GEOGRAPHICAL CORRELATES OF ABUNDANCE VS. RARITY IN SOME NORTH AMERICAN WINTER LANDBIRDS

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ABSTRACT.—Using Christmas Bird Count (CBC) data, I compared range sizes and within-range abundances of 70 species of apodiform, piciform, and passerine landbirds whose ranges are 75% or more restricted in winter to the contiguous U.S. and southern Canada. Range size was computed as the number of occupied 5° latitude-longitude blocks. Three abundance measures were calculated: (1) mean birds counted/census hour across all occupied blocks, (2) maximum birds/hour in a single block, and (3) maximum birds/hour on a single CBC. Range size was positively but weakly correlated with each abundance measure, and the abundance measures were very strongly correlated with one another.

Geography was a powerful predictor of the species' positions in a two-dimensional space defined by the axes of range size and average within-range abundance. Taxa that breed and winter at higher latitudes had larger total populations, and had significantly larger ranges and average local abundances. Species grouped by longitudinal areas of greatest local abundance had distinct range sizes but did not differ in average within-range abundance. Eastern species had larger ranges than comparably abundant western forms, probably because the eastern U.S. is characterized by relatively widespread habitat types.

Results of this study suggest that a species' within-range abundance is influenced by the degree of its habitat generalization, whereas its range size will be larger if it is a habitat generalist or a specialist on widespread habitats. Because individual CBC's include many habitats, the same ecological attribute—habitat generalization—could cause species to be both widespread and abundant inside CBC circles. Carefully standardized within-habitat censuses will be required to determine whether or not these generalist species also dominate the individual habitats occupied by their more specialized and narrowly distributed relatives.
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DISTRIBUTION and local abundance are fundamental ecological properties that combine to determine a species' total population size. Hanski (1982: 212) suggested as a "rule in nature" that species occupying the largest number of local or regional sites also tend to be the most abundant, on average, within sites. While this has not been found to apply in all cases (Ricklefs 1972, Adams and Anderson 1982), a positive correlation between habitat breadth and local abundance has been demonstrated for certain groups of vascular plants (McNaughton and Wolf 1970, Raup 1975), insects (Price 1971; Hanski and Koskela 1977, 1978; Muhlenberg et al. 1977), rodents (Dueser and Shugart 1979), and birds (Shugart and Patten 1972, Able and Noon 1976). Because this sort of relationship appears to be emerging as a general, if not universal, principle, it is important to search for its possible causes.

In previous studies, abundance has been compared with habitat breadth or distribution only locally or, at best, regionally. Audubon Society Christmas Bird Counts (CBC's) provide an unusual opportunity to examine these relationships for a large number of species on a continent-wide scale (e.g. Bock and Ricklefs 1983). In the present study, I used CBC data to compare range sizes and abundances of 70 landbird species whose winter ranges are largely confined to the U.S. and southern Canada (Fig. 1). I then searched in an empirical manner for biogeographical attributes that distinguished locally abundant and wide-ranging species from rare and narrowly distributed forms.

METHODS

It is important to determine whether or not positive correlations between distribution and abun-

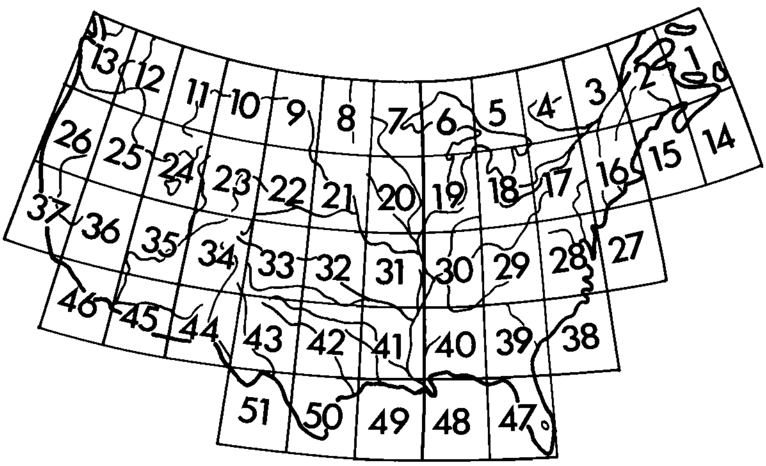

Fig. 1. The study area, divided into 51 5° blocks.

dance are inherent properties of whole species populations. Grinnell (1922) suggested that species reach higher densities at the centers of their ranges than near the edges. If distribution and abundance were studied in some limited geographic area, then species only peripherally present in the area might also be scarce locally compared to widespread species whose centers of maximum abundance occurred there. This could lead to a positive distribution-abundance correlation when no such relationship actually existed among species populations taken as a whole (Bock and Ricklefs 1983).

I estimated the winter ranges of North American landbirds from descriptions in the A.O.U. Check-list (American Ornithologists' Union 1983) and selected for analysis 70 species whose New World winter ranges appeared to be largely (≥75% by area) confined to the contiguous U.S. and southernmost Canada (Fig. 1, Appendix). This is the area where CBC's have been sufficiently numerous to yield meaningful abundance information. It is doubtful that any two ornithologists would arrive at identical lists by this subjective method. My list (Appendix), however, certainly excludes all species whose winter ranges lie primarily outside the study area. The analysis also was limited to species in the orders Apodiformes, Piciformes, and Passeriformes, because they form a reasonably cohesive ecological unit. Other aquatic, raptorial, or gallinaceous species have unusual characteristics of habitat, body size, and trophic position that strongly influence their distribution-abundance relationships (e.g. Brown 1981). Inclusion of such species would have masked many of the purely geographical aspects of abundance vs. rarity that were the focus of the present study.

Strengths and limitations of CBC's have been considered elsewhere (Bock and Root 1981). From a data bank including results of 7,189 CBC's conducted between 1962 and 1971, I computed the 10-yr mean number of each species counted per party-hour of census effort in each of 51 5° blocks (Fig. 1). The number of blocks in which a species was detected on CBC's was used as a measure of range size. Three within-range abundance measures were calculated: (1) mean individuals per party-hour of census effort in all occupied blocks, (2) birds per party-hour in the single block with the highest 10-yr mean, and (3) the average annual record number per party-hour of each species recorded on a single CBC.

Results and Discussion

Range size vs. abundance.—The number of occupied blocks was positively but weakly correlated with each abundance measure, taking all 70 species together (Table 1, Fig. 2). The three abundance variables were all very highly intercorrelated. Species of Icterinae have very large total populations compared with other North American landbirds, perhaps because of their use of agricultural ecosystems. The Rusty Blackbird (see Appendix for scientific names) and Common Grackle met the winter distribution criterion for inclusion in this study but occupied an unusual position in a two-dimensional space defined by range size and mean abundance (Fig. 2, species 64 and 65). Their presence in the sample, however, had only a modest impact upon overall correlations between distribution and abundance (Table 1).

The relationship between range size and mean abundance was far from linear. Many

TABLE 1. Product-moment correlations between range size and logs of three within-range abundance measures for 70 North American landbirds whose ranges are at least 75% restricted in winter to the study area (Fig. 1). See Methods for a full description of each variable. All values are significant at the $P < 0.01$ level. Numbers in parentheses = same calculations excluding three species of Icterinae.

	2	3	4
1. Range size	0.427 (0.471)	0.476 (0.501)	0.346 (0.349)
2. Mean abundance within range	—	0.965 (0.952)	0.882 (0.821)
3. Maximum abundance in one 5° block		—	0.895 (0.843)
4. Maximum abundance on a single CBC			—

species with relatively small ranges were just as abundant within occupied blocks as those with large ranges (Fig. 2). Locally rare species usually had small ranges, however, and species with large ranges usually were locally common—leading to the overall positive correlation between distribution and abundance.

Relatively abundant species might be detected on more CBC's and thus be perceived to have larger ranges, in part simply due to their overall abundance. Regardless of this possible artifact, two facts seem clear from the data set. First, certain species have much larger total populations than others by virtue of their occurrence in higher numbers in more places than other species. Second, there is no evidence that species with small ranges (or those that are so rare as to be undetectable in most places) in any way compensate by reaching very high abundances locally. Not all species had abundance patterns of the same statistical shape. Some (e.g. the Winter Wren, species 29 in Fig. 2) were detected in many blocks but reached high numbers in only 1 or 2, while others (e.g.

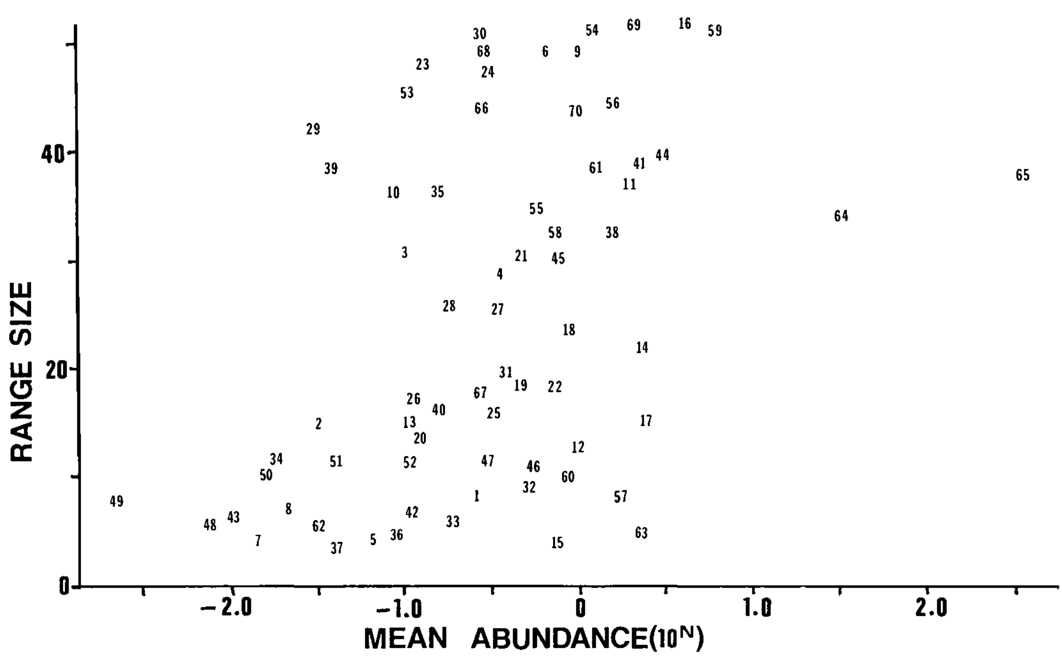

Fig. 2. Range size vs. within-range abundance of 70 winter landbirds. Numbers correspond to the list of species given in the Appendix.

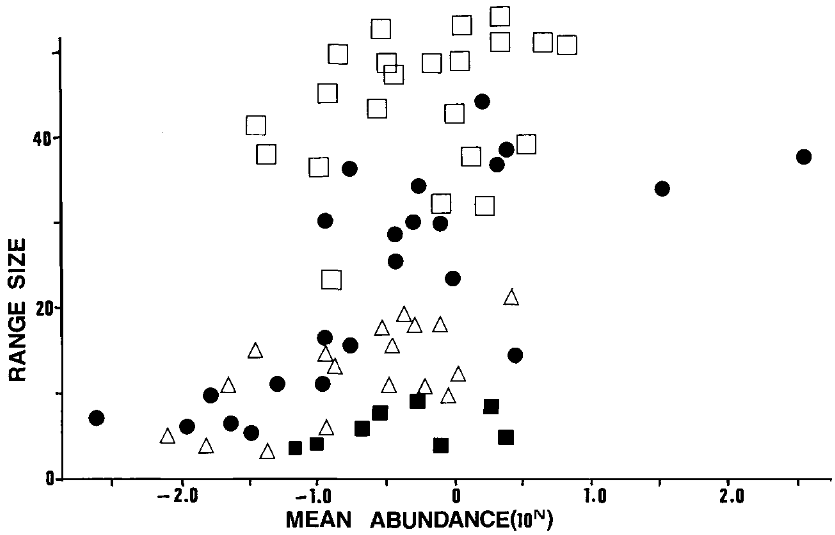

Fig. 3. Range size vs. within-range abundance of 70 landbird species. Open squares = species ubiquitous in the study area; dots = eastern species; triangles = western species; closed squares = Pacific Coastal species.

the Tricolored Blackbird, species 63) were abundant in most blocks where they were found. Overall, however, those same species with the highest average within-range abundances also reached the highest maximum abundances within single blocks and within single 9.3-km-diameter CBC circles (Table 1).

Relationship to longitude.—A consistent pattern emerged when the species were separated into groups based upon the longitudinal positions of their centers of abundance (Fig. 3). Species concentrating generally east of the 100th meridian had larger ranges than western species, and ubiquitous species had the largest ranges of any group (Table 2A). Species with centers of abundance restricted to the Pacific slope had the smallest ranges and occupied a unique position in distribution-abundance space (Fig. 3). None of the longitudinal groups differed in average abundance within occupied blocks (Table 2A), however, so longitudinal area did not explain the overall positive range size-

TABLE 2. Comparisons of range size and abundance among 70 taxa of North American winter landbirds. See Methods for descriptions of variables.[a]

Comparison	n	Range size $\bar{x}$ (SD)		Log_{10} mean abundance $\bar{x}$ (SD)	
A. Ubiquitous species	21	43.17 (7.6)		−0.32 (0.62)	
Eastern species	23	22.9 (12.2)	$F = 52.9$***	−0.54 (0.53)	$F = 0.74$*
Western species	18	12.2 (4.9)		−0.70 (1.03)	
Pacific Coast species	8	5.4 (2.0)		−0.46 (0.54)	
B. Breed above 55°N lat.	30	33.4 (15.0)	$t = 4.94$***	−0.38 (0.66)[b]	$t = 2.17$**
Breed only below 55°N lat.	40	16.6 (12.5)		−0.74 (0.69)	
C. Winter only below 40°N lat.	19	9.7 (7.5)		−1.09 (0.70)	
Winter at least partially above 40°N lat.	51	29.1 (15.6)	$t = 6.97$***	−0.39 (0.61)[b]	$t = 3.83$***

[a] * = not significant; ** = $P < 0.05$; *** = $P < 0.001$.

[b] These abundance figures were calculated excluding the atypically abundant Rusty Blackbird and Common Grackle (note positions in Fig. 2). Their inclusion resulted in higher t-scores.

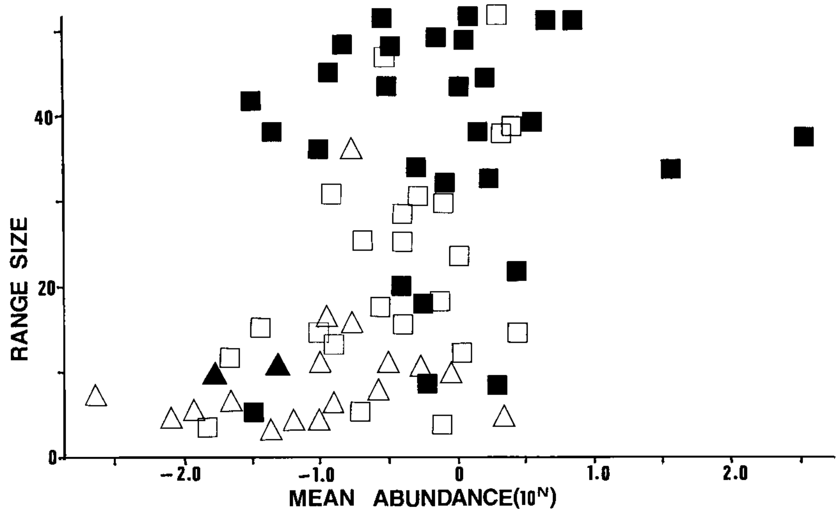

Fig. 4. Data as in Fig. 3, but closed symbols = species that breed at least partially above 55°N; open symbols = species that breed only south of 55°N. Squares = species that winter at least partially above 40°N; triangles = species that winter only below 40°N.

abundance correlation. In fact, distribution and abundance were much more highly correlated within the eastern and western groups than for all species combined (Table 3).

The assignment of species to the different longitudinal groups was not based upon range limits. For example, the Blue Jay was considered an eastern species even though it occupied 40 blocks, 9 of which are west of the 100th meridian. The general criterion used for placing a species in one of the four longitudinal groupings was the location of blocks supporting at least 20% of the abundance in its maximum block. This is important, because it means that each species in theory could occur in all 51 blocks and still be assigned to any of the longitudinal groups.

The major difference between eastern and western species occurred among the more abundant forms, which had much larger ranges in the east (Fig. 3). An inspection of any sort of vegetation map (e.g. Küchler 1964) suggests a possible cause. Eastern bird species have wider distributions than western forms because certain habitats (mixed hardwood forest types) are themselves more broadly distributed than most western vegetation types. That is, western bird species would in most cases have access to a smaller land area for an equivalent degree of habitat specialization. This apparently has little impact, however, upon their abundances in the places where they do occur. Rare eastern species generally had ranges as restricted as their western counterparts (Fig. 3). Significantly, none of these species is characteristic of the broadly distributed eastern hardwood or mixed forests. Rather, they are restricted to habitats such as pine forest of the coastal plain (e.g. Red-cockaded Woodpecker, Bachman's Sparrow), or tidal marshes (e.g. Sharp-tailed Sparrow, Seaside Sparrow).

Relationship to latitude.—Thirty of the 70 species have breeding ranges extending at least partially beyond the 55th parallel into boreal and/or arctic habitats. These species apparently have very large total populations, perhaps associated with their widespread breeding habitats. They had significantly larger winter ranges and higher average abundances than did species nesting only below 55°N (Fig. 4, Table 2B). Nineteen of 70 species wintered only south of 40°N, and this group had smaller ranges and lower abundances than did species wintering at least partially farther north (Fig. 4, Table 2C).

A major cause, or at least correlate, of the distribution-abundance relationship emerges from these data. U.S. winter landbird assemblages, at the level of 5° blocks and CBC circles, generally are dominated numerically by widespread and abundant species that breed north into arctic, subarctic, and boreal habitats and that migrate south in winter in large numbers into the study area. Such species contrast in particular with a second group of largely resident species, restricted to lower latitudes and much less abundant or widely distributed in winter.

Conclusions and Speculations

Geography was a powerful predictor of species' positions in distribution-abundance space in ways that, at least partially, explain the positive correlations found in this study. The U.S. landbird fauna is dominated in winter by high-latitude breeders that have much greater winter abundances and larger ranges than do species confined to lower latitudes (Fig. 4). If we accept the idea that resident low-latitude species generally are more ecologically specialized (e.g. MacArthur 1972), then the results of this study suggest that species' positions along both the range-size and mean local abundance axes are driven by degrees of habitat generalization. From an analysis of the longitudinal groupings (Fig. 3), it appears that a second factor, association with specific habitat types, can influence range size but not within-range abundance.

A remaining problem is why range size and abundance were positively correlated in the eastern and western groups (Table 3) but not in the ubiquitous or Pacific Coastal forms. We cannot rule out statistical chance due to small sample sizes, particularly for the Pacific Coastal group. Nevertheless, it is tempting to speculate that range size and abundance were uncorrelated in the ubiquitous and Pacific Coastal groups because species whose presence would cause such positive correlations necessarily are missing from each data set (Fig. 3). Among the ubiquitous forms, species even more generalized in their choice of habitat would have such large ranges that they could not meet the criterion for inclusion in this study. The Red-winged Blackbird (*Agelaius phoeniceus*) is a possible real example. It has an average winter within-range abundance much like that of the Common Grackle (Fig. 2, species 65) but a range that puts it outside the limits of the study area and off the range-size scale in Fig. 3. If rare Pacific Coastal species had much smaller ranges than their locally common relatives (as was the case among eastern and western forms), those ranges would have to be very close to zero (see Fig. 3). The land area available to such species might be insufficient to support minimally viable total population sizes.

Table 3. Product-moment correlations between range size and average within-range abundance for various groups of North American winter landbirds.

Group	n	r	P
Ubiquitous species	21	0.210	NS
Eastern species	23	0.717	<0.01
Western Species	18	0.618	<0.01
Pacific Coast species	8	0.242	NS

Christmas Bird Count data provide important glimpses of large-scale patterns in avian geographical ecology, but they also have certain serious limitations. Perhaps the most critical is that they provide no information on the abundances of species within habitats. Each CBC circle is 24 km in diameter, and most circles include a wide variety of habitat types. This study strongly suggests that widespread species are the most abundant, on average, inside their winter ranges, but we do not know if these same species dominate individual habitats where their more specialized relatives live. The answer to this question is important in shaping the nature of any search for "structure" (e.g. Ricklefs and Travis 1980, Wiens and Rotenberry 1981, Pulliam 1983) in avian winter bird communities. If within-habitat winter-bird assemblages are numerically dominated by habitat generalists, then the organization of those assemblages is less likely to be intrinsically understandable than if they are dominated by habitat specialists whose ecology, morphology, and behavior are more purely a consequence of selective forces operating in those habitats.

The Audubon Society's Winter Bird Population Study (WBPS; Boyd and Cink 1983) is a presumed within-habitat winter census. I have examined certain of these data (C. Bock unpubl.), and they suggest that, even in habitats where the narrowly distributed species reach maximum densities, they still are outnumbered in winter by widespread species. WBPS census areas are of varying sizes and heterogeneity, however, and they poorly sample many habitats restricted to the Southeast or Southwest. A more carefully standardized and systematic field study of this problem clearly is needed.

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APPENDIX. Seventy species of landbirds with New World winter ranges at least 75% restricted to the study area (Fig. 1). Numbers correspond to those shown on a plot of range size vs. abundance (Fig. 2).

1. Anna's Hummingbird (*Calypte anna*)
2. Lewis' Woodpecker (*Melanerpes lewis*)
3. Red-headed Woodpecker (*M. erythrocephalus*)
4. Red-bellied Woodpecker (*M. carolinus*)
5. Nuttall's Woodpecker (*Picoides nuttallii*)
6. Downy Woodpecker (*P. pubescens*)
7. White-headed Woodpecker (*P. albolarvatus*)
8. Red-cockaded Woodpecker (*P. borealis*)
9. Northern Flicker (*Colaptes auratus*)
10. Pileated Woodpecker (*Dryocopus pileatus*)
11. Blue Jay (*Cyanocitta cristata*)
12. Pinyon Jay (*Gymnorhinus cyanocephalus*)
13. Clark's Nutcracker (*Nucifraga columbiana*)
14. Black-billed Magpie (*Pica pica*)
15. Yellow-billed Magpie (*P. nuttalli*)
16. American Crow (*Corvus brachyrhynchos*)
17. Fish Crow (*C. ossifragus*)
18. Carolina Chickadee (*Parus carolinensis*)
19. Mountain Chickadee (*P. gambeli*)
20. Plain Titmouse (*P. inornatus*)
21. Tufted Titmouse (*P. bicolor*)
22. Bushtit (*Psaltriparus minimus*)
23. Red-breasted Nuthatch (*Sitta canadensis*)
24. White-breasted Nuthatch (*S. carolinensis*)
25. Pygmy Nuthatch (*S. pygmaea*)
26. Brown-headed Nuthatch (*S. pusilla*)
27. Carolina Wren (*Thryothorus ludovicianus*)
28. Bewick's Wren (*Thryomanes bewickii*)
29. Winter Wren (*Troglodytes troglodytes*)
30. Golden-crowned Kinglet (*Regulus satrapa*)
31. Mountain Bluebird (*Sialia currucoides*)
32. Varied Thrush (*Ixoreus naevius*)
33. Wrentit (*Chamaea fasciata*)
34. Sage Thrasher (*Oreoscoptes montanus*)
35. Brown Thrasher (*Toxostoma rufum*)
36. California Thrasher (*T. redivivum*)
37. LeConte's Thrasher (*T. lecontei*)
38. Bohemian Waxwing (*Bombycilla garrulus*)
39. Northern Shrike (*Lanius excubitor*)
40. Pine Warbler (*Dendroica pinus*)
41. Northern Cardinal (*Cardinalis cardinalis*)
42. Abert's Towhee (*Pipilo aberti*)
43. Bachman's Sparrow (*Aimophila aestivalis*)
44. American Tree Sparrow (*Spizella arborea*)
45. Field Sparrow (*S. pusilla*)
46. Black-throated Sparrow (*Amphispiza bilineata*)
47. Sage Sparrow (*A. belli*)
48. Baird's Sparrow (*Ammodramus bairdii*)
49. Henslow's Sparrow (*A. henslowii*)
50. Le Conte's Sparrow (*A. leconteii*)
51. Sharp-tailed Sparrow (*A. caudacutus*)
52. Seaside Sparrow (*A. maritimus*)
53. Fox Sparrow (*Passerella iliaca*)
54. Song Sparrow (*Melospiza melodia*)
55. Swamp Sparrow (*M. georgiana*)
56. White-throated Sparrow (*Zonotrichia albicollis*)
57. Golden-crowned Sparrow (*Z. atricapilla*)
58. Harris' Sparrow (*Z. querula*)
59. Dark-eyed Junco (*Junco hyemalis*)
60. McCown's Longspur (*Calcarius mccownii*)
61. Lapland Longspur (*C. lapponicus*)
62. Smith's Longspur (*C. pictus*)
63. Tricolored Blackbird (*Agelaius tricolor*)
64. Rusty Blackbird (*Euphagus carolinus*)
65. Common Grackle (*Quiscalus quiscula*)
66. Purple Finch (*Carpodacus purpureus*)
67. Cassin's Finch (*C. cassinii*)
68. Pine Siskin (*Carduelis pinus*)
69. American Goldfinch (*C. tristis*)
70. Evening Grosbeak (*Coccothraustes vespertinus*)