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THE DISTRIBUTION OF WINTERING BIRDS IN CENTRAL MAINE: THE INTERACTIVE EFFECTS OF LANDSCAPE AND BIRD FEEDERS

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Abstract.—The abundances of birds at 50 stops along a 43-km route were determined by 10 censuses in the winter of 1992–1993 in central Maine. Each stop was classified as one of the following: Agricultural, Edge, Deciduous Forest or Coniferous Forest. Habitat preferences for 16 landbird species were documented. For five of these species, Edge stops with feeders were preferred over Edge stops without feeders. When stations with feeders were removed from the habitat preference analysis, four of these five species showed significant changes in their habitat preferences. The data underscore the necessity of knowing the location of supplemental food in any field ornithological study.

LA DISTRIBUCIÓN DE AVES INVERNALES EN EL CENTRO DE MAINE: EFECTOS INTERACTIVOS DEL PAISAJE Y LOS COMEDEROS PARA AVES

Sinopsis.—Se determinó la abundancia de aves siguiendo una ruta de 50 paradas en 43 km usando 10 censos en el invierno de 1992 a 1993 en el centro de Maine. Cada parada se clasificó como agrícola, lindero, bosque deciduo o bosque conifero. Se documentaron las preferencias de hábitat de 16 especies. Para cinco de éstas, paradas con comederos en los linderos fueron preferidas a paradas en los linderos donde no había comederos. Cuando se removieron las paradas con comederos del análisis de preferencias de hábitat, cuatro de estas cinco especies mostraron cambios significativos en sus preferencias de hábitat. Estos datos subrayan la necesidad de conocer la localización de alimentos suplementarios en cualquier estudio de campo ornitológico.

The understanding of the determinants of bird distributions requires knowledge over a range of scales. Christmas Bird Count data (National Audubon Society) provide a useful means of comparing the distributions of birds across North America, using the 24-km diameter count circles as the units of comparison (e.g., Root 1988). Winter Bird Counts (currently published as annual supplements to the Journal of Field Ornithology) are standardized censuses within a relatively small, homogenous area (usually 40 ha or smaller). Counts are made regularly during the winter. In the present study, I seek to combine the advantages of both of these types of censuses by examining winter bird distribution over a broader range than the Winter Bird Counts. The scale of sampling is on the order of a Christmas Count Circle but repeated sampling and classification of the habitat of each sampling stop increase the precision of the census data. In addition, the proximity of bird feeders to each stop was noted and feeder effects were analyzed statistically.

MATERIALS AND METHODS

The data for this study were derived from 10 censuses of the winter birds along a fixed route in central Maine over a period of 12 wk in the winter of 1992–1993. The sampling design was patterned after that used by the Breeding Bird Survey (Robbins et al. 1986), administered by the U.S. Fish and Wildlife Service, in which an observer stops every 0.8 km along a 39.2-km route and counts all birds, heard and seen, during a 3-min observation period. The accuracy of the Breeding Bird Survey data depends on the fact that males of most breeding birds sing on a fixed territory and that therefore many birds can be detected on a single sampling. Most wintering birds, however, do not sing or maintain nesting territories. Some birds may forage widely in mixed-species flocks (Smith 1992). This tendency for winter bird distributions to be clumped increases the variance in census data. The counts at a site for many species are likely to be bimodal: either zero or, if a feeding flock is present at that stop, high. Accordingly, multiple sampling is required to determine the avian use of the habitat at each site.

The route consisted of 43 km of mainly secondary roads in Vassalboro and China, Maine, which were chosen because of the lack of traffic that might interfere with vocal identification of birds. The route lies between 44°23′44″N and 44°26′52″N and between 69°40′53″W and 69°29′54″W.

The habitat of each station was classified *a priori* into one of four habitat types: Agricultural, Edge, Deciduous Forest or Coniferous Forest. Agricultural habitat included fields, barnyards and pastures. Trees were rarely found in this type of habitat. Edge was used to describe habitats with some trees, usually not dense, adjacent to residences, lawns, brushy fields or bodies of water. Suburban areas were classified as Edge. Deciduous Forest included woods dominated by deciduous trees, especially maples (*Acer rubrum* and *A. saccharum*), oaks (mostly *Quercus rubra*), American beech (*Fagus americanus*) and ash (*Fraxinus* spp.). Coniferous forests were dominated by cone-bearing trees, particularly white pine (*Pinus strobus*) and eastern hemlock (*Tsuga canadensis*) with occasional balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*). There were nine Agricultural sites, 18 Edge sites, nine Deciduous Forest sites and 14 Coniferous Forest sites. The distribution of each habitat type was widely spaced along the survey route.

A separate classification was used to test the effect of bird feeders on bird distribution. If a survey stop was located within 100 m of a feeding station, that survey stop was classified as a "Feeder" stop. If no feeders were within 100 m, that station was classified as a "No Feeder" stop. Except for one feeding station located at a home in a Deciduous Forest habitat, all of the feeders were located in Edge habitat. Of the 18 Edge stations, seven had feeding stations present. All the feeding stations provided sunflower seed. Suet, niger seed and millet were provided at some feeders. All of the feeding stations were well-supplied during this study.

All surveys were begun within an hour after dawn. The order in which stations were visited was maintained throughout the study. At each stop, I got out of my car and counted all birds seen and heard in a 2.5-min period. The 2.5-min period was used so that the survey could be completed by 1100 hours when a noticeable decline in bird activity, and hence detectability, occurred.

The number of individuals of each bird species in each habitat type was totaled for each sampling date. The mean number of each species per stop was calculated by dividing the total number of birds for each habitat type by the number of stops, given above.

The sampling periods were *a priori* divided into early (14 and 23 December, 6 and 13 January), middle (20 January, 4 and 11 February) and late (18 and 25 February, 6 March). These three intervals were used as blocks in the statistical analysis to test for differences in abundance over the course of the study. With the exception of the data for Rock Doves (*Columba livia*), the block effect was not significant by one-way analysis of variance and the different blocks were combined for subsequent analysis. Habitat-use for each species was gauged by a one-way analysis of variance using the mean number of individuals/stop for each habitat type on the 10 sampling days. If the ANOVA showed that there were significant differences between means, Scheffé *post hoc* comparisons (Sokal and Rohlf 1981) were used to determine where the significant differences lay.

RESULTS

A total of 28 species was detected on these surveys. Of these, only 16 were sufficiently abundant to justify statistical analysis. Although data on the population dynamics of each species will not be presented, an ANOVA testing time of the season (early, middle and late season sampling) indicated that no significant differences occurred among blocks ($P > 0.05$ for all cases), with the exception of Rock Doves (*Columba livia*) for which there was an increase in numbers toward the end of the sampling. This increase did not result in a significant interaction between habitat and season in a two-way ANOVA, indicating that the increased numbers of Rock Doves did not lead to a different distribution of individuals among habitat types.

Fourteen of the 16 species were observed at feeders during these surveys. With the exception of a feeder at a Deciduous Forest station, all of the feeders were located at Edge stations. A comparison of the abundance of these 14 species between Edge stations with and without feeders is given in Table 1. Five species showed significantly different abundances in feeder versus non-feeder sites. Downy Woodpeckers (*Picoides pubescens*), Blue Jays (*Cyanocitta cristata*), Black-capped Chickadees (*Parus atricapillus*), American Goldfinches (*Carduelis tristis*) and House Finches (*Carpodacus mexicanus*) were all significantly more abundant in Edge habitats with feeders compared to Edge habitats without feeders ($P < 0.05$). The abundances of the remaining species were not significantly affected by the presence of bird feeders.

The distributions by habitat type, irrespective of feeder proximity, of the 16 most common species are given in Table 2A. Seven species showed no significant difference in abundance among the four habitat types (Mourning Dove (*Zenaida macroura*), Hairy Woodpecker (*Picoides villosus*), Common Raven (*Corvus corax*), Red-breasted Nuthatch (*Sitta canadensis*), Purple Finch (*Carpodacus purpureus*), Evening Grosbeak (*Coc-

TABLE 1. A comparison of the abundance of 14 species of birds in Edge habitat as a function of the presence/absence of bird feeders. The results of paired *t*-tests are shown. The mean abundance per stop is given with the standard deviation in parentheses.

Species	Feeders	No feeders	*P*
Rock Dove *Columba livia*	0.31 (0.508)	0.14 (0.293)	>0.05
Mourning Dove *Zenaida macroura*	0.36 (0.342)	0.0 (0.0)	>0.05
Downy Woodpecker *Picoides pubescens*	0.33 (0.214)	0.0 (0.0)	<0.01
Hairy Woodpecker *Picoides villosus*	0.06 (0.104)	0.06 (0.104)	>0.05
Blue Jay *Cyanocitta cristata*	1.07 (0.587)	0.03 (0.043)	<0.001
Black-capped Chickadee *Parus atricapillus*	1.03 (0.670)	0.46 (0.218)	<0.05
White-breasted Nuthatch *Sitta carolinensis*	0.11 (0.102)	0.03 (0.067)	>0.05
Red-breasted Nuthatch *Sitta canadensis*	1.28 (2.478)	0 (0)	>0.05
Eurasian Starling *Sturnus vulgaris*	1.20 (1.972)	0.05 (0.121)	>0.05
American Goldfinch *Carduelis tristis*	1.92 (1.513)	0.06 (0.113)	<0.01
Purple Finch *Carpodacus purpureus*	0.14 (0.203)	0 (0)	>0.05
House Finch *Carpodacus mexicanus*	1.32 (0.817)	0.01 (0.032)	<0.01
Evening Grosbeak *Coccothraustes vespertinus*	0.62 (0.826)	0.06 (0.104)	>0.05
House Sparrow *Passer domesticus*	0.36 (0.685)	0.10 (0.120)	>0.05

cothraustes vespertinus) and House Sparrow (*Passer domesticus*)). The remaining nine species showed a preference for one or more of the four habitats. Rock Doves were significantly more abundant in Edge habitats compared to the other three habitat types. Similarly, Downy Woodpeckers and Blue Jays were significantly more abundant in Edge habitat. American Crows (*Corvus brachyrhynchos*) were significantly more abundant in Agricultural habitat compared to Coniferous Forest habitat; no other significant differences in habitat preference were found for this species. Black-capped Chickadees were significantly less abundant in Agricultural habitat than in the other three habitat types. White-breasted Nuthatches (*Sitta carolinensis*) were significantly more abundant in Edge habitat compared to Agricultural habitat. European Starlings (*Sturnus vulgaris*) were equally common in Edge and Agricultural habitat but significantly more abundant there than in ether Coniferous or Deciduous Forest habitat; abundances between Coniferous and Deciduous Forest habitat were not statistically different. American Goldfinches and House Finches were significantly more abundant in Edge habitats than in the other three habitat types.

To remove the effect of feeders from the analysis of habitat preferences, the seven Edge stations with feeders and the single Deciduous Forest station with feeders were removed from the ANOVAs used to test for differences among habitat types. The habitat rankings (Table 2B) were changed for four species. Downy Woodpeckers were significantly more abundant in Deciduous Forest habitat compared to the other three habitats; the significantly higher number of Downy Woodpeckers in Edge habitat (Table 2A) was removed when the effect of feeders was removed. Blue Jay abundances did not differ among habitat types after feeder effects were removed (Table 2B); with feeding stations present, a significant

TABLE 2. Mean number of birds for 16 landbird species among four different habitat types. Standard deviations are given in parentheses. A. All 50 stations are included. B. The seven Edge stations and the one Deciduous Forest station with feeders are removed from the analysis. The mean abundance per stop is given with the standard deviation in parentheses. Key to Abbreviations: = signifies that two means are not statistically different; < signifies a significant difference with $P < 0.05$.

Species	Agri-cultural	Edge	Decid-uous	Conif-erous	Statistical comparison of means
		A. All Stations Included			
Mourning Dove	0.01	0.14	0	0	A = E = D = C
Zenaida macroura	(0.005)	(0.047)	(0)	(0)	
Rock Dove	0.04	0.22	0	0	D = C = A < E
Columba livia	(0.057)	(0.288)	(0)	(0)	
Downy Woodpecker	0	1.0	0.07	0	A = C = D < E
Picoides pubescens	(0)	(0.09)	(0.082)	(0)	
Hairy Woodpecker	0	0.05	0.02	0.01	A = E = D = C
Picoides villosus	(0)	(0.047)	(0.049)	(0.03)	
Blue Jay	0.12	0.43	0.15	0.16	A = D = C < E
Cyanocitta cristata	(1.51)	(0.24)	(0.14)	(0.21)	
American Crow	0.62	0.50	0.26	0.04	C = D = A, D = E = A
Corvus brachyrhynchos	(0.56)	(0.33)	(0.25)	(0.07)	
Common Raven	0.04	0.03	0.04	0.02	A = E = D = C
Corvus corax	(0.03)	(0.04)	(0.02)	(0.04)	
Black-capped Chickadee	0.16	0.73	1.13	0.76	A < E = C = D
Parus atricapillus	(0.18)	(0.29)	(0.46)	(0.36)	
White-breasted Nuthatch	0	0.06	0.01	0.03	A = D = C, D = C = E
Sitta carolinensis	(0)	(0.041)	(0.04)	(0.04)	
Red-breasted Nuthatch	0	0.02	0.04	0.05	A = E = D = C
Sitta canadensis	(0)	(0.04)	(0.06)	(0.08)	
European Starling	0.56	0.31	0	0	C = D < E = A
Sturnus vulgaris	(0.46)	(0.62)	(0)	(0)	
American Goldfinch	0	0.78	0.02	0	A = C = D < E
Carduelis tristis	(0)	(0.61)	(0.05)	(0)	
Purple Finch	0	0.06	0.03	0.14	A = E = D = C
Carpodacus purpureus	(0)	(0.08)	(0.06)	(0.30)	
House Finch	0	0.52	0.01	0	C = A = D < E
Carpodacus mexicanus	(0)	(0.33)	(0.04)	(0)	
Evening Grosbeak	0	0.17	0.04	0.1	A = E = D = C
Coccothraustes vespertinus	(0)	(0.26)	(0.10)	(0.12)	
House Sparrow	0.43	0.21	0	0	A = E = D = C
Passer domesticus	(0.51)	(0.29)	(0)	(0)	
		B. Stations with Feeders Removed			
Downy Woodpecker	0	0	0.07	0	A = E = C < D
Picoides pubescens	(0.0)	(0.0)	(0.08)	(0)	
Blue Jay	0.12	0.03	0.15	0.16	A = E = D = C
Cyanocitta cristata	(1.51)	(0.04)	(0.14)	(0.21)	
American Goldfinch	0	0.06	0.02	0	A = E = D = C
Carduelis tristis	(0)	(0.11)	(0.05)	(0)	
House Finch	0	0.01	0.01	0	A = E = D = C
Carpodacus mexicanus	(0)	(0.03)	(0.04)	(0)	

preference for Edge habitat was noted (Table 2A). Similarly, no significant differences among habitat types were found for American Goldfinches and House Finches (Table 2B). Both of these species were significantly more abundant in Edge habitats (Table 2A) when a feeder effect was present.

DISCUSSION

Food availability can influence avian distributions over a range of scales. On the scale of hundreds of kilometers, augmentation of natural food at bird feeders has been invoked to explain changes in bird distribution. With over 80 million people feeding birds in North America (U.S. Fish and Wildlife Service 1988), most wintering landbirds are likely to encounter feeders. The northward extension of several species (e.g., House Finch [*Carpodacus mexicanus*] in the east, Tufted Titmouse [*Parus bicolor*] and Northern Cardinal [*Cardinalis cardinalis*]) has been attributed to the provision of food during the winter (Andrle and Carroll 1988, Erskine 1992, Laughlin and Kibbe 1985). LeGrand (1992a, b) has claimed that "shortstopping" of irruptive winter finches at feeders in the northern United States has precluded recent invasions into the southeastern U.S. The influences of feeders in these changing patterns are suggestive, but compelling data are lacking. Indeed, to demonstrate such large-scale patterns, correlative data are probably the best data that can be acquired within the constraints of most research programs.

The present study addresses bird distribution on the scale of kilometers. By regularly censusing birds over the course of the winter of 1992–1993, I documented habitat preferences for nine of the 16 most common landbirds (Table 2A) among Agricultural, Edge, Deciduous Forest and Coniferous Forest habitats. The more novel portion of this study is the inclusion of the proximity of bird feeders as a factor in the analyses (Table 1). Seven of the 18 Edge stations had feeding stations within 30 m of the stop. Except for a single feeding station in a Deciduous Forest stop, the other stations had no proximate feeders, constraining the analysis of feeder effects to the Edge habitat only. For five species (Table 1), bird density was higher in the vicinity of the stops with feeders.

To determine any influence that feeders had on the distribution of birds among the different habitats (Table 2), the ANOVAs were recalculated after removing the seven Edge stations and the single Deciduous Forest station that were close to bird feeders. In four of the five cases where significant feeder effects were seen (Table 1), the habitat distribution of those birds was significantly changed (Table 2B). Without the presence of supplemental food, the Edge habitat was less preferred in four of the five cases, resulting in different rankings of the four different habitats.

The present data suggest that the proximity of supplementary food can influence habitat preferences. Other local effects of supplementary feeding have been documented as well. A number of studies have documented correlations between the abundance of naturally occurring food and winter survivorship (Enoksson and Nilsson 1983; Källander 1981; Nilsson 1985, 1987; Perrins 1966). The physiological condition of four woodland birds, as measured by ptilochronology, improved with supplemental winter feeding (Grubb and Cimprich 1990). In a controlled, but unreplicated experiment, Jansson et al. (1981) showed that supplementary feeding in the winter nearly doubled the survivorship of Willow Tits (*Parus montanus*) and Crested Tits (*Parus cristatus*) in Sweden. Desrochers et al. (1988) experimentally, but without replication, showed that Black-capped Chickadees in Alberta had higher survivorships when provided with supplementary food. The most compelling data for an effect of supplementary food on winter survivorship have been provided by Brittingham and Temple (1988, 1992a, b) who used replicated, controlled experiments to show supplementary feeding in winter increased survivorship of Black-capped Chickadees in Wisconsin.

Supplementary feeding can affect foraging behavior. Berner and Grubb (1985) showed that winter supplementary feeding led to a decrease in mixed-species flocking in Ohio woodlands. Grubb (1987) and Székely et al. (1989) found a similar effect on tits in England and Hungary, respectively.

On local scales (meters to kilometers), supplementary feeding can therefore influence habitat preference of wintering birds (Table 2), survivorship and foraging behavior. With the ever increasing interest in bird feeding, many wintering birds can take advantage of a feeder's largesse. The documented effects of food supplementation underscore the caveat of Grubb and Cimprich (1990) that ornithological studies must account for the proximity of bird feeding stations.

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