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PIONEERING AND NATURAL EXPANSION OF BREEDING DISTRIBUTIONS IN WESTERN NORTH AMERICAN BIRDS

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Abstract. Using as a baseline the distributional literature of the late 1950s–early 1960s, I compiled records for 24 species of birds from *Audubon Field Notes, American Birds,* and other sources which document massive pioneering and large-scale expansion of nesting distributions over the last three decades in the contiguous western United States. Four northern species have extended their ranges southward, three eastern species have expanded westward, 14 southwestern or Mexican species have moved northward, one Great Basin-Colorado Plateau species has expanded radially, and two Great Basin-Rocky Mountain subspecies have expanded westward. Breeding range expansions in migratory bird species are led predominantly by pioneering males. These range adjustments are not responses to anthropogenic influences. Instead, climatic change in the new regions of occupancy apparently has provided regimes of increased summer moisture and higher mean summer temperature typical of pre-expansion distributions.

Key Words: Birds; pioneering; distributional change; climatic change; western United States.

Because of unusual conspicuousness and mobility, birds are superior organisms for the documentation of rapid distributional change. Such change is often an obvious consequence of widespread, human-induced environmental modification. Given the pervasiveness of avian response to the direct and indirect activities of humans, small wonder that the simultaneous undercurrent of natural distributional change often passes unnoticed.

My purposes are (1) to review records of selected species that document apparently natural examples of pioneering and expanding breeding distributions in western North America, (2) to search for patterns among the taxa reviewed, (3) to discuss processes potentially responsible for any patterns discerned, and (4) to comment on the dynamics of range expansion.

METHODS

Documentation of avifaunal change requires a temporal baseline against which subsequent records can be compared and evaluated. For the western United States, such a baseline was lacking at the turn of the century because avian distributions were too poorly known. From the early 1900s through the 1950s, however, regional avifaunal surveys accompanied by mass collecting established reasonably precise breeding ranges for most species. Thus, the range for each species in the Fifth Edition of the *Check-list of North American Birds* (American Ornithologists' Union [= AOU] 1957) was chosen as the baseline in this study except where noted.

Distributional changes for selected species were identified by comparing this mid-century baseline with subsequently published regional avifaunal compilations, including AOU (1983). For detailed information on pioneers and extralimital nesting over the last three decades, I tallied nesting season records cited in *Audubon Field Notes* (1963–1970) and its successor, *American Birds* (1971–1992). I emphasize extralimital late spring records because they often point to pioneering and imminent summer residence. I define pioneering as the presence of a singing male or a pair in appropriate breeding habitat. Restriction of the tally to late spring vagrants ("overshoots") listed in nesting season reports reduced the chance of including true spring migrants typically listed in the spring migration reports. To save space, records are cited by year, journal abbreviation (either AFN or AB), volume, and page rather than by regional editor. References cited are neither geographically nor temporally exhaustive; instead, they provide an overview of the direction and relative timing of distributional change. Range

expansions represented by abundant records are documented in an Appendix. Because my primary goal was to review natural range expansions, I deliberately excluded species whose distributional histories provided clear evidence of association with human-modified habitats. Scientific and vernacular nomenclature follow the American Ornithologists' Union (1983, 1989).

RESULTS

Northern Species Expanding Southward

Four species of birds with basically northern distributions have expanded their nesting ranges southward over the last several decades. For a number of species, the pioneering and range expansions are continuing.

Larus pipixcan. Franklin's Gull. Alcorn (1988) reported nesting of this species at Carson Lake, Nevada in 1971 and 1975. Malheur Lake, Oregon (Littlefield 1990) and Great Salt Lake, Utah (Behle and Perry 1975), are the nearest persistent nesting colonies, either of which presumably served as the source of the Carson Lake birds. Nesting at Malheur Lake itself only dates from 1948 (Jewett 1949). An expansion of the breeding distribution in Montana is also indicated (Skaar et al. 1985), with either positive or circumstantial evidence of nesting in five and six latilongs, respectively. The American Ornithologists' Union (1957) listed only a single breeding record for Montana. Taylor (1992) documented widespread breeding sites and greater abundance in recent years in Idaho. Spring and summer nonbreeding records in Idaho also have increased. Moreover, the species also now nests in northwestern Wyoming (AOU 1983), a state not included in the breeding distribution outlined in AOU (1957). Finally, pioneering (without definite nesting) is strongly indicated for Colorado, where the species has increased dramatically since the 1920s and where non-breeders are uncommon in early summer (Andrews and Righter 1992). A broad pattern of expanded southerly nesting, spring and summer pioneering, and increased abundance in the northwestern United States is indicated.

Aegolius funereus. Boreal Owl. The AOU (1957) gave the southern limit of the breeding range of this species in western North America as northern British Columbia and central Alberta, with wintering birds spreading southward to southern British Columbia and northern Montana. As Figure 1 illustrates, in recent decades the Boreal Owl has been recorded during the breeding season from southern British Columbia (Campbell et al. 1990) southward through the subalpine forests of northern and eastern Washington, northern and eastern Idaho, western Montana (Hayward et al. 1987, Skarr et al. 1985, Stephens and Sturts 1991, Whelton 1989), to eastern and southern Wyoming (AB 34:917, AB 40:1235, AB 42: 1323), Colorado (Andrews and Righter 1992), and northern New Mexico (Stahlecker and Rawinski 1990, AB 46:1163). Thus, the *entire* mapped nesting distribution in Figure 1 dates from August 1963, when Baldwin and Koplin (1966) discovered juveniles in north-central Colorado. Note that the current nesting distribution extends for hundreds of miles south of the previously known southern limits of the *winter* range.

Many new records were obtained through nocturnal surveys in remote regions in late winter and spring, when this elusive species is calling independently or can be induced to respond either to tape recordings or to whistled imitations of vocalizations. A significant number of summer records, however, surfaced without such surveys: one killed by car (AB 29:1012), one dead on ground (AB 30:984), one dead on road and another found in chimney (AB 33:885), a juvenile in campground (AB 40:1247), and a juvenile being mobbed by chickadees (AB 46:1158). Other owls have been discovered by hikers and forest workers. These records suggest that recent numbers are at least sufficient to have increased the probability of such random encounters.

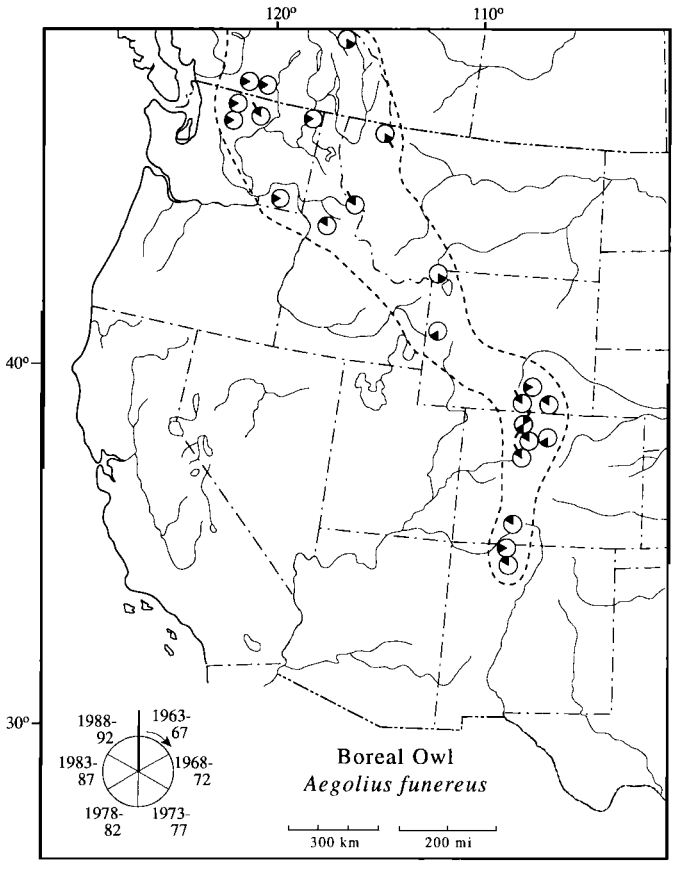


FIGURE 1. The dashed line indicates the approximate border of the current nesting distribution of the Boreal Owl in southwestern British Columbia and the contiguous western United States. *All* symbols represent specific localities of summer presence since 1963. Blackened pie slices denote occurrence in the half-decade period indicated by the diagram in the lower left. A line protruding from the pie slice represents positive evidence of breeding.

Although it will never be possible to establish either former absence or rarity in regions where the species can now be found in numbers, the pattern of records at least suggests an explosive increase since the 1950s in the Cascades and Rocky Mountains. Even if uncommon, this owl would not have been overlooked by naturalists and others active throughout this region during the early part of this century. Whether current populations in the United States resulted from (1) a major southward incursion from Canadian nesting populations, (2) expansion from local and rare relictual distributions surviving in the western mountains since the Pleistocene, or (3) a combination of both sources, cannot be determined.

Seiurus noveboracensis. Northern Waterthrush. Contreras (1988) summarized summer records in the central Cascades of Oregon, where this warbler has been found since 1977. Formerly the species was known in the state only as a straggler (Gabrielson and Jewett 1940). Contreras also cites reports that indicate breeding in Washington, where Jewett et al. (1953) listed it as hypothetical, and recent range expansion and increase in abundance in British Columbia. With reference to Oregon, he states that, "The area was not often visited by observers prior to discovery of the waterthrushes, so the birds may have been present unobserved for many years." Nonetheless, the region of the Cascade Mountains where wa-

terthrushes now occur regularly during the summer was not ignored by bird collectors and other naturalists in the first half of the present century. The large number of new records for Oregon, nesting in Washington, and expansion in British Columbia all point to a population increase and southerly extension of nesting range in the Pacific Northwest in the past 15 years or earlier.

Loxia leucoptera. White-winged Crossbill. AOU (1957) listed this species as breeding sporadically south to Washington, northeastern Oregon, and Montana. Records in the ensuing decades document more continuous summer presence at the southern edge of the known range as well as a major southward range expansion. Positive nesting records have been obtained in Utah in 1977 (Smith 1978), Colorado in 1987 (Groth 1992), and probable breeding either in New Mexico or (nearby) elsewhere in the southern Rockies (AB 36:207). Numbers began to swing upward in the mid-1970s. Widespread summer reports, sometimes of flocks of up to 100 individuals, which indicate extensive nomadism and at least occasional breeding in the subalpine forests of southwestern Canada and the western United States, are provided in the Appendix.

Eastern Species Expanding Westward

In recent decades the following three species of birds of fundamentally eastern North American distribution have invaded western North America.

Strix varia. Barred Owl. Although by the middle of the present century the breeding range of this species reached only as far west as northern British Columbia and eastern Montana (AOU 1957), in recent decades this owl has dramatically expanded westward to the Pacific Coast from southeastern Alaska (AOU 1983) to southwestern British Columbia (Campbell et al. 1990), Washington (Taylor and Forsman 1976), western Oregon (1990, AB 44:1178; 1991, AB 45: 1152–1156), northwestern California (1990, AB 44:1182), southeastern Idaho (Stephens and Sturts 1991), and western Montana (Skaar et al. 1985). The speed with which the expansion occurred has been just as impressive as the distance traversed.

Several authors (Hejl 1994, Root and Weckstein 1994, and references cited therein) have opined that the westward incursion of the Barred Owl is a response to forest fragmentation and increased proportion of second-growth in the Northwest. I see no evidence for this. Indeed, in British Columbia, the region for which the best information on habitat use is available, the species is "primarily a bird of deep forests" (Campbell et al. 1990:374). Moreover, this owl has been recorded in pristine habitats in many regions, e.g., Glacier National Park (AFN 1969, 23:677) and, most recently, near Jackson, Wyoming (AB 1992, 46:1158). Finally, it is relevant to note that widespread logging in northwestern North America antedated the invasion of the Barred Owl by many decades. Until the possible role of human habitat modification is proved, I hypothesize that the range expansion in the Barred Owl has resulted from natural causes.

Empidonax minimus. Least Flycatcher. In the last two decades, a plethora of pioneers, mostly singing males, have moved westward and southwestward in North America from the previously known breeding range of this species (Fig. 2). Nesting has occurred at several sites in British Columbia (1966, AB 20:587; 1968, AB 22:630), northern Washington (1975, AB 29:1009; 1990, AB 44:1179), and at least once in northeastern California (1984, AB 38:1058). The majority of the records fall in the period 1973–1992. The Appendix documents presence and timing by province and state. Note that the distribution of records in space and time is most continuous near the margin of the former range.

Passerina cyanea. Indigo Bunting. From a status in the mid-1950s of rare vagrant, this species has massively invaded the southwestern United States in the last several decades; in several regions it breeds commonly (see map in Payne 1992). Al-

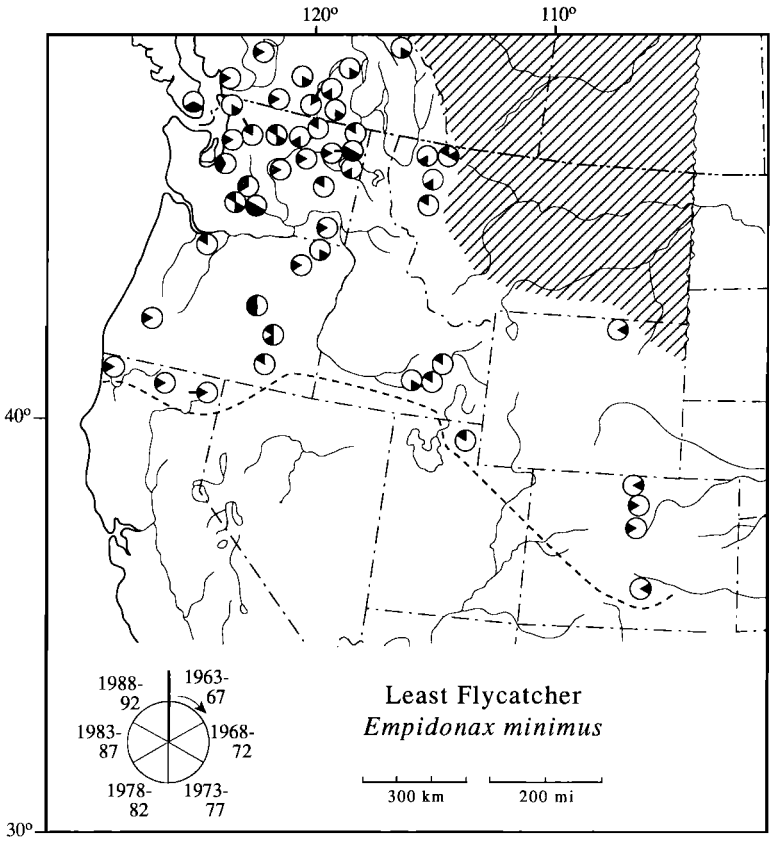


FIGURE 2. The pattern of diagonal lines indicates the approximate nesting range of the Least Flycatcher as of the mid-1950s in southwestern Canada, Montana, and Wyoming. The dashed line demarcates the approximate outline of occurrence of pioneers and new extralimital nesting localities of the species in southwestern British Columbia and the contiguous western United States. See legend to Figure 1 for explanation of symbols.

though some invaders have used thickets and secondary growth resulting from human habitat modification, many have occurred in undisturbed vegetation. Furthermore, secondary growth was available for decades prior to occupancy in much of the southwest and similar seral growth is still unoccupied over vast sections of the northwestern United States. These facts provide evidence that humans have played no obvious role in this expansion. I have not attempted to compile the abundant records.

Southwestern Species Expanding Northward

Fourteen species with traditional ranges in Mexico and the southwestern United States have moved northward since the mid-decades of the present century:

Buteogallus anthracinus. Common Black-Hawk. The AOU (1957) considered Central Arizona to be the northern nesting limit of this species, a status corroborated by Phillips (1968). By the early to mid-1960s it had nested in the Virgin River Valley in Utah and Arizona (Carter and Wauer 1965, Wauer and Russell 1967, Behle and Perry 1975). The AOU (1983) reported attempted breeding in southern Nevada, and Alcorn (1988) included reports from the 1970s and early 1980s from sites as far north as Elgin, Lincoln County. The first occurrence in California was of a spring vagrant in Riverside County, April 1985, reported by Daniels et

al. (1989). In sum, the records indicate persistent recent pioneering and rare nesting at the northern limits of the Mojave Desert.

Buteo albonotatus. Zone-tailed Hawk. This species first appeared in the Santa Rosa Mountains, California, in 1978 and unsuccessfully attempted to nest in 1979–1981 (Weathers 1983). From 1986–1992, Zone-tailed Hawks either definitely or probably nested on Hot Springs Mountain, San Diego County, California (AB 1992, 46:1178). These localities extended the range from nearest known sites in the San Pedro Martír region, northern Baja California (AOU 1957), and at Bill Williams Delta, Lower Colorado River Valley (Rosenberg et al. 1991). Garrett and Dunn (1981) cited several spring records of nonbreeding birds in southern California. The increasing frequency of these records in the 1970s suggests persistent pioneering from the south and southeast. Spring and early summer sight records from southern Nevada from 1975–1980 (Alcorn 1988) also fit this pattern.

Caprimulgus vociferus. Whip-poor-will. Although extralimital breeding has not been reported because of the difficulty of finding nests, numerous late spring and summer records of calling birds document a clear pattern of northward pioneering in the southwestern United States (Fig. 3). Citations for specific records are listed in the Appendix.

Euptilotus neoxenus. Eared Trogon. Although rare in adjacent Mexico, this species has appeared irregularly in the summer months since 1977 in the mountains of southeastern Arizona (1989, AB 43:1350; 1991, AB 45:1146; 1992, AB 46:1161). Two reports for east-central Arizona in June 1992 (AB 46:1161) require confirmation.

Myiarchus tyrannulus. Brown-crested Flycatcher. Traditionally a Colorado Desert or Sonoran species, in recent decades this flycatcher has expanded northwestwardly to the limits of the Mojave Desert in California, Nevada, and Utah (Fig. 4). Documentation for the new mapped localities is given in the Appendix.

Dendroica graciae. Grace's Warbler. This warbler pioneered to appropriate habitat in California from 1974–1977 (Johnson and Garrett 1974, Garrett and Dunn 1981), and was established for breeding by the early 1970s in at least five mountain ranges in southern Nevada where previously unknown (Johnson 1965, 1973, 1974).

Cardellina rubrifrons. Red-faced Warbler. This is a weakly expanding species, with scattered records of pioneers from 1973–1978 in California (AB 27:920; AB 29:1036; Garrett and Dunn 1981) and Arizona (AB 29:1017; AB 31:1174; AB 32: 1197) and an extralimital nesting in New Mexico in 1982 (AB 36:1007). New localities are plotted in Figure 5.

Setophaga picta. Painted Redstart. A pattern of irregular northern pioneering in this species is evidenced by repeated spring records of visitants and at least one nesting record in southern California (Johnson and Garrett 1974, Garrett and Dunn 1981), southern Nevada (Johnson 1965, Alcorn 1988), southwestern Utah (Behle and Perry 1975), central-western Colorado (Andrews and Righter 1992), Arizona (Monson and Phillips 1981), and New Mexico (Hubbard 1978).

Piranga flava. Hepatic Tanager. Recent decades have seen extralimital nesting of this tanager in California and Colorado and a scattering of late spring and summer pioneers (Fig. 6). Citations for these records are in the Appendix.

Piranga rubra. Summer Tanager. Reflecting their common preference for riparian habitats, this species and the Brown-crested Flycatcher show strikingly similar range expansions in southern California, southern Nevada, and southeastern Utah (Fig. 7). In contrast to the flycatcher, however, the tanager has also spread northward in New Mexico, apparently from the Rio Grande Valley. The Appendix lists specific citations for new records.

Guiraca caerulea. Blue Grosbeak. This species has expanded its summer range northward by several hundred miles over the last three decades (Fig. 8). A surprising

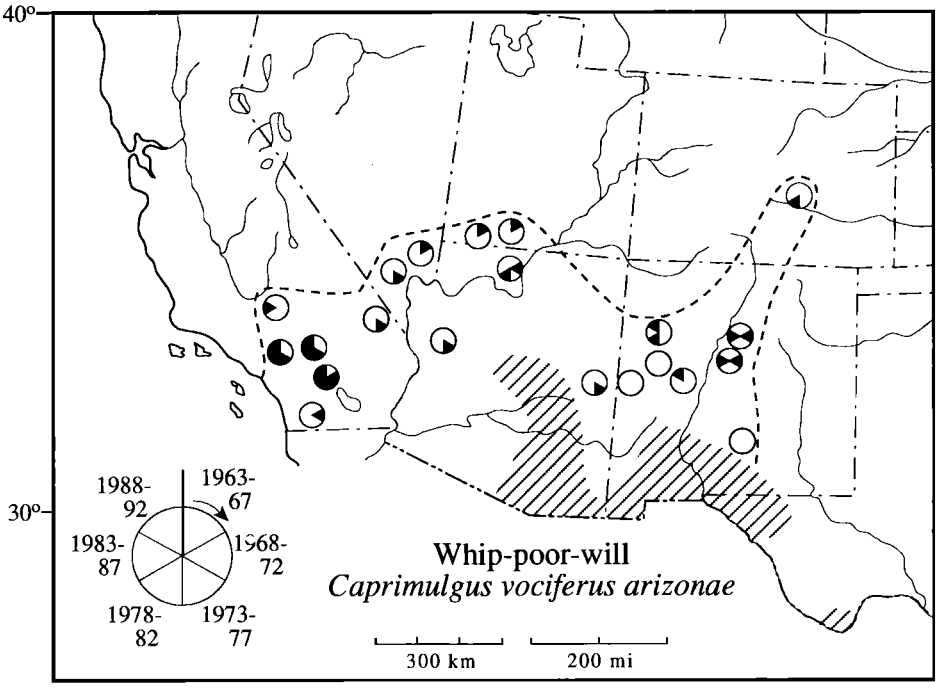


FIGURE 3. The pattern of diagonal lines indicates the approximate nesting range of the southwestern form of the Whip-poor-will as of the mid-1950s in Arizona, New Mexico, and Texas. The dashed line indicates the approximate northern limit of occurrence in the last three decades of extralimital summer birds without proof of nesting. Empty circles represent localities without specific dates in the literature. See legend to Figure 1 for explanation of other symbols.

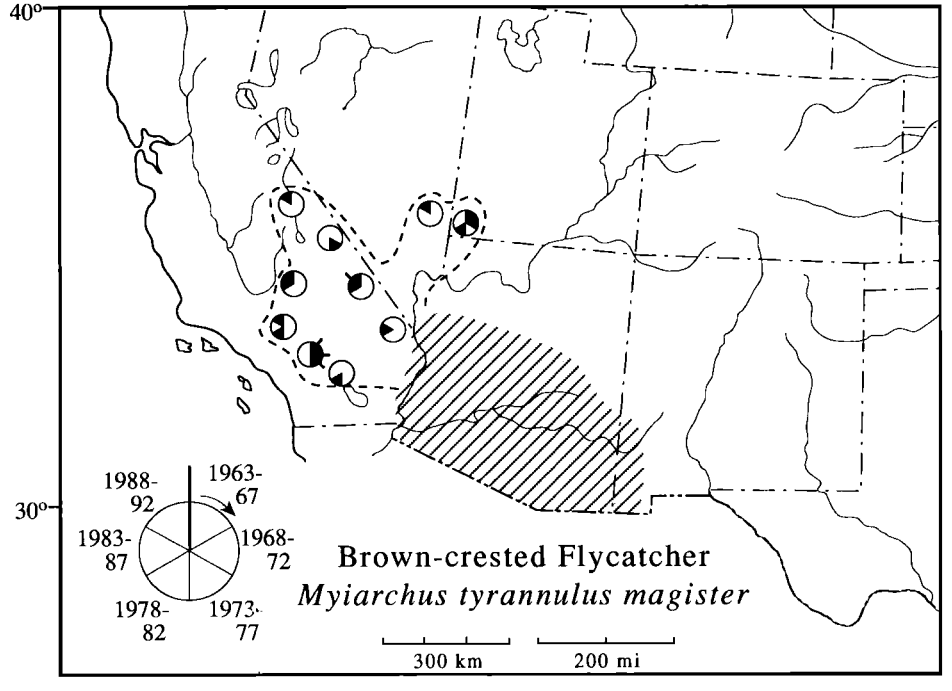


FIGURE 4. The Pattern of diagonal lines indicates the approximate nesting range of the northwestern form of the Brown-crested Flycatcher as of the mid-1950s in southeastern California, Arizona, and southwestern New Mexico. The dashed line indicates the approximate limits of pioneering and of nesting (symbols with protruding lines) in the last three decades. See legend to Figure 1 for explanation of symbols.

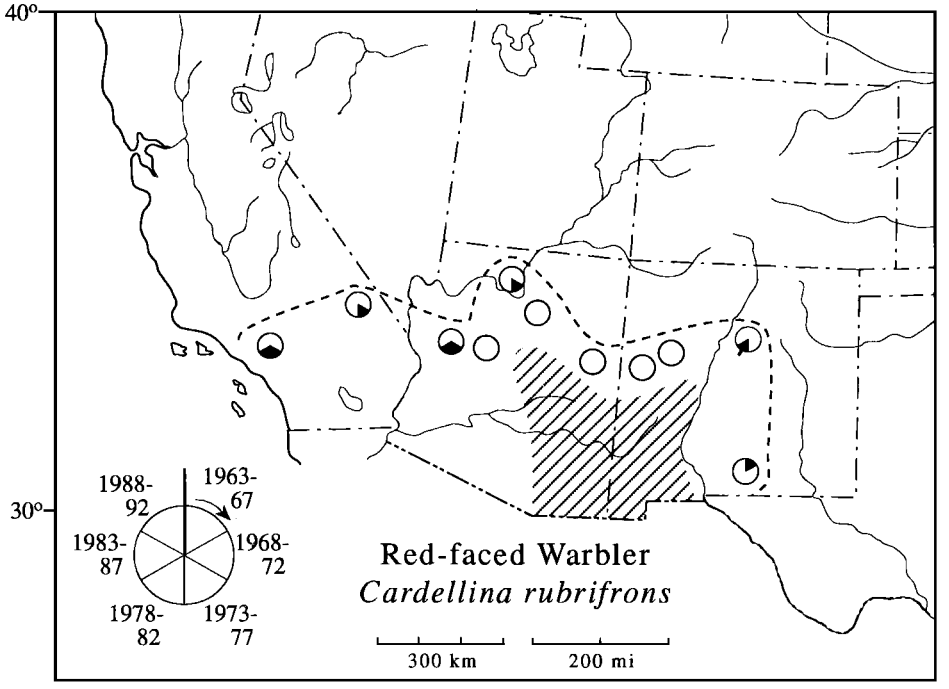


FIGURE 5. The pattern of diagonal lines indicates the approximate nesting range of the Red-faced Warbler as of the mid-1950s–early 1960s in Arizona and southwestern New Mexico. The dashed line shows the northern limit of the occurrence of pioneers and one extralimital nesting in northcentral New Mexico in the last three decades. See legend to Figure 1 for explanation of symbols.

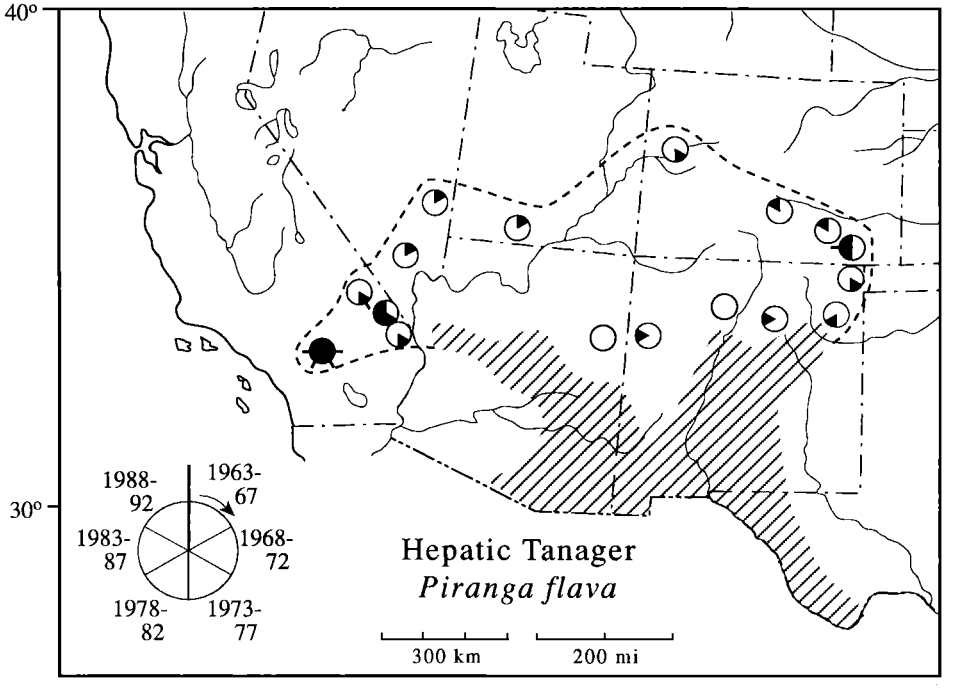


FIGURE 6. The pattern of diagonal lines indicates the approximate nesting range of the Hepatic Tanager as of the mid-1950s–early 1960s in Arizona, New Mexico, and western Texas. Symbols denote localities of westward and northward pioneers and colonists in the last three decades. See legend to Figure 1 for explanation of symbols.

number of positive nesting localities are plotted: southern Idaho (1981, AB 35:963; 1986, AB 40:1232), west-central Nevada (1969 [Alcorn 1988], Utah (1990, AB 44: 1163), Wyoming (1982, AB 36:1002; 1985, AB 39:944), and Colorado (1971, AB 25: 887; 1984, AB 38:1047; 1987, AB 41:1470). Specific references documenting these mapped records, and a few recent occurrences near the periphery of the former known range, are provided in the Appendix.

Icterus parisorum. Scott's Oriole. Since the 1960s, this oriole has steadily pioneered northward and colonized the interior of the contiguous western United States. Probable or certain nesting has been reported in southeastern Idaho (1972, AB 26:886), northern Nevada (1976, AB 30:985; 1980, Alcorn [1988]), central Utah (1963, AFN 17:474; 1965, AFN 19:568; 1971, AB 25: 887; 1980, AB 34:917), southwestern Wyoming (1982, AB 36:1002), and western Colorado (1980, AB 34:917; 1983, AB 37: 1012). Principal new late spring and summer localities are plotted in Figure 9. Citations of reports which document these mapped localities and other peripheral nesting season stations are given in the Appendix.

Aimophila cassinii. Cassin's Sparrow. Faanes et al. (1979:164) reported that "In a period of only 5 years [1974–1979], Cassin's Sparrow has apparently extended its breeding range into Wyoming, Nebraska and South Dakota. Maximum extension was the Wyoming record, a distance of 350 km." These authors also mention other reports from the same time period of range expansion in more southern regions of the western United States.

Amphispiza quinquestriata. Five-striped Sparrow. The first record of this species for the United States was from southern Arizona in June 1957. The next report (1969) was from Patagonia, Arizona where it had not been found previously despite repeated earlier visits by ornithologists, but where it has been found every year since. Mills (1977) reported a substantial number of local populations in southern Arizona which held a combined minimum estimate of 57 adults in 1977. Monson and Phillips (1981:195) termed the species, "A presumed recent immigrant from Mexico."

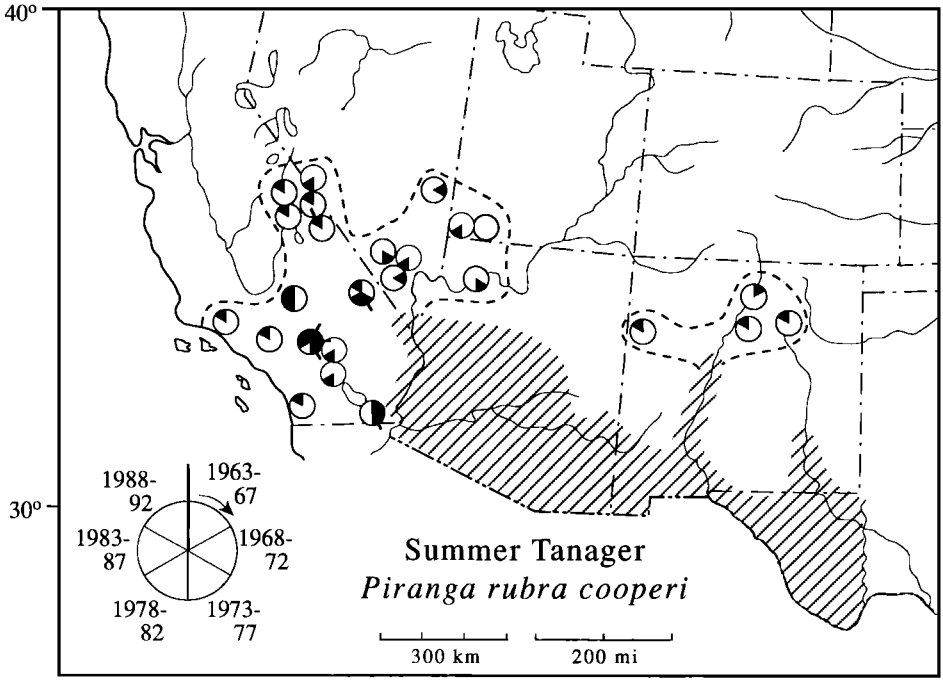
Great Basin-Colorado Plateau Species Expanding Radially

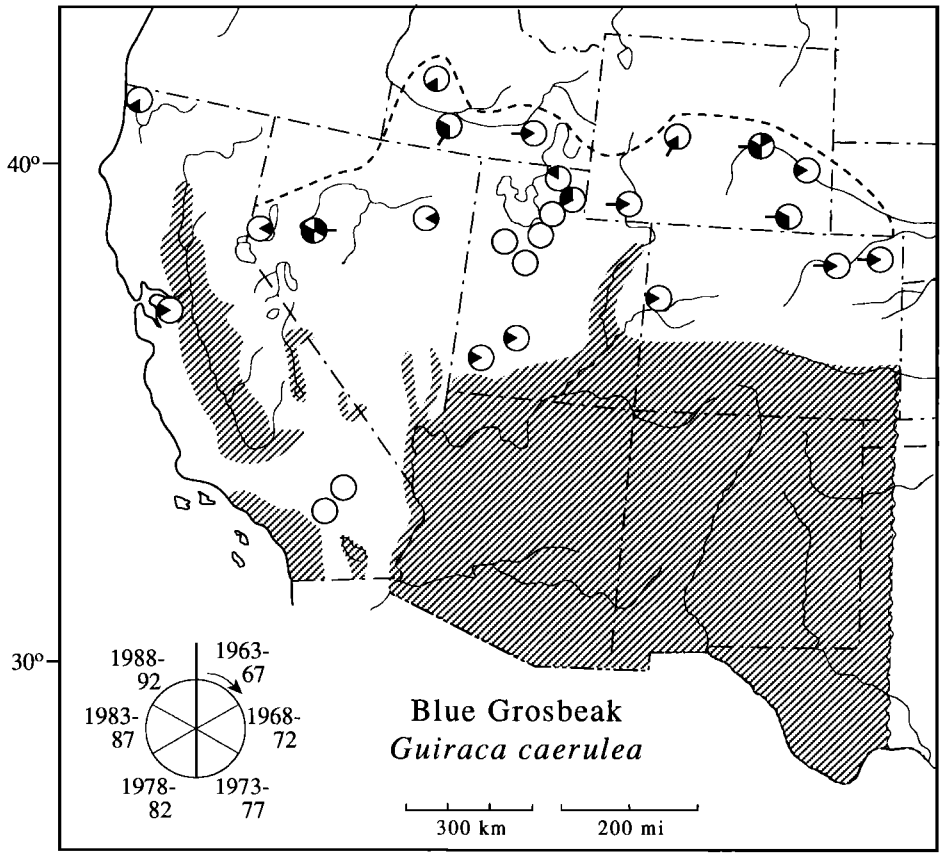
Empidonax wrightii. Gray Flycatcher. This species has expanded its nesting range in all directions from the former stronghold in the Great Basin and Colorado Plateau (Fig. 10). Furthermore, it is now common or abundant at many of the new localities and nests to the periphery of the new distribution. Johnson and Garrett (1974) and Johnson and Cicero (1985) provided detailed records for new localities in southern and central California, and Cannings (1987) discussed the extension into Washington state and British Columbia. Documentation for additional mapped locality symbols is found in the Appendix.

Great Basin-Rocky Mountain Subspecies Expanding Westward

Vireo solitarius plumbeus. Solitary Vireo. Johnson (1965, 1973, 1974) documented the spread of this form in southern Nevada, and Johnson and Garrett (1974) reviewed records for westward colonization in California, where it was first detected in the summer of 1962. This major adjustment in breeding range continues, for in June 1988, *V. s. plumbeus* was found in Alpine County, California and recently it reached northern Lander County (June 1991), Pershing County (June 1992), and Humboldt County (June 1993), Nevada (NKJ ms).

Anthus rubescens. American Pipit. Miller and Green (1987) carefully chronicled the westward incursion of the form *A. r. alticola* into the alpine zone of the central and southern Sierra Nevada. The first breeding season reports date from 1971–1972, and the first nests were found in 1975. By the mid-1980s, the species was nesting commonly. Importantly, prior to the discovery of breeding pipits in the Sierra Nevada, many early or-


40°
30°
1988-92
1963-67
1983-87
1968-72
1978-82
1973-77
Summer Tanager
Piranga rubra cooperi
300 km
200 mi


40°
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1988-92
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1983-87
1968-72
1978-82
1973-77
Blue Grosbeak
Guiraca caerulea
300 km
200 mi

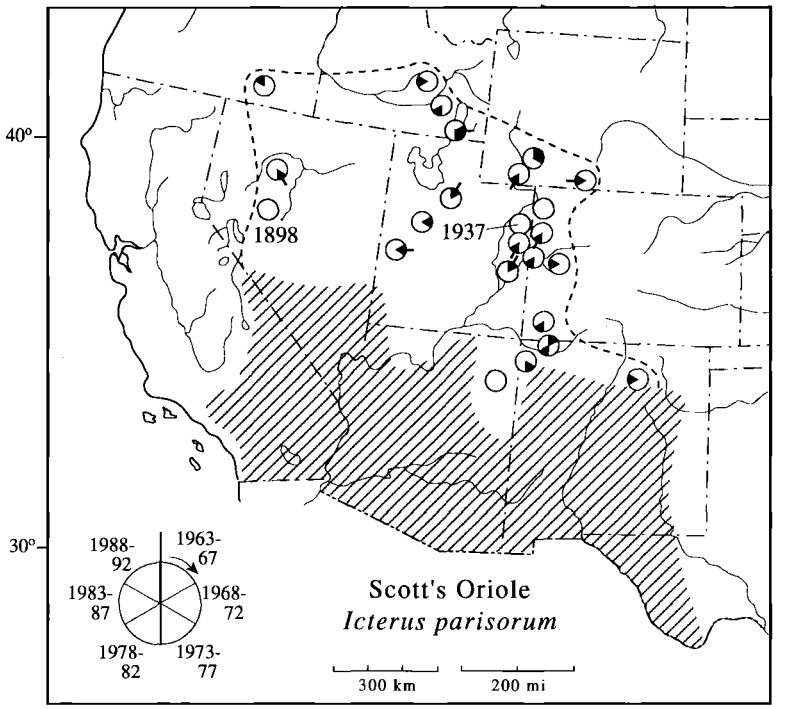

FIGURE 9. The pattern of diagonal lines shows the approximate nesting range of the Scott's Oriole in the Southwest as of the middle of the present century. The northern limit in Nevada is based in part on records in Linsdale (1936). The two dated locality symbols are documented in Oberholser (1918) and Twomey (1942). Records of the last three decades document pioneering and extralimital nesting to the extent of the dashed line. See legend to Figure 1 for explanation of symbols.

nithologists and other naturalists had spent extended periods in the alpine zone of that range without encountering this species as a summer resident.

DISCUSSION AND CONCLUSIONS

Patterns of Distributional Change

In common with ecologic niches, breeding distributions of birds are species-specific. Unique geographic ranges presumably reflect the unique spatial distribution of places which satisfy the innate requirements of each species. These needs include particular kinds of food, foraging and nesting sites, refuges, and innately selected habitats, all within preferred daily and seasonal regimes of temperature and humidity (Grinnell 1914, 1917; Salt 1952). Given these idiosyncratic requirements, broad distributional congruence among species is not to be expected. Nonetheless, four disparate taxa, a gull, an owl, a warbler, and a finch, demonstrated southwardly-expanding ranges. Similarly,

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FIGURE 7. The pattern of diagonal lines shows the approximate breeding range of the western form of the Summer Tanager as of the mid-1950s–early 1960s in the Southwest. Localities of range expansion by pioneers and colonists in the last three decades are denoted by the symbols and dashed line. See legend to Figure 1 for explanation of symbols.

FIGURE 8. The pattern of diagonal lines demarks the approximate breeding regions of the Blue Grosbeak in the southwestern United States as of the mid-1950s–early 1960s. Symbols for the occurrence of pioneers and new nesting localities in the last 30 years are enclosed by a dashed line that indicates the approximate boundary of the range expansion. See legend to Figure 1 for explanation of symbols.

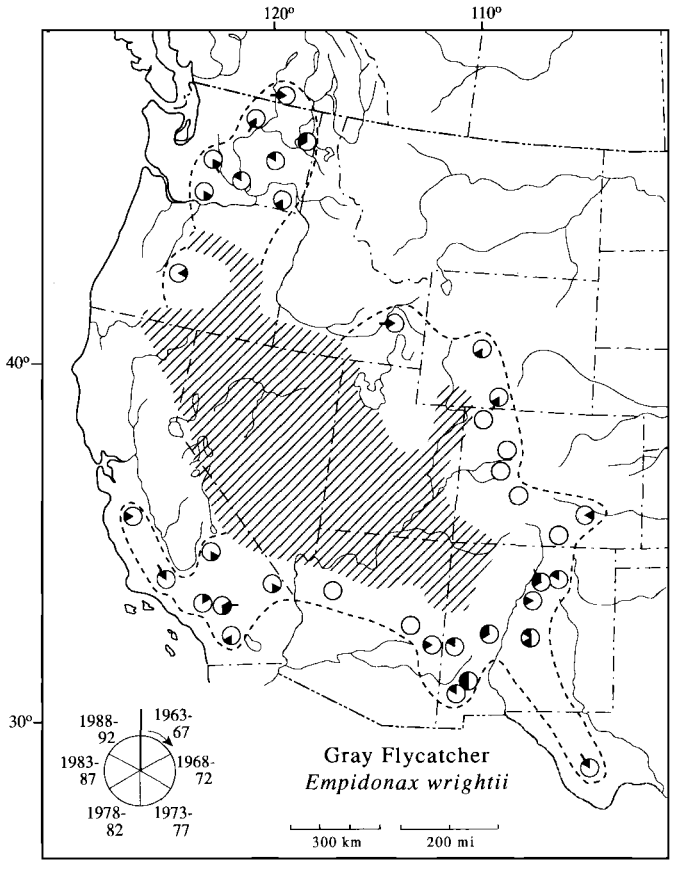

FIGURE 10. The pattern of diagonal lines shows the approximate breeding range of the Gray Flycatcher as documented by Johnson (1963). Localities of extralimital nesting and a few pioneers in the last 30 years are indicated. See legend to Figure 1 for explanation of symbols.

three species traditionally with eastern distributions, an owl, a flycatcher, and a bunting, have moved westward. Remarkably, an even more diverse group of species of southwestern distribution, two hawks, a nightjar, a trogon, a flycatcher, three species of warblers, two tanagers, a grosbeak, an oriole, and two sparrows, have enlarged their nesting distributions toward the north. (This pattern is not confined to birds. Davis and Callahan [1992] reported similar northward movement of 19 species of mammals in the Southwest.) Such broad-scale range adjustments that transcend taxonomic boundaries suggest that coincidental distributional barriers for groups of species have been lifted.

Are these expanding species reclaiming ground occupied in the past? Other "eastern" species, e.g., Ruffed Grouse (*Bonasa umbellus*), Veery (*Catharus fuscescens*), and Red-eyed Vireo (*Vireo olivaceus*), currently breed northwestward to British Columbia and Washington state or beyond. Perhaps the Barred Owl and Least Flycatcher, two species with broadly similar nesting ranges, are returning to regions of former occurrence. Their "expansions" could thus reflect the ebb and flow expected at range margins. Furthermore, some distributional "expansions" described here may actually be range *shifts* in which regions are evacuated in one part of the distribution as a wave of colonization advances elsewhere. The Franklin's Gull and Cassin's Sparrow, for example, may be retreating locally in the Great Plains (Knopf 1994) with simultaneous ex-

pansion elsewhere. For the southwestern species whose southern limits are in Mexico, data to answer this question are unavailable. For the Barred Owl and Least Flycatcher, however, possible population reduction and range shrinkage in the eastern United States concomitant with expansion in the northwest could be investigated.

Suggested Explanation for Natural Range Expansions

The 24 species dealt with here have enlarged their breeding ranges for reasons apparently unrelated to direct human modification of the environment. Instead, I propose that pervasive climatic change over the past several decades in the contiguous western United States is the most likely explanation. Although climatic warming is probably involved, especially for those southwestern species that are invading northward, it is probably neither the sole explanation nor even the primary cause for range adjustments among the expanding species as a group. First, despite an overall global trend in warming, parallel mean temperature increases for specific regions are not to be expected (Schneider 1993). Second, it is difficult to comprehend how climatic warming could assist either the southward expansions of northern species or the westward expansions of eastern species. Instead one must seek a regional common denominator of climatic change that could encourage movement into the western United States by clusters of species with pre-expansion ranges in either the north, east, or southwest.

Increased summer moisture is such a common denominator. Except for the Gray Flycatcher, whose radial expansion remains unexplained, most expanding species had former nesting distributions in regions with higher summer rainfall and humidity than in regions now being colonized. For example, wet summers and high humidity typify the eastern distributions of the Barred Owl and Least Flycatcher, and the northern distributions of the Boreal Owl and White-winged Crossbill. Similarly, convective, monsoonal precipitation characterizes summer climatic regimes of the American southwest and northern Mexico, where many species are now advancing northward. I hypothesize that many of these species are responding primarily to a decades-long increase of summer rainfall in regions beyond their former ranges. A concomitant rise in mean temperature during the nesting season may have encouraged range adjustments of some species.

Climatic information for the contiguous western United States offers broad support for wetter and warmer summers in recent decades. Specifically, Diaz and Quayle (1980:259), in comparing rainfall patterns of the period 1921–1954 with 1956–1977, stated that "summer precipitation in the far western United States was greater in the recent period compared to the previous one." Moreover, summer patterns showed that "the West was much wetter while the East was generally drier" since the mid-1950s.

Selected climatic data from California provided by Goodridge (1992) are also in agreement. Both temperature and rainfall increased dramatically from the mid-1970s to mid-1980s over much of the state. (A reversal in total precipitation initiated a half decade of drought in the late 1980s and early 1990s.) Goodridge (1992) also documented the "strong heating trend" of 0.026 degrees per year for 10 stations on the southeastern deserts of California from 1909–1991, as well as an unspecified increase in rainfall at interior versus coastal California stations from 1889–1991. These trends could have promoted extralimital colonization of Brown-crested Flycatchers and Summer Tanagers, for example. At the base of the Santa Rosa Mountains, California, Weathers (1983:12–13) recorded sharp increases in rainfall in the period 1976–1980, over averages from 1961–1975, and specifically attributed to wetter summers the unprecedented nesting of Zone-tailed Hawks in 1978.

Climatic information from southern Ne-

vada clearly conforms with the hypothesis of increased summer moisture in recent decades in the American Southwest. From 1965–1970, when the record ended, the Palmer Drought Index reflected a series of wet years which contrasted with a long span of relatively continuous drought from 1953–1964 (Houghton et al. 1975).

Thus, regional climatic trends agree broadly with the hypothesis that increased summer moisture, perhaps coupled with a higher mean temperature, has encouraged recent avian range expansions in the western United States. Nonetheless, detailed correlations of local climatic data with the temperature and moisture requirements of individual species will be necessary to establish causality. The classic research of Salt (1952), who demonstrated the close association of preferred ranges of temperature and vapor pressure with distribution and metabolic efficiency in three species of finches (*Carpodacus*), represents the approach ultimately necessary for a real understanding of the relationship between changing regional climatic patterns and major range expansions. The investigation of climatic adaptation in species of magpies (*Pica*) by Hayworth and Weathers (1984) represents a careful modern study of similar issues. Williamson (1975) and Brewer (1981) offered general discussion of the relationship of avian distributions to climatic change.

Pioneering and the Dynamics of Expanding Nesting Distributions

Grinnell (1922) proposed that individuals occurring irregularly beyond the usual distributional limit of the species ("accidentals") are the chief instruments of range expansion. Such accidentals were hypothesized to typically emanate from peripheral or "frontier" populations, to be prone to pioneering, and to be adapted to marginal conditions. Such peripheral populations, with death rates exceeding birth rates, were thought to be sustained by the continual input of individuals from more successful, central populations where birth rates exceed death rates. Thus, nearly three-quarters of a century ago, Grinnell (1922) clearly captured the essence of the theoretical process known to modern ecology as the "Source-Sink hypothesis" (Pulliam 1988). Grinnell emphasized (1922:378) that the "great majority of these pioneers . . . [occur in the] autumnal season when the movement is most in evidence. . . ." Such accidentals typically represent strong flying, migratory species; some, however, include "the most sedentary of species" (Grinnell 1922:375).

In considering the role of the accidental as discussed by Grinnell, Newman (1976: 921) questioned how "*autumnal* straying leads to expansion of the *breeding* range" (italics his) and noted that, "no such explanation seems required in the case of summer rarities . . . the transformation from stray to breeder seems simple and direct."

Grinnell's and Newman's apparently contradictory views can be reconciled and refined. In support of Grinnell's position, I suggest that for *permanently resident species* it is easy to envision pioneering by fall immatures which eventually find extralimital sites in which to breed the following spring. But, as Newman suggests, spring vagrants, not fall accidentals, would serve more logically as colonists during the season when the nesting range is actually expanding. Although Newman does not explicitly identify *migratory species* as being more likely than resident species to produce such vagrants during the spring movement, I suggest that such a distinction is significant. Furthermore, increasing evidence on the nature of spring and summer vagrants, as documented by accumulated records in *American Birds* and other sources, points to *males* as the predominant sex of individuals leading the vanguard of spring-summer range expansion. Importantly, in many species males often preceed females in northward migration (Welty and Baptista 1988). These extralimital males are often discovered because they are singing and holding territories; witness the astounding numbers of vagrant

eastern vireos and warblers singing on territories in several western states during the spring–summer of 1992 (AB 46:1159, 1162, 1175–1176, 1179–1180; Terrill et al. 1992). Although the initial discovery of males versus females is somewhat biased by the easier detectability of the former (singing and, in some species, more vivid coloration), I note that many of these birds defended territories for days or weeks without evidence of the presence of a female. This point is also vividly illustrated by the westwardly invading Indigo Bunting in which spring-summer vagrants are overwhelmingly males.

An especially illuminating example of the nature of breeding range expansion is provided by the American Redstart (*Setophaga ruticilla*). In 1981, this basically eastern species formed an unprecedented pioneering colony (evidently without nesting) at the mouth of the Klamath River, California (1981, AB 35:976–977). The first individual (sex unmentioned) was recorded on June 9. On June 21, *nine* singing males and *one* female were noted. By July 5, the number of males had decreased to four and the number of females had increased to five. None could be located on July 31. The species had nested twice before in the same region of northwestern California (1972, AB 26:898; 1980, AB 34:928).

The Biological Significance of Rapid Distributional Change in Birds

Rapid natural adjustments over long distances in nesting distributions of birds must be dealt with by diverse kinds of biologists. For example, avian biogeographers (e.g., Mengel 1964 and others) who have proposed models of speciation in which avian distributions track the migration and disjunction of vegetation across vast distances and over millenia should be disconcerted by range shifts over equally great distances, but over decades, time spans too brief for significant vegetational change. Likewise, the concept of "indicator species" for particular regions should be reconsidered. How can we describe Scott's Oriole as an indicator of upland Mojave Desert given that it nests in Idaho and Wyoming? Similarly, the Gray Flycatcher, now nesting from British Columbia to west Texas, should no longer be termed a "Great Basin-Colorado Plateau" species.

Community ecologists have long been impressed with invasions of plants and animals. Most examples of invasions, however, are in response to anthropogenic activity (Elton 1958). The natural range changes described here are thus of special interest. Several species (e.g., Barred Owl, Gray Flycatcher, Summer Tanager, Indigo Bunting) are now common or abundant in sections of their new ranges and would be expected to significantly alter local interspecific relationships. How could the addition of numbers of a large predator such as the Barred Owl not influence prey dynamics in the forests of southwestern British Columbia? The extralimital establishment of 32 territories of Gray Flycatchers in the Davis Mountains, Texas (1991, AB 45: 1137), of 60 Summer Tanagers along the South Fork of the Kern River, California (1991, AB 45:1162), and a minimum of 55 singing male Indigo Buntings in June–July 1977 at several sites along the Lower Colorado River Valley (Rosenberg et al. 1991), surely has also altered biotic relationships in those areas.

Finally, natural range extensions offer an important message to the conservationist. Namely, populations of at least some species of birds are healthy enough to provide sources for significant numbers of pioneers and potential colonists. However, as my conservationist colleague, Robert C. Stebbins, feared when informed of these data, this optimistic news may conceal a problem. Those either unaware of or oblivious to the deleterious effects of widespread environmental deterioration on many bird species may seize upon these few examples of range expansion as evidence that habitat destruction is not only inconsequential to bird populations but that it may actually benefit them. Whereas I anticipate such

misrepresentations, they can readily be countered by a mounting body of evidence to the contrary.

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APPENDIX I. (Sequence of species follows AOU 1983.)

Caprimulgus vociferus. Whip-poor-will. California (Jones 1971; 1968, AB 22:649; 1970, AB 24:717; 1971, AB 25:907; 1973, AB 27:919; 1974, AB 28:950; 1975, AB 29:1033; 1976, AB 30:1004; 1977, AB 31:1190; 1978, AB 32:1209; 1979, AB 33:897; 1980, AB 34:930; 1981, AB 35:979; 1982, AB 36:1016; 1983, AB 37:1028; 1984, AB 38:1062; 1985, AB 39:963; 1986, AB 40:1256; 1987, AB 41:1488; 1990, AB 44:1187; 1991, AB 45:1162); Nevada (Johnson 1965, Alcorn 1988); Utah (Behle and Perry 1975); Colorado (1981, AB 35:965; Andrews and Righter 1992); Arizona (Phillips et al. 1964; Brown et al. 1987; Rosenberg and Terrill 1986; 1973, AB 27:904; 1975, AB 29:1016); and New Mexico (1971, AB 25:890; 1972, AB 26:889; 1981, AB 35:967; 1982, AB 36:1006; 1983, AB 37:1015; 1990, AB 44:1168; 1992, AB 46:1163).

Empidonax minimus. Least Flycatcher. Alaska (1982,

36:1008); British Columbia (1966, AB 20:587; 1968, AB 22:630; 1969, AB 23:677; 1973, AB 27:895; 1974, AB 28:927; 1975, AB 29:1009 and 1023; 1978, AB 32: 1189; 1979, AB 33:882 and 892; 1982, AB 34:924; 1983, AB 37:1009; 1984, AB 38:1055; 1985, AB 39: 940 and 955; 1986, AB 40:1247); Washington (1968, AB 22:630; 1974, AB 28:927; 1975, AB 29:1009; 1976, AB 30:981 and 995; 1977, AB 31:1165; 1979, AB 33: 882; 1981, AB 35:962; 1983, AB 37:1021; 1984, AB 38:1043; 1985, 39:940; 1986, AB 40:1231; 1987, AB 41:1465 and 1480; 1988, AB 42:1320; 1989, AB 43: 1344; 1990, AB 44:1179; 1991, AB 45:1153; 1992, AB 46:1172); Oregon (1977, AB 31:1165; 1982, AB 36: 999; 1983, AB 37:1009; 1984, AB 38:1043 and 1055; 1985, AB 39:940; 1988, AB 42:1320; 1989, AB 43: 1344; 1990, AB 44:1179; 1991, AB 45:1153; 1992, AB 46:1172); California (1983, AB 37:1025; 1984, AB 38: 1058; 1986, AB 40:1252); Idaho (1977, AB 31:1165; 1989, AB 43:1344); Montana (1971, AB 25:886; 1978, AB 32:1189; 1989, AB 43:1344; 1990, AB 44:1160); Wyoming (1971, AB 25:886; 1986, AB 40:1235); Utah (1989, AB 43:1348); Colorado (1971, AB 25:886; 1972, AB 26:885; 1983, AB 37:1012; 1986, AB 40:1235).

Empidonax wrightii. Gray Flycatcher. British Columbia (1986, AB 40:1175, 1231); Washington (1973, AB 27:895; 1974, AB 28:927; 1975, AB 29:1009; 1976, AB 30:981; 1977, AB 31:1165; 1978, AB 32:1189; 1980, AB 34:913; 1985, AB 39:940; 1990, AB 44:1179; 1991, AB 45:1154; 1992, AB 46:1172); Oregon (1970, AFN 24:701); California (1968, AFN 22:649; 1969, AFN 23:696; 1975, AB 29:1033; 1979, AB 33:898; 1989, AB 43:1368–1369; 1990, AB 44:1188); Idaho (1985, AB 39:940); Montana (1990, AB 44:1160); Wyoming (1981, AB 35:963, 965; 1982, AB 36:1001; 1985, AB 39:944), Colorado (1971, AB 25:886); New Mexico (1977, AB 31:1173; 1978, AB 32:1196; 1982, AB 36: 1006; 1984, AB 38:1051; 1986, AB 40:1241; 1987, AB 41:1474; 1988, AB 42:1327; 1990, AB 44:1168; 1992, AB 46:1164); Arizona (1984, AB 38:1049); Texas (1991, AB 45:1137).

Myiarchus tyrannulus. Brown-crested Flycatcher. California (1964, AFN 18:536; 1965, AFN 19:578; 1967, AFN 21:605; 1970, AFN 24:718; 1971, AB 25: 907; 1973, AB 27:919; 1974, AB 28:950; 1978, AB 32: 1209; 1986, AB 40:1256; 1987, AB 41:1488; 1988, AB 42:1341; 1989, AB 43:1369; 1990, AB 44:1188; 1991, AB 45:1162; 1992, AB 46:1179); Nevada (Alcorn 1988, N. K. Johnson specimen in breeding condition from Meadow Valley Wash, Lincoln County, May 25, 1989); Utah (Behle and Perry 1975; 1978, AB 32:1193; 1981, AB 35:965 [record requires confirmation]).

Piranga flava. Hepatic Tanager. California (Johnson and Garrett 1974; 1971, AB 25:907; 1972, AB 26:907; 1973, AB 27:920; 1974, AB 28:951; 1975, AB 29:1036; 1976, AB 30:1005; 1977, AB 31:1191; 1978, AB 32: 1210; 1981, AB 35:980; 1982, AB 36:1017; 1983, AB 37:1028; 1984, AB 38:1063; 1985, AB 39:963; 1986, AB 40:1256; 1987, AB 41:1489; 1992, AB 46:1180); Nevada (Johnson 1965; one at Eureka [not plotted on map], June 19 [1977, AB 31:1170]); Utah (Behle and Perry 1975); Colorado (1973, AB 27:901; 1979, AB 33:886; 1983, AB 37:1012; 1985, AB 39:944; 1989, AB 43:1348; 1990, AB 44:1163); Arizona (Phillips et al. 1964; Rosenberg and Terrill 1986); New Mexico (1976, AB 30:989; 1980, AB 34:920; 1983, AB 37: 1017; 1984, AB 38:1051; 1985, AB 39:950; 1986, AB 40:1241).

Piranga rubra. Summer Tanager. California (1964, AB 18:536; 1966, AB 20:600; 1967, AB 21:605; 1968, AB 22:650; 1972, AB 26:907; 1973, AB 27:920; 1974, AB 28:951; 1977, AB 31:1191; 1978, AB 32:1210; 1979, AB 33:898; 1981, AB 35:980; 1985, AB 39:963; 1987, AB 41:1489; 1988, AB 42:1341; 1989, AB 43: 1369; 1991, AB 45:1162; 1992, AB 46:1180); Nevada (1977, AB 31:1170; 1982, AB 36:1002; Alcorn 1988); Utah (Behle and Perry 1975; 1978, AB 32:1193); Arizona (Brown et al. 1987); New Mexico (Hubbard 1978; 1992, AB 46:1164).

Guiraca caerulea. Blue Grosbeak. California (1977, AB 31:1187; 1979, AB 33:895; 1985, AB 39:960; 1992, AB 46:1176); Idaho (1981, AB 35:963; 1982 AB 36: 1000; 1986, AB 30:1232); Nevada (1969, AFN 23:680; 1984, AB 38:1047); Utah (1985, AB 39:944; 1986, AB 40:1236; 1987, AB 41:1470; 1989, AB 43:1348; 1990, AB 44:1163); Wyoming (1965, AFN 19:568; 1982 AB 36:1002; 1984, AB 38:1047; 1985, AB 39:944; 1987, AB 41:1470); Colorado (1971, AB 25:887; 1984, AB 38:1047; 1987, AB 41:1470).

Icterus parisorum. Scott's Oriole. Oregon (1991, AB 45:1155 [a female and, hence, perhaps not a pioneer); California (1975, AB 29:1036; 1977, AB 31:1191; 1992, AB 46:1176); Idaho (1972, AB 26:886; 1973, AB 27: 901; 1981, AB 35:963; 1986, AB 40:1232); Nevada (1976, AB 30:985); Utah (1963, AFN 17:474; 1965, AFN 19:568; 1971, AB 25:887; 1980, AB 34:917); Arizona (Rosenberg and Terrill 1986); Wyoming (Findholt and Fitton 1983; 1982, AB 36:1002; 1987, AB 41:1470); Colorado (1980, AB 34:917; 1982, AB 36:879 and 1002; 1983, AB 37:1012); New Mexico (1967, AFN 21:594; 1977, AB 31:1174; 1978, AB 32: 1197; 1980, AB 34:920; 1983, AB 37:1016; 1984, AB 38:1052; 1987, AB 41:1475; 1992, AB 46:1165).

Loxia leucoptera. White-winged Crossbill. British Columbia (1978, AB 32:1203; 1981, AB 35:972; 1985, AB 39:941 and 956; 1989, AB 43:1361); Washington (1977, AB 31:1182; 1978, AB 32:1203; 1981, AB 35: 972; 1984, AB 38:995, 1044; 1985, AB 39:941, 956; 1986, AB 40:1248; 1987, AB 41:1480; 1990, AB 44: 1180; 1992, AB 46:1173); Oregon (1981, AB 35:972; 1984 [Gordon et al. 1989]; 1986, AB 40:1232, 1248; 1987, AB 41:1480; 1989, AB 43:1361; 1990, AB 44: 1180); California (1978 [Gordon et al. 1989]); Idaho (1977, AB 31:1165; 1985, AB 39:941; also see records in Stephens and Sturts [1991], who denote, without dates, a breeding latilong in the far northern part of the state and records of "transients" from nine other latilongs); Nevada (1984, AB 38:995); Utah (1965 [Worthen 1973], 1977, AB 31:1170; 1982, AB 36:1003; 1985, AB 39:945; 1989, AB 43:1348); Montana (1984, AB 38:1044; also see Skaar et al. [1985] who present, without dates, records of probable breeding in nine latilongs and presence without evidence of breeding in 16 others); Wyoming (1977, AB 31:1170; 1980, AB 34:918; 1984, AB 38:995; 1987, AB 41:1470); Colorado (1976, AB 30:985; 1978, AB 32:1193; 1981, AB 35:966; 1982, AB 36:1003; 1983, AB 37:1012; 1987, AB 41:1470; 1988, AB 42:1323; 1989, AB 43:1348); and New Mexico (1982, AB 36:207; 1984, AB 38:995; 1985, AB 39:951).