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CHANGES IN DISTRIBUTION PATTERNS OF SELECT WINTERING NORTH AMERICAN BIRDS FROM 1901 TO 1989

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Abstract. Range and abundance patterns of birds change with time. We used National Audubon Society's Christmas Bird Count data and similar census data recorded in the *Canadian Field Naturalist* to examine such changes in select birds by comparing distribution and maps from 1901–1940 with those from 1960–1989. For both time periods, we plotted average winter abundances within each of the 48 conterminous United States and eight southern-most provinces in Canada for all species examined. Many more birds exhibit range expansions than contractions. Introduced and managed species show the most dramatic expansions. Although changes are less extensive, native non-managed birds also show expansions that apparently are linked to environmental modifications by humans. For example, water management programs provide winter habitat for the prey of Bald Eagles, and, coincidentally, the eagle expanded its winter range into these areas. In addition, abundance patterns changed over time for most species. The locations of the highest abundances shifted and the number of states and provinces with maximum abundance changed. Due to extensive habitat alterations over the past century, most of the observed avian distributional changes appear to be linked either directly or indirectly to human causes.

Key Words: Conservation biology; Christmas Bird Counts; landscape ecology; range expansions; range contractions; abundance shifts.

Biogeographic patterns of species are dynamic, not static; ranges expand and contract, and abundance patterns shift over time. Such changes can be precipitated by factors intrinsic to populations (e.g., dispersal of juveniles), by factors extrinsic to populations (e.g., habitat modification), or by a combination of both. Species exist in habitats where the environment provides at least minimum requirements for survival. Ranges and abundances can expand when suitable new habitat develops, or when surplus individuals from nearby areas continually immigrate into habitats unsuitable for sustained survival (Pulliam 1988, Pulliam and Danielson 1991). Ranges can contract when population sizes decline and individuals abandon less-than-ideal habitats (Fretwell 1972), which are often at the edges of ranges. Environmental modifications can render habitats unsuitable for survival, causing localized extirpations, which along with stochastic, demographic, or genetic changes can also result in range contractions. Abundance patterns can shift when less extreme cases of any of the above situations occur inside the ranges of species. In addition, changes in species abundances can have cascading effects on abundances of other species, by changing, for example, competitive or predator/prey interactions (e.g., Terborgh 1986, Spencer et al. 1991, Flecker 1992). Introductions of exotic species can have a similar effect, thereby reducing abundances of native species (e.g., Savage 1987, Coblentz 1990). Hunting can also reduce abundances, but the enactment and enforcement of various laws (e.g., Migratory Bird Act) have ameliorated its impact in most cases (Williams and Novak 1987). Management of species for hunting, however, has dramatically changed the ranges and abundance patterns of game species by changing the carrying capacities of habitats (see below). Therefore, changes in distributional patterns of birds wintering throughout North America can be due to habitat modifications, immigration among populations, and indirect effects such as changing competitive interactions.

The purpose of this paper is to compare historical and recent distributional patterns of selected wintering North American birds to determine if shifts occurred in the ranges

and abundance patterns, and, if so, what type of changes they were and to speculate on possible causes. We found that the majority of birds examined exhibit range changes; most species expanded their ranges and only a very few showed range contractions. Some shift in abundance patterns occurred in almost all species.

METHODS

We used data collected by volunteers for the National Audubon Society's Christmas Bird Counts and similar census data recorded in the *Canadian Field Naturalist* from 1924 through 1939. Wing (1947) summarized data from 1901 to 1940 (from winter 1900/1901 to winter 1939/1940), which included 6853 censuses. We obtained data for 32,167 censuses from U.S. Fish and Wildlife Service for 1960 through 1989, excluding those for 1969, which were missing. All data were collected on a day around Christmas and, for each species, observers recorded all individuals seen. Count effort was recorded as total number of census hours (total census hours) for the earlier (1901 to 1940) data, and as total number of census hours per censusing party (total party hours) for the later (1960 to 1989) data.

For each species Wing (1947) calculated the average number of individuals seen per total census hour in each state or province. We attempted to analyze the later data in a similar manner: for each species we calculated the average number of individuals seen per total party hour in each state or province. The absolute abundances from the two time periods cannot be compared directly because count efforts were recorded in two different ways. Consequently, we converted all state and province averages for each species into proportions of the maximum averages for each time period. This normalization forced the value to run between 0 and 1, which we then plotted by state or province. The use of political boundaries is not biologically meaningful, but is unfortunately necessary due to the way Wing compiled the earlier data. Because we used states and provinces as plotting units, ranges appear larger than they actually are; we plotted species as "present" in an entire state or province, even if its distribution was limited to a small portion of that unit. This is of little consequence in this comparative study, given that we plotted data for both time periods similarly. More census sites and more participants with better equipment during the later time period, however, may have biased the observed distributional patterns. For example, our analysis could indicate an apparent range expansion if a bird occurred only in a part of a state or province, and a census site was not established at that location until after 1940. Consequently, we noted expansions only when individuals were recorded in states and provinces beyond those neighboring the earlier range.

Because we were looking for shifts in distributions, we identified 58 wintering North American species or subspecies that we expected would show such changes. This included 27 non-passerines and 31 passerines. Very rare or extremely gregarious species are poorly represented by these types of censuses (Bock and Root 1981). Thus, we ignored those taxa. Additionally, we disregarded difficult to distinguish species (e.g., Black-capped and Carolina chickadees, *Parus atricapillus* and *P. carolinensis,* respectively). Although House Sparrows (*Passer domesticus*) and European Starlings (*Sturnus vulgaris*) are gregarious, we included them in our analysis because the range and abundance patterns of these introduced birds have not only changed dramatically (Forbush 1929, Robbins 1973), but those changes have affected greatly the patterns of native birds (Zeleny 1976, Robbins et al. 1986, Ehrlich et al. 1988:459–463).

RESULTS

As we expected, given the biased manner in which we selected the species examined, most of these birds exhibit some type of

change in their winter ranges and abundance patterns.

Range Changes

Range expansions were much more common than contractions. This is true even though we recorded expansions only when individuals were present in states beyond those neighboring their 1901–1940 range. The most extreme expansions are evident in introduced and managed species. These include Mute Swan (*Cygnus olor*), Wild Turkey (*Meleagris gallopavo*; Fig. 1), European Starling (*Sturnus vulgaris*), and House Finch (*Carpodacus mexicanus*). Several birds moved into the northeastern region: Northern Harrier (*Circus cyaneus*), Mourning Dove (*Zenaida macroura*; Fig. 1), Tufted Titmouse (*Parus bicolor*), and Northern Cardinal (*Cardinalis cardinalis*). A couple of species expanded into the northwestern region: Ferruginous Hawk (*Buteo regalis*) and Barred Owl (*Strix varia*; Fig. 1). No species expanded south except irruptive species (see below), perhaps because most wintering North American species have southerly ranges. The Golden Eagle (*Aquila chrysaetos*; Fig. 2) and red-shafted race of the Northern Flicker (*Colaptes auratus*) moved east, whereas the yellow-shafted race expanded west. The Bald Eagle (*Haliaeetus leucocephalus*; Fig. 2) expanded its range into the center of the continent.

Irruptive species irregularly expand their winter ranges south (Bock and Lepthien 1976, Widrlechner and Dragula 1984). Consequently, we expected differences in these species' southern range limits between the two different time periods. Red Crossbill (*Loxia curvirostra*) and Evening Grosbeak (*Coccothraustes vespertinus*; Fig. 2) fit this expectation. The other irruptive species we examined, Boreal Chickadee (*Parus hudsonicus*), Pine Siskin (*Carduelis pinus*), Common Redpoll (*Carduelis flammea*; Fig. 3), White-winged Crossbill (*Loxia leucoptera*), and Pine Grosbeak (*Pinicola enucleator*), do not.

We found relatively few species with contracted ranges. Of these, most associate with water and only one is a passerine: Pied-billed Grebe (*Podilymbus podiceps*), Northern Pintail (*Anas acuta*), Common Merganser (*Mergus merganser*), and Brown-headed Cowbird (*Molothrus ater*; Fig. 3). The cowbird, which benefits from habitat fragmentation (Brittingham and Temple 1983, May and Robinson 1985, Ehrlich et al. 1988:495–501), has expanded its winter range into the northeastern region (Maine and Nova Scotia), but has contracted its range elsewhere, particularly along its northern border (Pennsylvania, Michigan, Wisconsin, Iowa, Montana and Washington).

Shifting Abundance Patterns

Abundance patterns of most species changed. The areas of peak abundances for many species shifted into the northeastern region. These include: Bufflehead (*Bucephala albeola*), Hairy Woodpecker (*Picoides villosus*), Blue Jay (*Cyanocitta cristata*), Brown Creeper (*Certhia americana*), White-breasted Nuthatch (*Sitta carolinensis*), Red-breasted Nuthatch (*S. canadensis*), and Evening Grosbeak (Fig. 2). Other species have become more abundant toward the center of the continent in recent years. Some of these are managed and/or introduced; Northern Bobwhite (*Colinus virginianus*; Fig. 3), Ring-necked Pheasant (*Phasianus colchicus*), House Sparrow (*Passer domesticus*); others are native and non-managed; Northern Harrier, Ferruginous Hawk, and Red-headed Woodpecker (*Melanerpes erythrocephalus*). The data, unfortunately, do not allow us to know if these shifts were due to increases or decreases in absolute abundances.

Another measure of changing abundance patterns is a difference in the absolute number of states and provinces with very high abundances. This number decreased in roughly three times as many species (e.g., Fig. 3, bottom) as it increased (e.g., Fig. 1, middle). About half of the birds examined

have the same number of states and provinces with maximum abundance peaks (e.g., Figs. 1–3).

DISCUSSION

North America has experienced dramatic changes over the last 100 years that have strikingly altered its natural resources and environment. The human population in Canada and the United States has increased from about 150 million at the end of World War II to around 280 million in 1991 (Ehrlich et al. 1992). Along with habitat fragmentation (Wilcove et al. 1986), air and water pollution have greatly degraded the environment by affecting the productivity of our forests, lakes and streams (Bormann 1985). Furthermore, we have been draining our wetlands at an alarming rate (WRI 1992), and climatic change has the potential to disrupt communities due to differential relocation of species' ranges (Peters 1992, Root and Schneider 1993). All of these alterations have had and will probably continue to have major impacts on the biogeographic patterns of birds.

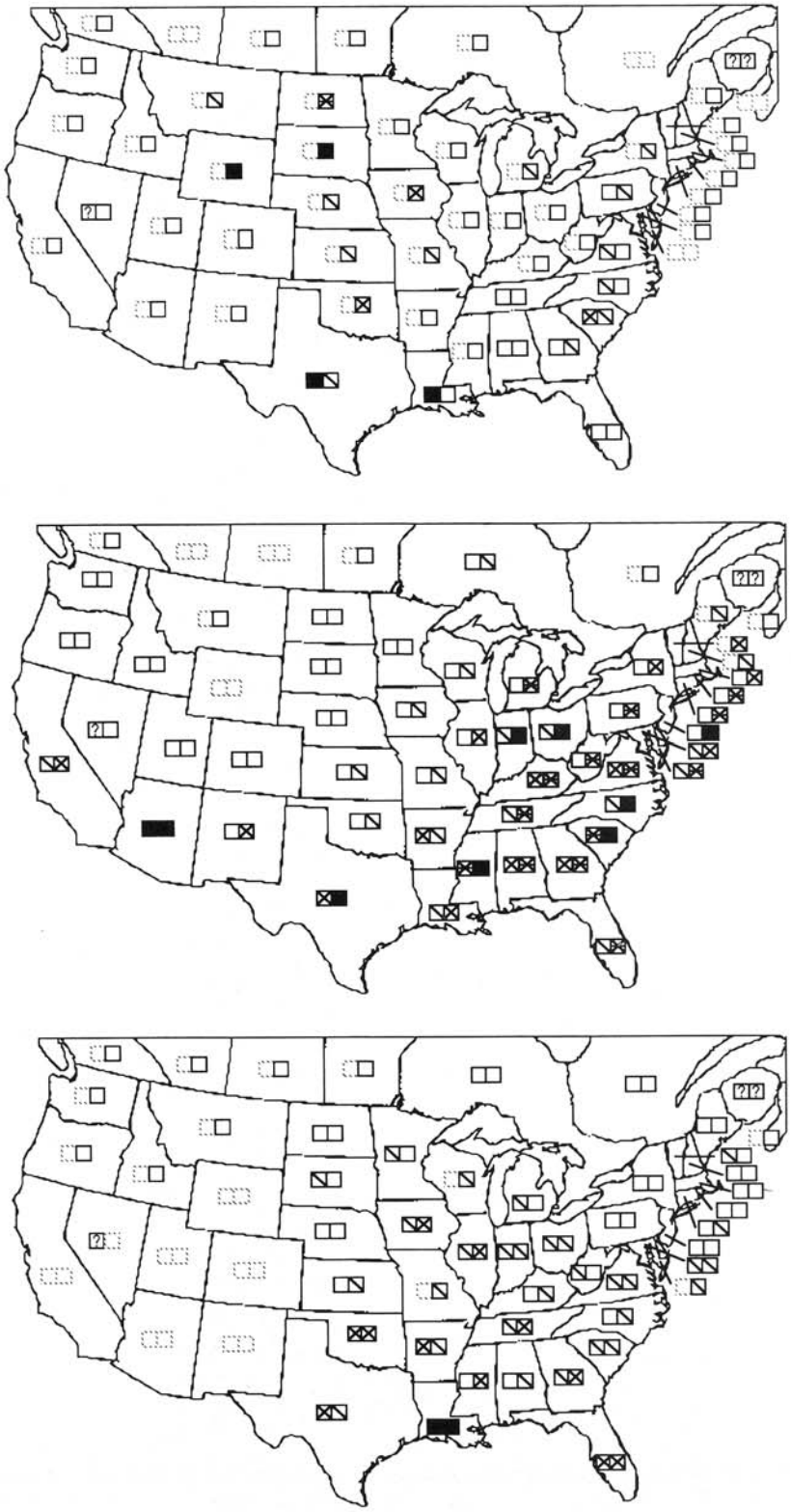
Range Expansions

Along with introduced species that have strong dispersal abilities (e.g., House Sparrow and European Starling), successfully managed birds show extensive range expansions. Up to 1940 the Mute Swan was recorded only in Pennsylvania and Michigan. Since that time, programs to introduce and establish it—primarily in parks—have allowed it to spread to 19 states and three provinces. The Wild Turkey (Fig. 1) shows even a more dramatic change. Its original range covered all the states east of the 100th meridian, except for North Dakota and most of Minnesota. Additionally, Merriam's subspecies (*M. g. merriami*) ranged throughout New Mexico, Texas and Arizona (Schorger 1966). Hunting pressures, habitat loss, and disease spread by domestic poultry all contributed to a dramatic range contraction (Schorger 1966, Hewitt 1967, Lewis 1973). From 1901 to 1940 it was recorded in only ten states. According to Schorger (1966), turkeys were reintroduced into all but three states within its original range, and introduced into all the states outside its original range. Additionally, individuals were introduced into Alberta, Saskatchewan, Manitoba and probably Ontario (AOU 1983). Obviously, management has had a major impact on the distribution of the Wild Turkey, because it is now found in 52 states and provinces.

Supplemental feeding of birds by humans has also contributed to a change in both the presence and abundances of various seed-eating birds in the northeastern region. On average, a third of the households in North America provide about 60 pounds of supplemental feed a year, with the average being even higher in New England (Ehrlich et al. 1988:349). Feeders apparently have contributed strongly to both the expansion of winter ranges (e.g., Mourning Dove, Fig. 1) and increased winter densities (e.g., Blue Jay; White-breasted Nuthatch; Tufted Titmouse; Northern Cardinal; and Evening Grosbeak, Fig. 2). Birds that frequent feeders are attracted to a steady food supply at feeders, and by urbanized habitats with thickets and shrubbery that ornamental plantings often provide (Eaton 1959, Beddall 1963, Kircher 1981, Ehrlich et al. 1988: 349–353).

Habitat manipulation, albeit of another sort, may have contributed to the extensive distributional changes of the Barred Owl (Fig. 1). This owl has moved into the north-

FIGURE 1. Top: Map showing distributional pattern of Wild Turkey. The data from 1901 to 1940 are provided on the left-hand side of the rectangle, while those from 1960 to 1989 (except 1969) are on the right-hand side. The six different symbols (open squares with dashed margins, open square, diagonal line, crossed lines, asterisk, and filled square) correspond respectively with the following proportion of the maximum value: 0.0, 0.01 to 0.10, 0.11 to 0.25, 0.26 to 0.45, 0.46 to 0.70, and 0.71 to 1.00. Question marks indicate that no data were available. Middle: Mourning Dove. Bottom: Barred Owl.



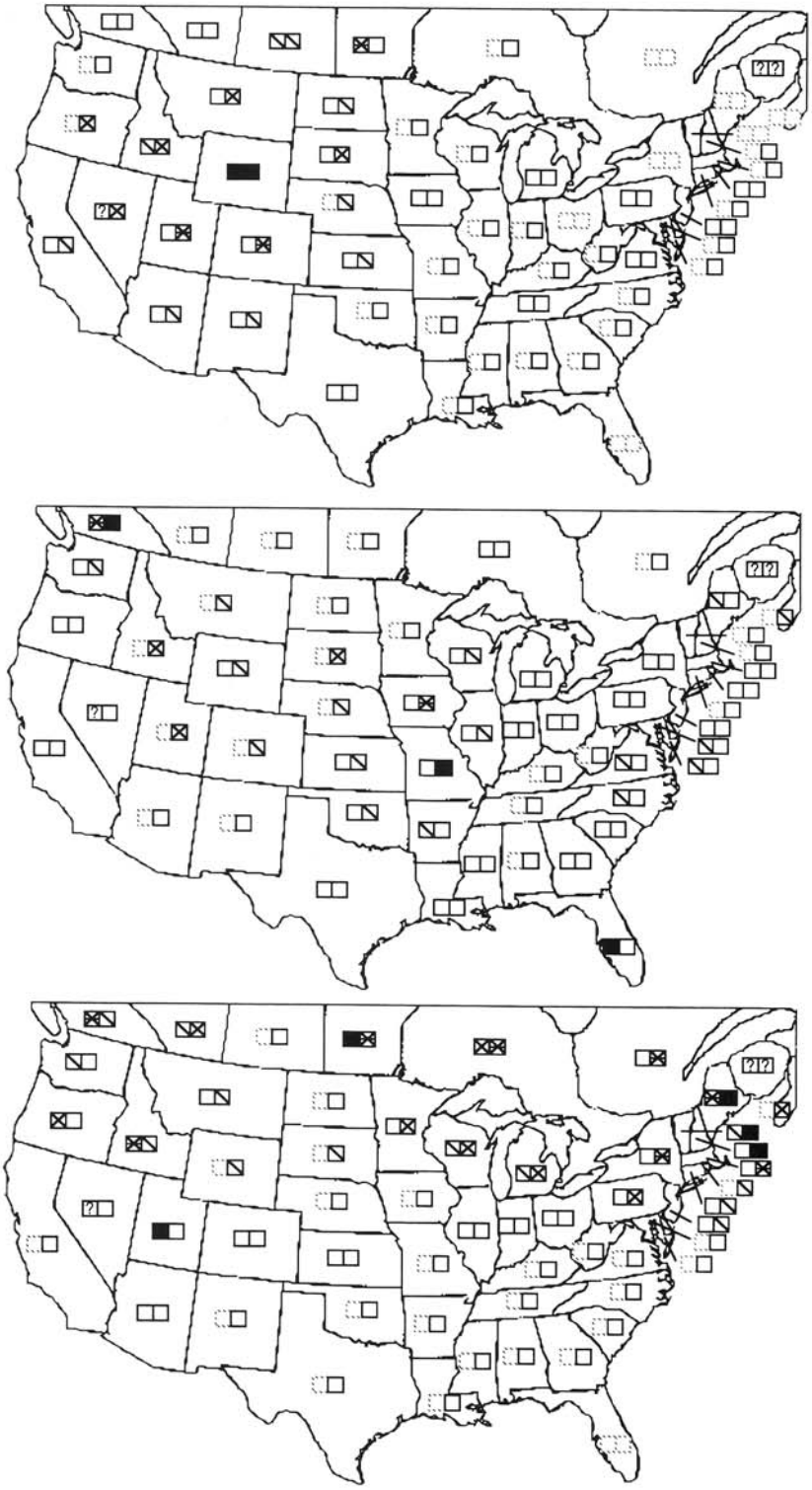


FIGURE 2. Top: Map showing distributional pattern of Golden Eagle. Middle: Bald Eagle. Bottom: Evening Grosbeak. See Figure 1 for key.

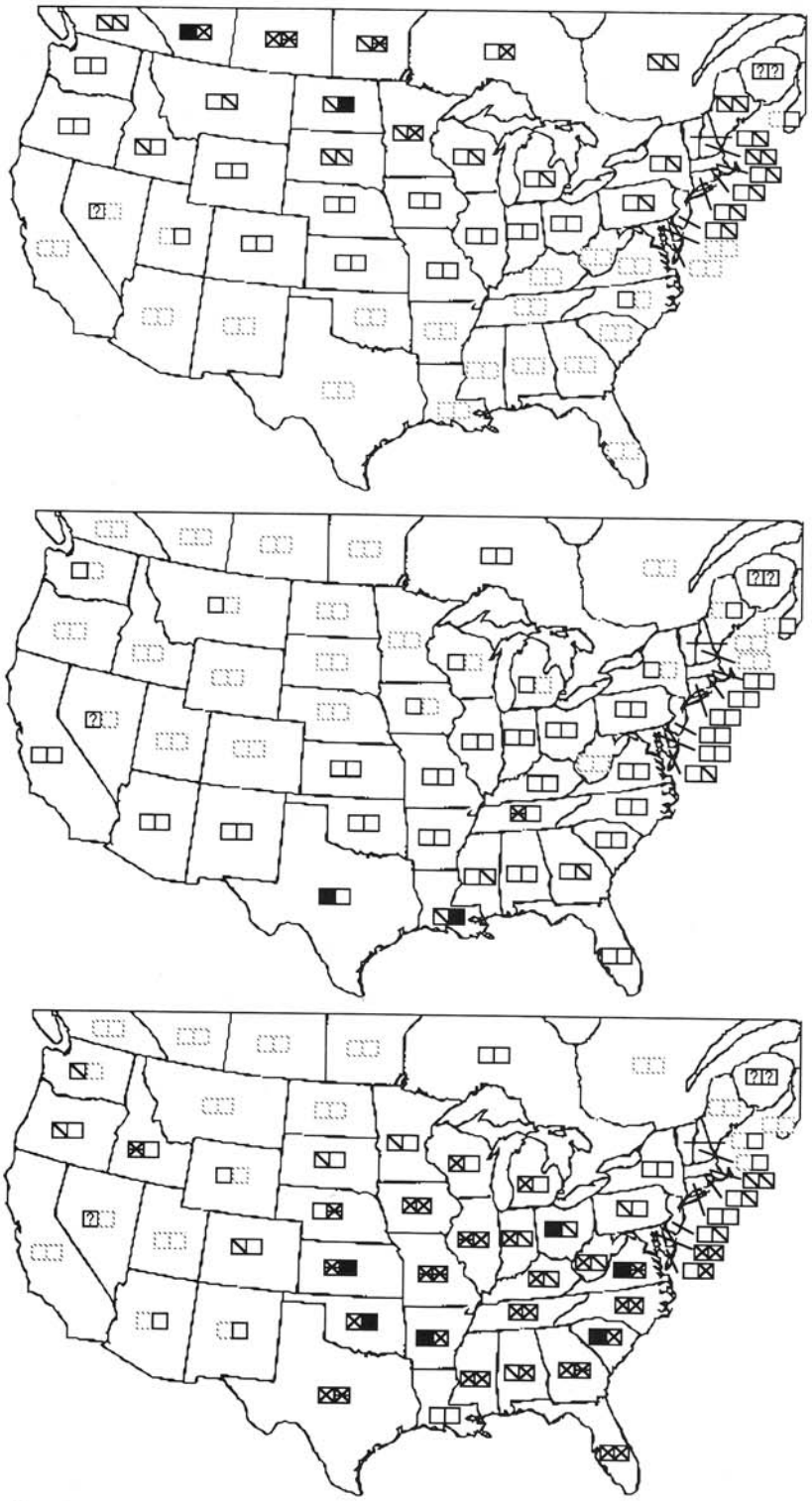


FIGURE 3. Top: Map showing distributional pattern of Common Redpoll. Middle: Brown-headed Cowbird. Bottom: Northern Bobwhite. See Figure 1 for key.

western region relatively recently (Holt and Hillis 1987, Sharp 1989, Taylor and Forsman 1976). From 1963 to 1972 no northern populations were reported west of the 100th meridian, and only one individual was recorded north of the 50th parallel—in Pinawa, Manitoba (Root 1988). Logging and associated activities in the northwestern region may have facilitated invasions (T. E. Hamer, unpubl. data).

The Barred Owl expansion is of major interest, because its range is now partly sympatric with that of the endangered Northern Spotted Owl (*Strix occidentalis occidentalis*). The consequences of interspecific competition between these two species have not yet been quantified, but nesting sites, foraging activities, and diet are similar, particularly in the Northwest (Taylor and Forsman 1976). Anecdotal evidence suggests that the larger, more aggressive Barred Owl may be able to displace the smaller Spotted Owl; on the Olympic Peninsula in Washington, territories previously held by Spotted Owls, which have strong territory fidelity, have been taken over by Barred Owl pairs (Sharp 1989). This range expansion provides an excellent opportunity to quantify the effects of invasion. Given the endangered status of the Northern Spotted Owl, such research will not only help us understand basic biological problems but it could help in the assessment of different forestry policies.

Other raptors, specifically the two North American eagles, have significantly expanded their ranges; the Golden Eagle (Fig. 2) has moved east, while the Bald Eagle (Fig. 2) has spread into the center of the continent. The Golden Eagle is uncommon throughout its newly established range in the east. Higher abundances occur in the west, even though ranchers previously hunted them from small planes. This practice began in the late 1930s and for over 20 years people killed between 1000 and 2000 individuals each year in west Texas and southeastern New Mexico (Spofford 1969). The location of peak abundance, Wyoming, remained unchanged (Fig. 2).

Over the years humans have strongly influenced the expansion of the Bald Eagle's range by implementing various water management programs. Historically, birds were forced to move south during unusually cold winters because they need open water for hunting. This could help explain the high abundance recorded in Florida in 1901–1940. Large lakes and impoundments built in the 1930s, locks placed on major waterways, and numerous hydroelectric plants built with cooling ponds provide open water in winter. For example, core wintering areas adjacent to parts of the Mississippi, Illinois, and Missouri rivers accounted for 30% of the sightings in Millsap's study (1986). Dams on these and other rivers create sloughs and are therefore indirectly responsible for the open water used by eagles for feeding (Southern 1963). The turbines in the dams also kill or stun fish, thereby allowing the eagle easy access to food (Spencer 1976).

The winter abundance of the Bald Eagle throughout most of the contiguous United States dropped by about a third from 1957 to 1970 due to the use of persistent insecticides (e.g., DDT) and habitat destruction (Brown 1975). Since World War II, population declines in the East have been blamed on habitat destruction due to human disturbances in the form of waterfront housing and outdoor recreation (Sprunt 1969). Shooting by ranchers from small planes from the late 1930s to the early 1960s could have depressed the abundance during this time period, and for sometime after (Sprunt 1969).

Winter distributions of irruptive, boreal, seed-eating birds are highly variable from year to year (Benkman 1987, Bock and Lepthien 1976). The availability of seeds is assumed to be the primary factor driving the movements of the irruptive fringillids (Bock and Lepthien 1976) and perhaps even the Boreal Chickadee (Root 1988). For most species that we examined, however, long-term averages show little change, even when censuses are separated by 30 years (e.g., Common Redpoll, Fig. 3). This implies that

the response of these birds, and perhaps the factors driving their irruptive behavior, have been fairly constant over the past century. The average ranges of two species (Red Crossbill and Evening Grosbeak; Fig. 2) are quite different between the early and later part of the century; both species expanded their ranges much farther south. Dietary preferences might help explain why we found distributional changes in some species, but not in others.

Range Contractions

Given the amount of habitat modification that has occurred over the past century, we expected the ranges of many birds to contract significantly. Of the species examined, fewer than 10% showed such a pattern. This low percentage could have been partly an artifact of our sample, because we avoided species that have very restricted ranges. The plotting unit (state or province) may also have artificially decreased the instances of detectable range contractions, because individuals had to vacate entire states, not just part of them, before a contraction would be recorded. Of the four species showing range contractions, three of them depend on open water: Pied-billed Grebe, Northern Pintail and Common Merganser. The contraction of the Northern Pintail is particularly disconcerting. This game species has been extensively managed, yet estimates of its breeding population have shown a five-fold decrease since the mid-1900s (Migratory Bird Management Office 1992; also Banks and Springer 1994). The reasons for this large decline are not yet understood.

The fourth species with a contracted winter range is the Brown-headed Cowbird (Fig. 3). This result was unexpected, because this cowbird has reportedly expanded its range due to clearing of eastern forests and increased cattle grazing (Mayfield 1965, May and Robinson 1985, Ehrlich et al. 1988:495–497). Indeed, the percentage of Christmas Bird Counts east of Texas, and south of the 37th parallel reporting Brown-headed Cowbirds, increased from near zero to over 80%, suggesting this bird has been steadily increasing its numbers in this area (Brittingham and Temple 1983). Maps of average winter abundance do not show this large increase, except perhaps in Louisiana, and small increases in Mississippi and Georgia. This is because relative, not absolute, abundances are plotted in this study. A comparison of the relative data suggests that the absolute abundances throughout most of its range may have increased. This is not the case in the upper mid-west where the cowbird range has contracted. The reasons for this are undoubtedly complex, but one contributing factor may be that during the breeding season the U.S. Fish and Wildlife Service and Michigan Department of Natural Resources trap and remove cowbirds from Michigan. Its parasitism on the endangered Kirtland's Warbler (*Dendroica kirtlandii*) is extensive (over 70% in the 1960s) (Mayfield 1978). By 1980 they had removed over 40,000 cowbirds (Walkinshaw 1983).

Shifting Abundance Patterns

Shifts in abundance patterns could indicate whether changes in habitats had significantly increased or decreased the carrying capacity of species in various areas. If an increase in carrying capacity occurred, then more individuals could survive in the area, thereby forming a new peak. A new peak could also be formed by decreasing carrying capacity in areas around a particular habitat.

Due to feeders, the carrying capacity in the northeastern region has presumably increased. Besides ranges of species expanding into this region, abundance patterns of birds attracted to feeders also have shifted so that higher relative densities are reported in this region (e.g., Evening Grosbeak, Fig. 2). Consequently, feeding stations have apparently had major impact on the winter distribution patterns of select wintering birds.

Another common change in abundance pattern is toward the center of the country,

which corresponds to regions where the most winter wheat is grown (USGS 1970). Species such as Northern Bobwhite (Fig. 3) are apparently attracted to waste grain, unharvested areas along fence rows, and open fields. In the Great Plains, populations have increased as humans suppressed fires and brushy cover became established, and as farmers built more fence rows (De Vos 1964).

CONCLUSION

The National Audubon Society's Christmas Bird Count data and similar census data recorded in the *Canadian Field Naturalist* provide an excellent source for examining distribution patterns of wintering North American birds over both broad-spatial and long-temporal scales. We found extensive changes in the ranges and abundance patterns of the birds we examined. The primary cause of these shifts, directly or indirectly, was human activity. Although these include activities specifically designed to manifest a change (e.g., management of the Wild Turkey), most were not purposeful (e.g., water management programs and the Bald Eagle). Subsequent studies are needed to focus on possible factors regulating the distributional shifts we begin to explore here. One obvious approach would be to include more species, examine breeding-season data, and investigate directly possible effects of climate.

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