata* – *Ambrosia* spp.) vegetation. Puschock (1998) examined fall and spring use of pinyon-juniper (*Pinus* sp. – *Juniperus* sp.), mountain mahogany (*Cercocarpus betuloides*), mesquite scrub, and xeric riparian scrub (called 'canyon bottom-arroyo' by Puschock) and found that whereas migrants were more common in the riparian (where capture rates were comparable to those along the Rio Grande), migrants did occur in all habitats examined. Thus, whereas cottonwood- and willow-dominated riparian habitats receive the greatest use, migrants use other habitats as well.

Several early studies found evidence for migrant use of higher elevation habitats, especially during autumn migration (Austin 1970, Greenberg et al. 1974, Blake 1984, Hutto 1985), and recent findings have extended the geographic scope over which this pattern occurs (Carlisle et al. 2004, 2006, DeLong et al. 2005). In particular, montane deciduous and coniferous forests appear to support relatively high abundance and diversity of migrants during autumn migration. Both Carlisle et al. (2004) and DeLong et al. (2005) discussed the possibility that montane woodlands in and around the Great Basin may provide cooler microclimates and higher food availability during late summer and early autumn than surrounding lowlands and thus provide more favorable habitat to migrants at those times of year and Patten et al. (2003) suggested the same pattern for the Sonoran Desert. In fact, Carlisle (2005) found that whereas arthropod and fruit availability at an autumn stopover site in southwestern Idaho differed significantly among years, most migrant species were able to gain mass in each year, indicating the presence of adequate food sources for re-fueling at this montane site. Recently, Wightman et al. (2007) showed that ponderosa pine forests with a deciduous component were also important for autumn migrants.

Findings of migrants using different habitats during autumn than during spring migration raise the question of whether there are important seasonal differences in stopover habitat requirements between spring and autumn. For example, van Riper et al. (2008) found more birds present during spring than fall migration along the lower Colorado River in southwestern Arizona, suggesting that some species migrate via different routes and/or use different habitats during autumn. Wethington et al. (2005) found a similar pattern in hummingbirds in western North America. As suggested above, stopover habitat choices by migrants may ultimately be driven by patterns in food availability, which likely depends on variation in elevation, climate and weather, vegetation, and soil types.

Understanding the cues used by migrants to select stopover habitats requires knowledge of spatial patterning of habitats and how these patterns are perceived by migrants (Hilden 1965). The prevailing, and usually implicit, model for understanding migrant habitat selection is based on a spatial hierarchy, whereby the process of selecting a stopover site is thought to start with coarse level topographical cues and progress toward finer level distinctions among vegetation structure and floristics (Hilden 1965, Hutto 1980, Petit 2000, Deppe and Rottenberry 2008). This model implies a shift from a domain where factors extrinsic to local sites are prevalent at large spatial extents to one where factors intrinsic to local sites predominate at small spatial extents (Moore et al. 1995). In patchy landscapes of the interior West, understanding the spatial scale at which migrants shift from using extrinsic to intrinsic cues might be of greater importance to conservation of stopover sites than in more homogenous landscapes.

MOLT-MIGRATION

In North America, many migratory landbird species molt on the breeding grounds immediately after breeding, whereas others molt elsewhere (Pyle 1997). A higher proportion of western than eastern species and subspecies depart breeding areas before initiating flight feather molt (~50 % vs <10 %; Rohwer et al. 2005), and this east-west difference is attributed to arid conditions across much of the West during late summer that do not support the energetic demands of molt (Rohwer et al. 2005). Although some species likely migrate to their winter grounds to molt, many recent studies found that adults of several western North American species leave the breeding grounds in July or August, stop in the "Mexican monsoon region" in the southwestern United States and northwestern Mexico to molt, and resume migration to the winter grounds in southern Mexico and Central America when molt is complete

(e.g., Young 1991, Voelker and Rohwer 1998, Rohwer et al. 2005). Whereas not a complete list, species that undergo "molt-migration" to the desert southwest include Bullock's Oriole (*Icterus bullockii*; Rohwer and Manning 1990), Lazuli Bunting (*Passerina amoena*; Young 1991), western populations of Warbling Vireo (*Vireo gilvus*; Voelker and Rohwer 1998), and Western Tanager (*Piranga ludoviciana*; Butler et al. 2002). Many other species depart the breeding grounds before molting and are possible candidates for this list based on feather condition and timing of migration documented for birds passing through western banding stations (e.g., Richardson et al. 2003, Carlisle et al. 2005a). Specifically, Rohwer et al. (2005) speculate that Western Wood-Pewee (*Contopus sordidulus*), Dusky Flycatcher (*Empidonax oberholseri*), Cordilleran Flycatcher (*E. occidentalis*), Pacific-slope Flycatcher (*E. difficilis*), Ash-throated Flycatcher (*Myiarchus cinerascens*), Western Kingbird (*Tyrannus verticalis*), Hepatic Tanager (*P. flava*), Summer Tanager (*P. rubra*), Black-headed Grosbeak (*Pheucticus melanocephalus*), and Lesser Goldfinch (*Carduelis psaltria*) may also undergo molt-migration to the desert southwest. Based on observations at Southeast Farallon Island, P. Pyle (pers. comm.) speculated that some or all populations of Gray Flycatcher (*E. wrightii*), Cassin's Vireo (*V. cassinii*), Nashville Warbler (*Vermivora ruficapilla*), Townsend's Warbler (*Dendroica townsendi*), Hermit Warbler (*D. occidentalis*), Chipping Sparrow (*Spizella passerina*), Lark Sparrow (*Chondestes grammacus*), Hooded Oriole (*I. cucullatus*), and Orchard Oriole (*I. spurius*) also undergo molt-migration.

Because loss of habitat on molting grounds may adversely affect adult survival and, in turn, lead to population declines throughout the species' ranges, it is important to increase our knowledge of stopover ecology of molt-migrants in the desert southwest. We need information about species involved, habitat requirements, and duration of time spent in these molting areas (e.g., Leu and Thompson 2002). In areas that receive significant monsoon rainfall, riparian, mesquite, and montane (e.g., Hutto 1985) habitats and thorn forests in western Mexico (S. Rohwer, pers. comm.) may be especially important to molt-migrants. Molt-migrations to specific habitats also occur in waterbirds, such as waterfowl to large areas of protected wetlands, and Eared Grebes (*Podiceps nigricollis*) to Mono and Great Salt lakes. Much directed effort has been expended to conserve and manage these important areas to maintain population stability in these waterbirds (Jehl 1988, Hohman et al. 1992). Because some habitats used by landbird molt-migrants may be threatened by development and livestock grazing practices in the desert southwest, identification of critical molt-migration stopover habitats and regions will be an important first step toward establishing similar habitat protection and management for landbirds.

Two concurrent efforts to elucidate patterns of molt-migration are underway, including studies by Sievert Rohwer (University of Washington) and Peter Pyle (Institute for Bird Populations) and their colleagues. These efforts are assessing the species composition, ranges, and habitat requirements of landbird species undergoing molt-migration to the southwestern United States and northwestern Mexico using a combination of count surveys, mist-netting and banding, and collecting. Such studies will lead to a greater understanding of the stopover ecology of molt-migrants and will contribute greatly to conservation and management strategies for critical habitats in the region.

STOPOVER ECOLOGY AND ENERGETIC CONDITION

A host of recent studies have enhanced our knowledge of migrant stopover behavior in the West. In particular, applications of established techniques (mist-netting and associated analyses) to previously unstudied areas, and use of an important and novel technique (plasma metabolite sampling), have contributed to a growing body of literature pertaining to stopover ecology and habitat suitability (Wang et al. 1998, Kelly et al. 2002a, Cerasale 2004, Carlisle et al. 2005b, Guglielmo et al. 2005, Paxton et al. 2007b, Paxton et al. 2008).

Recent studies by Wang et al. (1998), Kelly et al. (2002b), and Paxton et al. (2008) of Wilson's Warbler migration in the West highlight important age and sex differences in stopover ecology as well as the role that competition may play in impacting stopover success. In particular, Wang et al. (1998) found that northbound males along the Rio Grande in New Mexico arrived earlier and with more fat than females and also had shorter stopover durations and faster mass gains. During autumn, southbound immature birds had lower fat stores, slower mass gain rates, and longer stopovers than adults. Among northbound spring migrants at a stopover site on the lower Colorado River, second-year birds displayed faster and more meandering movements than after-second-year adults, suggesting age-related differences in foraging efficiency (Paxton et al. 2008). In contrast, Carlisle and colleagues (unpubl. data) found no differences in stopover parameters between males and females in Wilson's Warblers or other species

during spring or fall migration in eastern Idaho, and found that immature Wilson's Warblers gained significantly more mass than adults (0.19 g vs. 0.05 g), albeit over a longer stopover period (~2.1 days vs. ~1.6 days). Interestingly, the arrival condition indices for immature birds were significantly lower than those for adults, suggesting that their need for mass gain was greater. Also, Carlisle et al. (2005b) investigated autumn stopover ecology at a southwestern Idaho montane site with deciduous shrubs adjacent to conifer forest and found that most species were able to gain mass, suggesting the potential importance of montane habitats to southbound migrants (see above).

Growing evidence suggests that competition may have a considerable effect on migrant refueling rates and thus warrants further attention (Hansson and Pettersson 1989, Moore and Yong 1991, Kelly et al. 2002b, Cerasale 2004). Competition among migrant birds is supported by several lines of evidence: (1) concentrations of intercontinental migrants can depress local food abundance during stopover (Moore and Yong 1991), (2) southbound migrants tend to have larger initial mass decreases when at high densities (Hansson and Pettersson 1989), and (3) migrant birds gain mass more slowly during refueling when densities of migrant birds, especially potential competitors, is highest (Moore and Yong 1991, Kelly et al. 2002b, Cerasale 2004). Competitive interactions may also occur between migrant and resident (either year-round or seasonally resident) species, as suggested by strongly negatively correlated abundances of breeding-season resident and northbound migrant shrub/canopy-foraging birds across many riparian sites in southeastern Arizona (Skagen and colleagues, unpubl. data). Collectively, these findings underscore the importance of assessing what impact the densities of both resident and passage migrant birds, in combination with the amount of available habitat at a site, have on migrant abundance and stopover site suitability.

Although mass changes among recaptured birds provide valuable insights into the suitability of stopover sites, such data require intensive (ideally daily) sampling, and recapture rates are low, often less than 10 % (e.g., Carlisle et al. 2005b). An emerging technique, plasma metabolite profiling, enables investigators to make among-site and between-season comparisons of fuel deposition rate with reduced sample size requirements (Guglielmo et al. 2005). With this technique, circulating levels of blood metabolites such as triglycerides, glycerol, and ß-hydroxybutyrate together reflect rates of mass change in individuals at the time of collection of the blood sample. Using this technique to assess the suitability of non-native tamarisk vegetation relative to native riparian vegetation for migrating Wilson's Warblers, Cerasale (2004) found higher triglyceride levels at tamarisk-invaded sites, suggesting that birds were gaining mass more quickly than in native vegetation. Cerasale (2004) concluded that lack of competition from other migrant species (significantly more abundant at native sites) was the most likely explanation. Smucker (2007) found that Wilson's Warbler triglyceride levels were highest in riparian areas with dense understory vegetation and declined with decreasing vegetation structure, suggesting faster rates of mass gain in areas with more subcanopy vegetation. Wider application of this tool and other measures of individual condition (e.g., immune function, hormonal state, haematological state, polychromatia, oxidative stress, uric acid, carotenoids) to address differences among individuals, habitats, and seasons holds great potential for revealing patterns of stopover site use and the factors influencing migrant habitat use patterns.

MIGRATORY CONNECTIVITY

Since the late 1980's, a major concern of ornithologists has been the downward population trajectories of many migratory bird species (Robbins et al. 1989). It now appears that the dynamics of most migrant population trends are characterized spatially by regions of decline and regions of increase (Sauer et al. 2008) and that population trends in the West are characterized by increases in some species and decreases in others (DeSante and George 1994). Emerging from the recent debates and research on migratory bird population trends is the concept of population connectivity (Webster et al. 2002). Whereas nascent versions of this idea have been traced to Salomonson (1955), the degree to which migration connects breeding and wintering populations has only recently been recognized as a driver of migrant population dynamics. The core idea is that at one extreme, specific wintering and breeding populations may be tightly linked, without any seasonal mixing of individuals from other populations (strong connectivity). At the other extreme, the population of birds at a particular wintering site may be a random mix of individuals from throughout the breeding range, or vice versa (weak connectivity). If connectivity is strong, the effects of local winter events will be limited to specific breeding populations and are likely to be more noticeable. In contrast, where connectivity is weak, local winter events will have only diffuse effects on breeding populations across a broader area.

Several good examples of tracing wintering individuals to their population of origin (breeding) have recently emerged. Koronkiewicz et al. (2006) linked Willow Flycatchers wintering in Costa Rica to a breeding population at Roosevelt Lake in Arizona. Kelly and Hutto (2005) concluded that connectivity at a regional scale on the wintering grounds is weak within the Orange-crowned Warbler (*Vermivora celata*) based on subspecies taxononomy. Using mtDNA, Smith et al. (2005) assigned overwintering individuals of five species of Neotropical migrants to either eastern or western lineages and then determined the degree of migratory connectivity between breeding and wintering populations. Their results varied, showing strong connectivity for Yellow-breasted Chat (*Icteria virens*) and Swainson's Thrush (*Catharus ustulatus*), and weaker connectivity for Common Yellowthroat (*Geothlypis trichas*), Nashville Warbler, and Wilson's Warbler. These examples, even at broad scales, indicate that understanding the degree of connectivity can have serious implications for the conservation of avian populations.

Whereas most research on migratory connectivity has focused on linking breeding and wintering populations, determining the degree of migratory connectivity during the *en route* period is also critical to understanding population dynamics of migratory birds, especially given the growing evidence of high mortality during migration (Sillett and Holmes 2002, Paxton et al. 2007a). Our understanding of many aspects of stopover ecology has been limited because departure and ultimate destination points are often unknown. However, the advent of more quantifiable ecological tracers (genetic and isotopic markers) has enhanced our ability to discern at broad scales how breeding populations are temporally and spatially distributed during migration. Kelly et al. (2002a) and Clegg et al. (2003) showed relatively strong connectivity for western breeding populations of Wilson's Warblers across their wintering range and revealed that Wilson's Warblers engage in leapfrog migration (i.e., birds breeding at higher latitudes winter farther south than con-specifics breeding at lower latitudes). These patterns have since been corroborated at additional sites in the West (Paxton et al. 2007b), and demonstrated for MacGillivray's Warbler (*Oporornis tolmiei*) as well (Paxton 2004, Paxton and van Riper 2006). Strong relationships between timing of migration and breeding location have been documented for western populations of Orange-crowned Warblers, Common Yellowthroat, and Yellow Warblers (*Dendroica petechia*), although the direction of the relationship varied (Kelly 2006). There is also evidence of strong temporal patterns and chain migration (i.e., birds originating at higher latitudes wintering farther north than those from lower latitudes) of populations of immature western Sharp-shinned Hawks (*Accipiter striatus*) during autumn migration (Smith et al. 2003). Additional information about the distribution of breeding populations on the wintering grounds is needed to ascertain the relative prevalence of leapfrog versus chain migration among western species.

Knowing the degree of temporal and spatial segregation of breeding populations during migration provides the foundation for in-depth questions about stopover ecology that were previously not possible. For example, we can now begin to address questions about how habitat alterations or loss of habitat along migration routes potentially affects different breeding populations. Whether breeding populations migrate in broad fronts or use distinct migration pathways greatly impacts management strategies for stopover habitat along migration routes. For example, Paxton et al. (2007b) found that Wilson's Warblers breeding in different geographic regions use different migration routes in the southwestern U.S. As a result, local habitat alterations could differentially impact different populations. Whereas our knowledge of migratory connectivity has greatly increased and its applications are and will be critical to the future of migrant conservation, the field is still new and there is an urgent need to improve the resolution of existing information and to expand the number of species for which data are available.

MIGRATION ROUTES AND BROAD-SCALE FLIGHT PATTERNS

Compared to the eastern U.S., our knowledge of migration routes through the West is in its infancy. That many migrants move across broad fronts at regional and continental scales is suggested by the influence of biogeographical factors (size of the breeding range, breeding bird density, and distance from the breeding range) on migrant abundance at stopover sites (Kelly et al. 1999). However, riparian associated birds migrating across the southwestern U.S. are less strongly influenced by biogeographical factors and may adjust their migration routes to maximize time spent in riparian zones (Skagen et al. 2005). Moreover, specific migration routes may be used by specific populations, as evidenced by migratory connectivity patterns of breeding and wintering populations of species with extensive ranges, such as Wilson's (Paxton et al. 2007b) and MacGillivray's warblers (Paxton 2004). Some species, such as the Nashville Warbler with a limited breeding distribution in the West, migrate within a small geographic region (Paxton 2004). Thus, alterations to particular habitats could have differential impacts on populations.

Many species and populations may use different routes and/or habitat types during northbound and southbound migrations. For example, a 'loop' migration pattern has been well documented in western hummingbirds, many of whom migrate north along the coast and at lower elevations during spring, and then travel south in autumn through several mountain ranges of the West – utilizing flowers in mountain meadows along the way (Wethington et al. 2005). Similarly, Patten et al. (2003) observed that spring migrants in southern California utilize the Salton Sink but that the area is largely avoided during fall, when fall migrants were found in Peninsular Ranges or further east into Arizona. In addition, several studies based on capture data during spring and fall migration at the same sites have found varying abundances between seasons (Finch and Wang 2000, van Riper et al. 2008, Carlisle, unpubl. data). For example, in eastern Idaho, Wilson's Warblers were captured more than six times more frequently during fall than during spring, whereas *Catharus* thrushes (especially Swainson's, *C. ustulatus*) were over 10 times more common during spring migration (Carlisle, unpubl. data). Together, these data suggest that use of migration routes and/or stopover habitats varies by season, and that patterns differ among species.

The application of NEXRAD (NEXt Generation RADar; a nationwide network of over 150 large-scale Doppler weather surveillance towers) data to the study of bird migration in the southwestern U.S. has recently provided valuable insights on flight patterns of migrants (Felix et al. 2008). NEXRAD stations detect birds during migration and return data that can be analyzed to determine migrant velocity, altitude, and direction. Using data from seven radars along the borderlands in Texas, New Mexico, and Arizona, Felix et al. (2008) determined that spring migrants fly faster and lower than fall migrants and that seasonal differences are partially explained by the altitudes of favorable winds. Future objectives of this effort are to estimate migrant density and describe habitat associations across the southwest. Once this study refines applications of this technique in the topographically diverse desert southwest, there will be potential to apply the use of NEXRAD data to study migration across the American West. Moreover, as radar technology continues to improve with the scheduled deployment of dual-polarimetric technology in the next three years, the capacity to monitor migration will also improve (Bachmann and Zrnic 2007).

SEASONAL INTERACTIONS AND CARRY-OVER EFFECTS

A conceptual framework likely to revolutionize how we view and study migratory landbirds has at its core the notion that conditions during one season in the life cycle of migratory birds can impact individual fitness and population size in a subsequent season (Webster and Marra 2005, Norris and Marra 2007). Formerly limited to waterbirds, there is now a growing body of information on how conditions at staging areas or stopover sites impact breeding success and winter population size, as well as how breeding success can impact arrival at autumn stopover sites (Newton 2006, Norris and Marra 2007). In migratory passerines, several patterns have emerged: conditions during winter or spring migration can impact the timing of arrival and population densities on the breeding grounds, individual condition, clutch size, and breeding success; conditions on the breeding grounds (including time spent and reproductive effort) can impact fall migration departure date as well as future physical condition; and the strength of seasonal interactions depends on migratory connectivity (e.g., Norris et al. 2004, Norris and Marra 2007). Using techniques described under *Migratory connectivity* (above), scientists can now study these "carry-over effects" by asking, for example, if early and late migrants from the same breeding populations differ in residency time at stopovers or physiological state at arrival and departure, all factors that can influence migration success, survival, and reproductive success (Sandberg and Moore 1996, Sillett and Holmes 2002, Smith and Moore 2003, Moore et al. 2005).

Norris (2005) incorporated carry-over effects into models of the response of populations to habitat loss and found relationships between habitat loss and reproduction that were not detectable with traditional single-season approaches. Population response differed with the quality as well as quantity of habitat lost, and carry-over effects may vary by specific demographic factor and season. Given the magnitude of the threat of habitat loss facing western birds, modeling exercises such as this should play a prominent role in the conservation of migratory species, and collecting data needed to develop such models (e.g., strength of density dependence on breeding and wintering grounds, magnitude and generality of individual carryover effects, extent to which carryover effects interact with population density), is a high priority. Identification of critical demographic factors and mechanisms driving migration behavior can help to prioritize potential conservation actions and help determine which drivers can be managed (e.g., habitat loss, degradation) and which cannot (e.g., weather).

EVOLUTIONARY CONSTRAINTS, PHENOTYPIC PLASTICITY, AND FLEXIBILITY OF MIGRANTS

Migration is a process that has been shaped over time by genotypic and phenotypic responses of individuals to environmental variability. Modern species of birds arose mainly in the late Pliocene and Pleistocene (0.08-5.3 mya; James 2005), yet their current migratory pathways across North America probably date back only 18,000 years, to the retraction of the last glacial ice sheets during the late Pleistocene (Joseph 2005). Long before European settlement of North America, *en route* migrants coped with intensive and extensive perturbations such as glaciation and decadal-long droughts. The "great evolutionary flexibility" associated with long-distance migration (Alerstam et al. 2003) allows for the continuing evolution of migration patterns in response to environmental changes. Changes can occur through microevolution (Bairlein and Hüppop 2006, Pulido and Berthold 2006) or through the expression of ecological flexibility of individuals. Some aspects of migration, such as migration routes of species with relatively short parental care, are believed to be genetically determined. Evidence of substantially changed migration routes in historic times is documented for 26 bird species (Sutherland 1998), including Blackcaps (*Sylvia atricapilla*). Through captive rearing and orientation experiments, Berthold et al. (1992) established the genetic basis of the recently evolved and novel westerly migration route of Blackcaps in continental Europe, and Bearhop et al. (2005) have recently demonstrated that assortative mating of Blackcaps with different migration strategies is contributing to this rapid evolution of a new migratory route. Whether bird populations can alter migration routes in response to loss of breeding or wintering habitats in western North America has strong implications for future population viability (Dolman and Sutherland 1995).

Phenotypic plasticity "indicates the general capacity for change or transformation within genotypes in response to different environmental conditions" (Piersma and Drent 2003). Although historically used in the context of character states and reaction norms which do not pertain to reversible, within-individual variation, the term "phenotypic plasticity" recently has been broadened to encompass both irreversible (developmental plasticity) and reversible (phenotypic flexibility) forms (Piersma and Drent 2003, Charmantier et al. 2008). Reversible plasticity within individuals, or flexibility, enables individual migrants to cope with unfamiliar and highly unpredictable environments they encounter throughout their annual cycles. Long-distance migrants exhibit several forms of flexibility, including structural and physiological plasticity, illustrated by the reversible structural changes in body composition (body fat, muscle mass, reproductive and digestive organs) associated with migration (Weber and Hedenstrom 2001, Piersma and Drent 2003), and ecological and dietary flexibility, behavioral responses that allow for the exploitation of the variable resources birds encounter throughout the year (Skagen and Oman 1996, Parrish 2000, Mettke-Hofmann and Greenberg 2005).

Although migrants have clearly coped with extensive change throughout time, rates of land-use change in North America in the past several decades and the expected rate of global climate change are more rapid than the changes birds have generally experienced in their evolutionary pasts. The capacity of migrants to adjust to these rapidly changing conditions is essentially unknown (van Noordwijk et al. 2006). Whereas aspects of migration assumed to be genetically determined, including timing of the onset of migratory activity (Pulido et al. 2001) and migration route (Sutherland 1998, Pulido and Berthold 2006), have evolved in historic times, the potential for widespread genetic adaptation may be constrained by the speed of anticipated environmental change. Phenotypic plasticity, the extent of which varies among species, enables migrants to track localized changes in resource quality and availability and to alter the speed of migration in response to weather conditions en route (Both et al. 2005, Marra et al. 2005). We hypothesize, however, that plasticity may be insufficient to enable some species to cope with the large-scale shifts in the timing and distribution of breeding, wintering, and migratory resources and habitats predicted by climate change forecasts. Moreover, we believe that short-distance migrants, especially those with a known capacity for facultative movements (e.g., Yellow-rumped Warbler, *Dendroica coronata*; Terrill and Ohmart 1984), will probably be better able to respond to a changing environment than will long-distance migrant birds with more fixed movement patterns. The potential for, and constraints on, genetic and phenotypic responses by migrating birds to changing environments are in great need of research attention to identify options for species conservation.

FUTURE RESEARCH NEEDS

Whereas many prior migration studies have focused on basic aspects of life history and migration ecology, extensive discussions and questionnaire responses at recent venues have explicitly or implicitly identified conservation issues, such as land use change and climate change, as driving forces in determining today's highest priority research needs. The discussions also illuminated a need for collaborative self-organizing approaches to studying highly complex

migration systems. In fact, collaborative study of landbird migration ecology may now be necessary to achieve the rapid scientific advances needed to confront urgent migration-related conservation issues (Heglund and Skagen 2005, Kelly and Hutto 2005).

Emerging questions for migration research have been identified by research ecologists and managers attending recent migration workshops, symposia, and meetings of MIGRATE (Migration Interest Group: Research Applied Towards Education; http://migrate.ou.edu), a National Science Foundation Research Coordination Network pursuing an integrated understanding of animal migration. Here we synthesize questions defined at four venues: (A) a southwest-focused migration workshop in 2004 (Skagen et al. 2004), (B) the inaugural meeting of MIGRATE in 2007, (C) questionnaires associated with a migration symposium at the Cooper Ornithological Society 2007 meeting (28 respondents), and (D) the Partners in Flight Research and Monitoring Needs 2008 database (www.partnersinflight.org/pifneeds/; Table 2). Figure 1 portrays the relationships between these perceived research needs, the review information presented earlier in this document, and potential conservation and management actions.

Several common themes emerged from the venues and are summarized in Table 2, which presents primary questions generated at two or more of the four venues. The full suite of proposed topics covers a broad range of disciplines including behavior, ecology, physiology, genetics, climate change, geology, and information management. As an example of questions generated by such efforts, MIGRATE participants defined priority research questions in which today's major conservation challenges were clearly identified. For example: *What is the impact of environmental change on migratory life histories? In particular, what are the effects of land use and climate change?* Two of the MIGRATE priority questions focus on connections between migration and the remainder of the annual cycle: *What are the determinants of individual fitness? What are the drivers of population dynamics in migratory animals?* MIGRATE participants also prioritized the need to know more about mechanisms of coping with change: *What are the determinants of behavioral plasticity in migrants and what are the constraints on behavioral adaptation?*

The answers to these and other priority questions will be essential for guiding management to effectively prepare for and respond to environmental change (Figure 1). In particular, coordinated efforts to protect migrants will rely on an understanding of the roles that specific habitats throughout the western hemisphere play in the annual cycles of migratory species. Targeting species, habitats, or sites for conservation action will be most effective when informed by research allowing prioritization of such actions based on relative need and expected benefits to birds. As our understanding of the interconnectedness among different stages of the annual cycle grows, so too will the need for international partnerships to protect migratory birds throughout their ranges. Knowledge of the capacity of birds to respond phenotypically or genetically to change will be another useful element to ranking species in terms of their need for management attention.

New collaborations are required to take full advantage of new technologies and conceptual frameworks to pursue coordinated investigations at multiple spatial and temporal scales over multiple continents (e.g., Bairlein 2003). Descriptions of the types of tools and approaches to address these questions were presented above; below, we offer brief suggestions for two fruitful lines of future investigation, on stopover habitat associations and migration routes, based on our own work.

STOPOVER HABITAT USE PATTERNS BY SEASON

In general, riparian areas are relatively productive during spring when conditions in much of the West are relatively cool and moist (Anderson et al. 2004, Hardy et al. 2004). In contrast, the productivity of riparian areas during the warmer and drier late summer likely depends on habitat structure and water availability. Larger streams and rivers with a year-round water flow likely remain more productive than smaller streams that are dry during summer. Diversions on streams or small rivers can reduce water availability, which could impact migrant stopover by reducing cover and food availability. Higher elevation habitats may be less productive during spring migration if plant and arthropod phenology does not coincide with migration timing, but would remain productive longer into the summer and autumn due to cooler temperatures and retention of moisture.

Thus, we predict that low to mid-elevation riparian habitats, especially throughout the Great Basin and Intermountain West (more xeric areas), will be especially important to migrants during spring migration. Although larger river systems (that retain water year-round) likely remain important during autumn migration as well (e.g.,

Rio Grande), we predict that autumn migrants also rely on mid- to high elevation deciduous shrublands, mixed woodlands, and coniferous forests because of moisture retention, fruit availability, and a delayed plant and arthropod phenology that provides greater food availability during late summer and autumn. Reliance on montane habitats in the northern Great Basin and Intermountain West should be most pronounced during early migration (late July into August) because the hot, dry conditions at lower elevations are alleviated by cooling temperatures and increasing storm frequency in September and October. One relatively simple and testable approach is to use remotely sensed net primary productivity (NPP) data on a biweekly basis to predict the number of migrants that occur on a regional scale. These NPP data integrate the existing vegetation potential as well as current climatic conditions and may reflect the types of cues that migrants are using to optimize migratory survivorship.

MIGRATION ROUTES

Identifying species- and population-level patterns in migratory routes for western migrants has important implications for how we approach conservation of habitats upon which birds depend, as well as how we predict the impacts of events affecting particular habitats. Based on our present knowledge, we suggest that landbird migration in the West occurs across a relatively broad front pattern (at the species level) but that, within species, routes may vary seasonally and specific populations are likely restricted to narrower migration routes. It is difficult to know whether seasonal differences that are routinely documented reflect relatively local differences in habitat use in spring vs. fall or whether these observations suggest that loop-type migrations are common in the interior West. It seems likely that these patterns will be tied both to potential for local productivity of habitats and regional drivers of that productivity (e.g., monsoons). Ultimately, understanding seasonal differences in the temporal and spatial dynamics of migration requires tracking of individual migrants.

Identifying the relevant scale at which to approach this issue for a given species might be accomplished by examining trends in populations across the breeding range. Species showing variability across populations (i.e., some increasing, others declining) might be displaying evidence of strong connectivity with wintering populations and are best studied at the population level. In contrast, species with weak connectivity would be predicted to exhibit little correlation among breeding population trends and would thus be appropriate for broader scale examinations of migratory routes.

Whereas some details of migration routes and connectivity have come from banding recoveries, more recently, natural markers such as isotope and genetic data have greatly increased our understanding of migration routes and connectivity. These natural markers become even more powerful as tools when combined with radio telemetry data. For example, the combined information from stable isotopes and radio telemetry indicates that different breeding populations of Wilson's Warblers use different migration routes when departing from a stopover site on the lower Colorado River (Paxton and van Riper unpubl. data). Considering the importance of route and connectivity information to migratory bird conservation, a large-scale, collaborative effort using these natural markers to map ranges and migration routes of all migratory species (and populations) is warranted. Further refinement of our knowledge of routes and connectivity will be enhanced by further miniaturization of satellite GPS and other technology to enable tracking of individual birds throughout the annual cycle (e.g., Stutchbury et al. 2009). The recent advent of radios weighing as little as 0.2 g (Naef-Denzler 2006) and the availability of archival tags have pushed the envelope for extrinsic tracking technology to and below the 20 g body size window (Wikelski et al. 2007). In the next decade it will be possible to track the movements of individuals that, heretofore, have been too small to sample.

CONCLUSIONS

Tens of millions of migratory birds depend on stopover habitats in western North America to provide refueling resources during migration. On this journey, birds depend on spatially and temporally restricted resources for water, habitat, and food in otherwise arid or semi-arid landscapes. It is this reliance on habitats of limited spatial extent, particularly riparian habitats, that makes western migratory birds highly vulnerable to environmental change and creates uncertainty for their future. Throughout the West, continued growth and expansion of human populations place increased demands on floodplains for water and land to support urbanization, agriculture, recreation, and other land uses. The result is that regions of the West with high population densities, such as the southwest, have suffered the loss or degradation of much riparian habitat during the last century (Webb et al. 2007). In addition to imperiling numerous obligate riparian breeders, this loss threatens birds during migration by disrupting the habitats upon which

en route migrants depend. Human activities may be affecting birds in non-riparian habitats as well, such as montane deciduous woodlands, and other habitat types and areas that we have yet to fully appreciate in terms of their importance to migrants.

Populations of western migrants will continue to persist only as long as the integrity of the chains of stopover sites connecting their breeding and wintering sites is preserved. This is a formidable challenge under current conditions, made even more daunting by projections of global climate change models (IPCC 2007) predicting changes, including higher temperatures and less precipitation in the North American southwest, likely to alter the suitability of existing stopover sites. Moreover, anticipated changes in bird distributions (northward, upward in elevation) in response to global warming may necessitate new migratory routes, rendering existing stopover sites less important. How migratory birds will respond to the rapid rate of current and future climate change poses an unprecedented challenge to our ability to protect birds and the habitats upon which they depend. The use of climate models to understand the scope and nature (e.g., negative, positive, or neutral) of effects of climate change on bird populations and to delineate ways to mitigate for and adapt to this far-reaching challenge is gaining in popularity (Seavy et al. 2008), as are interdisciplinary collaborative approaches that create opportunities to understand migratory birds within the context of global systems. We encourage these approaches and the advancement they are likely to achieve in securing the future of birds migrating through western North America.

ACKNOWLEDGMENTS

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Table 1. A partial list of primary research findings since 2000 that have altered how we view migration in western North America.

Taxon	Finding	Source
Charadriiformes	Migration occurs as a broad front	Skagen et al. 2008
Passeriformes	Migrant densities are high at high elevations, especially during autumn	Carlisle et al. 2004, DeLong et al. 2005
	Mesquite phenology affects migrant timing	McGrath et al. 2008
	Invasive saltcedar impacts stopover site quality	Walker 2008, Paxton et al. 2008, Cerasale 2004
	Molt migration is a common strategy	Rohwer et al. 2005
Parulidae	Migration timing is related to breeding latitude	Kelly 2006
	Migration routes differ among breeding populations	Paxton 2004, Paxton et al. 2007b
	Wilson's Warblers are leapfrog migrants	Kelly et al. 2002a, Clegg et al. 2003, Paxton et al. 2007b

Table 2. Emerging questions and research needs for migration research as identified by research ecologists and managers, 2004 – 2008.

Topic	Sample question(s) and research needs	Venues[1]
Land Use Change	What are the effects of land use change on migratory life histories?	A, B, C, D
Climate Change	How will climate change influence phenology of migrant passage and food resources, and the quality and distribution of stopover areas?	A, B, C
Habitat Use	What is the relative importance of all habitat types to migrants? What habitats and locations are used for molt migration? How can we determine and measure quality of stopover habitats?	A, C, D
Plasticity and Flexibility	What are the determinants of ecological flexibility in migrants? To what extent can birds alter behavior and physiology to accommodate changing environments? Is there a threshold of environmental change beyond which migrating birds cannot adapt?	A, B, C
Distribution	What migration routes, pathways, and corridors are currently being followed by migrants?	A, C, D
Population Monitoring	Identify gaps in monitoring data. Establish migration monitoring network and list-serve. Standardize protocols.	A, C, D
Linkages	Identify linkages in the annual cycle. Establish connectivity between breeding, migration, and wintering areas.	A, B, C

Population Dynamics	What are the drivers of population dynamics in migratory animals? What levels of mortality occur during migration?	B, C

[1]Venues: (A) a southwest-focused migration workshop in 2004 (Skagen et al. 2004), (B) the inaugural meeting of MIGRATE in 2007, (C) questionnaires associated with a migration symposium at the Cooper Ornithological Society 2007 meeting, and (D) the Partners in Flight Research and Monitoring Needs 2008 database.

Figure 1. Topics for priority research questions on bird migration (left), as defined by research ecologists and conservation practitioners at recent migration meeting venues, and their relationship to potential conservation and management practices (right). All topics relate to understanding migratory bird responses to land use and climate change.