RAINFALL AND WINTER SPARROW DENSITIES: A VIEW FROM THE NORTHERN GREAT BASIN

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ABSTRACT.—Rainfall is known to influence seed production markedly in arid habitats of the northern Great Basin. We tested the effect of between-year rainfall variation on the abundance of wintering seed-eating sparrows, using published data from Audubon Christmas Bird Counts for the period 1965–1981. Results do not support the proposition that wintering sparrows in the northern Great Basin are limited directly by competition for food. Other seasonal climatic factors, such as winter snow cover and temperature, appear to be more important than rainfall in influencing winter sparrow abundance. The winter densities of coexisting sparrows were found to be strongly correlated, suggesting that species in this guild respond similarly to variable winter conditions in different years. *Received 5 March 1984, accepted 18 September 1984.*

A CURRENT controversy in ecology concerns the degree to which competition is important in structuring ecological communities (e.g. Arthur 1982; Schoener 1982; Connell 1983; Lewin 1983a, b; Roughgarden 1983; Weins 1983a, b). Our perception of the role that competition plays in nature has been influenced markedly by studies of avian communities. Several workers (e.g. MacArthur 1958, Lack 1966, Cody 1968) have suggested that competition for food plays a key role in determining the structure of many avian communities and ultimately limits the density of many populations of small birds. With regard to food limitation, Pulliam and Brand (1975) showed a positive correlation between summer rainfall and grass seed production in southeastern Arizona, where increased summer rainfall resulted in greater food availability to wintering seed-eating sparrows. In addition, Pulliam and Parker (1979) showed a positive correlation between local seed production and numbers of wintering Chipping Sparrows (*Spizella passerina*) in southeastern Arizona.

In a recent paper, Dunning and Brown (1982) extended the generality of Pulliam and Parker's (1979) results by reporting positive correlations between summer rainfall and densities of wintering finches of the subfamilies Fringillinae and Emberizinae (hereafter sparrows) on five southeastern Arizona Christmas Bird Counts (hereafter CBCs).

Dunning and Brown (1982) assumed that increased summer rainfall resulted in increased seed production. They selected ten migratory sparrow species that were both relatively abundant in winter and variable in their winter population densities. They predicted that (1) winter sparrow densities would be positively correlated with summer precipitation, (2) a good year for one sparrow species would be a good year for all other co-occurring sparrow species, because they share a common limiting resource, and (3) species diversity of sparrows should be correlated positively with summer rainfall, because consumer species diversity should be correlated with greater productivity. They interpreted their findings as strongly supporting the first two hypotheses but only weakly supporting the third. They concluded that their analysis showed "strong support for the proposition that the local abundance of seed-eating birds, at least of sparrows in southeastern Arizona, are regulated primarily by the availability of food resources" (1982: 127).

We attempted to test the generality of Dunning and Brown's first two conclusions to CBCs in the northern Great Basin, where rainfall also is known to limit annual seed production in arid habitats. In addition, we explored the role of other seasonal climatic factors that also may affect the winter density and distribution of seed-eating sparrows.

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TABLE 1. Description of seven northern Great Basin Christmas Bird Counts used in this analysis.

Count locality	Lowest elevation (m)	Latitude, longitude	Years of census	Arid habitat (%)	$\bar{x}$ spring precipitation (mm)	$\bar{x}$ total sparrows/party-hour	$\bar{x}$ party-hours	Species examined[a]
Nampa, Idaho	675	43°40'N, 116°40'W	17 (1965–1981)	15	66.3	31.6	61.8	DJ, WS, HF, AG
Boise, Idaho	825	43°37'N, 116°11'W	16 (1966–1981)	50	84.1	24.7	39.4	DJ, WS, HF
Baker, Oregon	1,005	44°51'N, 117°50'W	15 (1965–1968 and 1970–1981)	35	59.2	15.9	33.4	DJ, HF, AG
Malheur, Oregon	1,275	42°54'N, 118°53'W	16 (1965–1968 snd 1970–1981)	15	46.7	4.8	43.3	DJ
Salt Lake City, Utah	1,285	40°46'N, 111°54'W	17 (1965–1981)	70	125.5	22.2	80.6	DJ, WS, HF, PS
Hyde Park, Utah	1,340	41°48'N, 111°50'W	7 (1975–1981)	20	134.9	10.5	35.8	DJ, WS
Truckee Meadows, Nevada	1,340	39°28'N, 119°49'W	15 (1966–1978 and 1980–1981)	54	57.9	29.8	53.5	DJ, WS, HF

[a] DJ = Dark-eyed Junco (*Junco hyemalis*), WS = White-crowned Sparrow (*Zonotrichia leucophrys*), HF = House Finch (*Carpodacus mexicanus*), AG = American Goldfinch (*Carduelis tristis*), PS = Pine Siskin (*Carduelis pinus*).

METHODS

Bird census data were taken from seven CBCs (Audubon Field Notes 1964–1970, American Birds 1971–1981). All CBCs in the northern Great Basin were examined. Because of concern about bias due to small sample sizes, we arbitrarily selected only those counts with a minimum of 20 party-hours/CBC sampling effort, a minimum of 5 sparrows/party-hour, more than 15% arid habitat for wintering sparrows, and CBCs of at least 7 yr duration (Table 1). All species selected for individual correlations with weather variables were migratory species exhibiting highly variable winter densities in excess of two birds/party-hour. We divided bird census data by the number of party-hours to compensate for the varying census efforts typical of many CBCs (Bock and Lepthien 1974). Christmas Bird Count data may exhibit several inherent forms of bias (see Bock and Smith 1971, Bock and Lepthien 1974, Confer et al. 1979, and Smith 1979 for discussion).

Weather data were taken from the U.S. Environmental Data Service monthly reports from the U.S. Weather Service station closest to, or most appropriate for, the 12-km CBC radius.

Our statistical analyses were similar to those used by Dunning and Brown (1982). All statistical procedures were carried out using the MINITAB statistical program package (Ryan et al. 1976). Our most powerful test of rainfall-sparrow abundance relationships used untransformed data in least squares regression analysis. Sparrow data were also $\log_{10}$ transformed because we had no a priori reason to assume that bird abundance over the period studied was normally distributed or that the relationship between rainfall and sparrow abundance was linear. Nonparametric Spearman rank correlations were used as a conservative statistical comparison of these relationships. Multiple regressions using untransformed sparrow abundance data were used in some cases to test for the possible effects of combinations of several seasonal climatic factors on winter sparrow density.

Climatic considerations.—The northern Great Basin and southeastern Arizona exhibit markedly different climatic regimes. Southeastern Arizona has a bimodal pattern of annual rainfall, in which precipitation peaks in spring and summer. The spring rains (December–April) are the remnants of Pacific storms that reach Arizona. They are sporadic in nature and result in seed production by annual plants with Rocky Mountain/Great Basin affinities. The summer rains (June–early September) are more dependable and result in seed production by a forb flora with Sonoran Desert affinities (Lowe 1964, Cable 1975). In the northern Great Basin, however, most effective precipitation comes in the winter and spring. Here, the precipitation that most influences plant growth and seed production falls between October and March. Summer rains consist of isolated thunderstorms that have negligible impact on seed production, because most important forbs have set seed by mid-July (Craddock and Forsling 1938, Tisdale and Hironaka 1981). Consequently, the vast majority of seeds available to granivores in arid habitats result from the previous spring and winter's precipitation (Pechanec et al. 1937, Stewart and Young 1940, Blaisdell 1958, Pearson 1979).

We used the combined precipitation for the months of February, March, and April (spring rainfall) as the independent variable for our initial attempts to find correlations with sparrow densities. Later analyses used either winter through late spring precipitation (September–June) or annual precipitation as an all-inclusive measure.

RESULTS

Our first series of tests examined possible relationships between spring rainfall and winter densities for each individual sparrow species at each locality. Our criterion of 2 birds/party-hour minimum density limited our analysis to 20 cases among the 7 CBCs. Using untransformed data, only 1 of the 20 regressions was statistically significant.

We repeated the analysis using $\log_{10}$-transformed sparrow data, and again only 1 of the 20 regressions was statistically significant, which would be expected stochastically at the $P < 0.05$ level. Nine of the 20 correlation coefficients were negative, which is also close to chance expectation. Results were similar when these tests were repeated using more conservative Spearman rank correlations.

Tests for relationships between spring rainfall and the combined densities of all sparrow species at each count locality also were nonsignificant, providing little support for a spring rainfall-winter sparrow abundance relationship in the northern Great Basin. Spring rainfall explained less than 3% of the total variability in winter sparrow abundance in our analysis.

TABLE 2. Spearman rank coefficients (r_s) for total sparrow abundance vs. spring and annual rainfall for seven northern Great Basin Christmas Bird Counts. Counts are ordered from lowest to highest elevation.

Count locality	Spring rainfall	Annual rainfall
Nampa, Idaho	0.238	−0.051
Boise, Idaho	0.226	0.248
Baker, Oregon	−0.014	−0.613[a]
Malheur, Oregon	−0.129	−0.006
Salt Lake City, Utah	−0.125	0.223
Hyde Park, Utah	0.179	−0.393
Truckee Meadows, Nevada	−0.071	−0.023

[a] $P < 0.05$.

Annual precipitation was somewhat more effective, explaining about 8% of the variability in winter sparrow abundance. However, only the Baker, Oregon CBC showed a significant rainfall-sparrow abundance relationship ($F = 6.30$, df $= 13$, $P < 0.05$), although the correlation actually was negative in this case. Correlations of September–June precipitation with total sparrow densities were not significant for any CBC.

We next tested Dunning and Brown's second hypothesis, that the densities of all sparrow species should be positively correlated with each other because these species share a common limiting resource that is subject to wide levels of annual variation. In all 20 cases, results were positive and highly significant ($P < 0.01$, Spearman rank correlation), strongly supporting this hypothesis. Because the densities of co-occurring species were thus strongly correlated, we combined the densities of all species at each count locality in the subsequent analyses.

To further examine the possible relationship between annual rainfall and winter sparrow densities, we conducted a comparison of total sparrow abundance for years having above-average vs. below-average rainfall on all seven CBCs, using a nonparametric Mann-Whitney U-test. Again, results were not significant at any count locality.

Because rainfall generally accounted for such a small proportion of the total variability in winter sparrow abundance, we elected to ex-

TABLE 3. A comparison of various climatic factors used in our regression models to predict winter sparrow abundance on seven Christmas Bird Counts in the northern Great Basin. Untransformed data were used in the regressions presented in this table. The first number in each column is the F statistic and the value in parentheses is the R^2 or predictor value. Counts are ordered from lowest to highest elevation.

	Weather on the day of the count					
Count locality	Median temperature	Median snow cover	Temperature and snow cover	December mean temperature and precipitation	December mean temperature and precipitation and annual rainfall	December mean temperature and precipitation, annual rainfall, and party-hours/CBC
Nampa, Idaho	2.796 (15.7%)	7.594[a] (33.6%)	6.452[a] (48.0%)	1.947 (21.8%)	1.438 (24.9%)	2.220 (42.5%)
Boise, Idaho	0.870 (5.9%)	0.112 (0.8%)	1.354 (17.2%)	1.281 (16.5%)	3.060 (43.3%)	2.112 (43.4%)
Baker, Oregon	0.176 (1.3%)	0.010 (0.1%)	0.082 (1.3%)	2.156 (26.4%)	4.824 (56.8%)	3.324 (57.1%)
Malheur, Oregon	0.406 (2.8%)	0.032 (0.2%)	0.288 (4.2%)	2.171 (25.0%)	1.344 (25.1%)	2.038 (42.6%)
Salt Lake City, Utah	1.007 (6.3%)	0.394 (2.6%)	0.966 (12.1%)	0.325 (4.4%)	0.202 (4.4%)	0.402 (11.8%)
Hyde Park, Utah	0.418 (7.7%)	0.328 (2.6%)	0.546 (21.4%)	0.071 (3.4%)	0.093 (8.6%)	1.068 (68.0%)
Truckee Meadows, Nevada	0.607 (4.5%)	0.650 (4.8%)	1.066 (15.1%)	0.309 (4.9%)	0.271 (6.9%)	3.080 (55.2%)
Mean R^2	6.3%	6.9%	17.0%	14.6%	24.3%	45.8%

[a] $P < 0.05$.

plore the possible role of several additional climatic variables. Other variables tested included median temperature and median snow cover on the day of the count, which accounted for 6.3% and 6.9% of the total variability, respectively (Table 3). Regressions were not significant for any count, although day-of-count temperature was negatively correlated with bird abundance for all seven CBCs and day-of-count snow cover was negatively correlated for five of seven CBCs.

We found that mean temperature and mean precipitation for the month of December served as an excellent predictor of snow cover ($R^2 = 0.89$, $F = 25.32$, df = 2,12, $P < 0.01$) during that month for the Truckee Meadows CBC (snow cover information was not consistently available for the other count areas). We therefore tested the effect of these two combined variables on total sparrow densities using multiple regressions with untransformed data. These predictors accounted for 22.5% of the variability in the Boise, Baker, and Malheur counts, but accounted for less than 3% of the variability for Salt Lake City, Hyde Park, and Truckee Meadows, the three counts occurring at the highest elevations (Table 3).

The inclusion of annual precipitation with the previous variables in multiple regressions produced marked improvements in R^2 values for the Boise and Baker counts but did not increase predictor values markedly for the other CBCs, explaining an average of 24% of the total variability (Table 3).

To assess the effect of varying census effort on bird density estimates, we regressed normalized sparrow abundance (birds/party-hour) on sampling effort (total party-hours/CBC) for each count. We found that four of seven correlations were significant, three negative, and one positive (Table 4). This suggests that the standard procedure for normalizing count data by dividing bird abundance by the number of party-hours may tend to under- or overestimate bird densities on some counts. We were able to assess the variability induced by this party-hour bias by including party-hours as an independent variable in our multiple regression model. Although party-hours and normalized bird densities (birds/party-hour) are not independent variables and thus should show at least some correlation, the fact that predictor values were improved considerably supports the proposition that some of the variability in sparrow density estimates is being induced by normalizing sparrow abundance data. Our model now explains 42–68% of the variability on all counts except Salt Lake City, for which only 11.8% of the variability is explained (Table 3).

DISCUSSION

Dunning and Brown's (1982) results were consistent with the Food Limitation Hypothesis. However, when we performed a similar analysis in a different arid ecosystem, we found a striking lack of correlation between precipitation, and hence food supply, and CBC winter sparrow densities.

Several factors could complicate this relationship between food and winter sparrow densities. First, northern Great Basin CBCs may be inadequate censuses of winter sparrow abundance. Second, competition with rodents and ants for available seed resources could confound a simple relationship between annual seed production and winter sparrow abundance. Third, annual population recruitment on the breeding grounds could be more important than food availability in determining the abundance of wintering sparrows. Finally, snow cover, inclement weather, and other climatic variables may overshadow annual variations in food supply.

Our CBCs have smaller sampling efforts and lower sparrow densities than the popular southeastern Arizona CBCs. Thus, the lack of significant correlations may simply be a function of inadequate sampling effort. However, our regressions of normalized sparrow densities on sampling effort are instructive. One correlation was positively significant (Hyde Park, $n = 7$ yr), three were not significant (Baker, Salt Lake City, Boise), and three were negatively significant (Nampa, Malheur, Truckee Meadows). If the small sampling efforts were biasing density estimates, there should be a significant, positive correlation between sampling effort and normalized density estimates. The fact that six of the seven correlations were not positive seems to indicate that sparrow habitats in the count areas had been saturated by birders. Thus, we feel that whatever the reasons for the negative correlations, the smaller sampling efforts of northern Great Basin CBCs are not responsible for the apparent lack of precipitation-sparrow density correlations.

An important difference between the northern Great Basin and southeastern Arizona is the time interval between seed production and the arrival of wintering sparrows. In southeastern Arizona, this interval is a few weeks at most. In the northern Great Basin, where most seed production occurs during early summer, there is a minimum interval of three months. During this time, seeds are subject to predation by rodents (Schreiber 1973) and ants. Thus, local or temporal variations in rodent or ant densities could reduce seed availability in ways not directly correlated with precipitation.

TABLE 4. Regression coefficients for total birds/party-hour vs. total party-hours to test the effects of varying sampling effort on estimates of bird density. Slopes of significant regressions are negative for all counts except Hyde Park.

Count locality	F[a]
Nampa, Idaho	4.600*
Boise, Idaho	2.255
Baker, Oregon	4.110
Malheur, Oregon	5.402*
Salt Lake City, Utah	1.687
Hyde Park, Utah	19.210**
Truckee Meadows, Nevada	11.893**

[a] * $P < 0.05$; ** $P < 0.01$.

At present, there appears to be no tractable method for assessing the effects of between-year variations in population recruitment during the breeding season on winter sparrow densities. However, sparrows wintering in the northern Great Basin breed in a variety of locales in which the occurrence of favorable breeding conditions probably is not directly correlated between years. Thus, it seems unlikely that variations in recruitment could explain the positive correlations seen between coexisting species in different years. A more likely explanation for the variability in winter sparrow densities is the facultative migration scenario proposed by Pulliam and Brand (1975) and further supported by Terrill and Ohmart (1984), in which the primary determinant of the abundance of small birds in winter is between-year variations in habitat suitability.

The consistently significant correlations we found between the densities of individual sparrow species and the combined densities of all co-occurring species suggests that species in this guild are responding similarly to variable winter conditions between years. This remarkably strong relationship may be enhanced somewhat by the fact that sparrows often occur in mixed flocks in winter, or that flocks of several species occur in the same habitats. Thus, when birders encounter one species in the field, they are likely to encounter other species simultaneously. Although this aspect of the winter flocking behavior of sparrows may induce some form of sampling bias, true deficits of any individual species should be reflected in the Spearman ranking tests.

Consequently, as a result of the consistent lack of correlations between rainfall and sparrow densities, and yet strong correlations between the densities of co-occurring species on each CBC, there appear to be some real patterns in our data. Our results suggest that a combination of climatic variables influence winter sparrow densities in the northern Great Basin. Our multiple-regression model incorporating mean December temperature and precipitation, total annual precipitation, and sampling effort/CBC explains more than half of the variability in winter sparrow abundance, with the exception of the Salt Lake City CBC, for which the model appears inadequate. The nonsignificant F values for these multiple regressions include some colinearity effects (Sokal and Rohlf 1981), probably between December precipitation and annual precipitation. Additional variability in sparrow abundance data may be induced by sampling errors on the CBCs, competition for seed resources by other granivores that may complicate a direct relationship between rainfall and winter seed availability, or between-year variations in sparrow population recruitment.

The analysis of weather on the day of the CBC suggests that sparrow densities increase at lower elevations with increased snow cover and conversely decrease under similar conditions at high elevations. We believe this reflects the tendency of bird flocks to move down elevational gradients to locate more optimal foraging conditions in areas with less snow cover. We contend that wintering sparrow flocks in the northern Great Basin select habitat patches based on snow cover, which profoundly affects seed availability, and other abiotic factors such as temperature, which in turn affect patch suitability.

Rotenberry (1978) and Weins (1981) have argued that multifactorial analyses of habitat and climatic variables provide little direct support for the proposition that breeding bird communities in the northern Great Basin are structured primarily by competitive interactions and the availability of food resources. Our analysis of wintering sparrow populations also provides little support for the notion that food limitation is of pervasive importance in this environment. We suggest that severe or variable winter conditions frequently may overshadow food availability as the major determinant of the distribution and density of wintering sparrow populations in the northern Great Basin.

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