

SUMMER RAINFALL AND WINTER SPARROW DENSITIES: A TEST OF THE FOOD LIMITATION HYPOTHESIS

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ABSTRACT.—We used published data on winter sparrow densities (from Christmas Bird Counts) and summer precipitation to test the hypothesis that local densities of wintering sparrows in southeastern Arizona are affected by the abundance of food. Our analyses rest on the assumption, justified by previous studies, that the abundance of seeds available to wintering granivorous birds is correlated with the quantity of rainfall the previous summer. Our results strongly supported two a priori predictions: (1) the density of sparrows should be positively correlated with summer rainfall, and (2) the density of individual sparrow species should be positively correlated with the total density of all other sparrow species. Our findings provide further evidence that winter finch populations are food-limited and suggest that interspecific competition may be important in at least some avian communities. Received 3 December 1980, accepted 25 May 1981.

ONE of the primary unresolved issues of current population and community ecology is the extent to which food supply and interspecific competition influence population size and community structure. Because competition is expected to occur primarily when essential resources are in short supply, the potential importance of competition can be assessed by determining how frequently and under what circumstances populations are resource-limited. Several investigators have suggested that food is the most limited resource for many populations of small passerine birds and that intra- and interspecific competition for food plays a major role in determining population size and community structure (e.g. MacArthur 1958, 1964; MacArthur and MacArthur 1961, Lack 1966; Cody 1968, 1974; Grant 1968; Fretwell 1972; Abbott et al. 1977; Pulliam and Parker 1979). This viewpoint has been criticized or modified by other investigators, some of whom argue that food is only occasionally and temporarily a limited resource for songbirds and, consequently, that competition plays, at most, a minor role in regulating population size and influencing community structure (e.g. Wiens 1974, 1977; Ricklefs 1975; Emlen 1978). The issue is further complicated because most investigators have studied migratory songbirds primarily on either their breeding or their wintering grounds. Even those investi-

gators and competition often stress its importance at different seasons (e.g. compare MacArthur 1958 and Cody 1974 with Fretwell 1972 and Pulliam and Parker 1979).

A number of studies (reviewed in Brown et al. 1979) suggest that seeds are the most important limited resource for granivorous animals inhabiting the deserts and arid grasslands of southwestern North America. In desert habitats heteromyid rodents and harvester ants appear to be the dominant seed eaters, but these two taxa decrease in abundance and species diversity in grasslands, where birds become the most conspicuous granivores. The most abundant and diverse of the seed-eating birds are the emberizine sparrows. Most species of this group are found in the arid habitats of southwestern North America only in the winter, when their diets consist primarily of seeds. Pulliam and his associates (Pulliam 1975, Pulliam and Brand 1975, Pulliam and Mills 1977, Pulliam and Parker 1979; see also Raitt and Pimm 1976) have studied the population biology and community ecology of wintering sparrows in the arid grasslands of southeastern Arizona. They have shown that the production of seeds available to sparrows in these habitats depends on summer rainfall, and they have presented evidence that competition for these seeds affects the density, distribution, and interspecific interactions of wintering sparrow populations. Pulliam and

TABLE 1. Description of censuses for five Arizona Christmas Bird Counts. All data from 1958 to 1979 were used; the Tucson Valley count was not run in 1975. Proportions of grassland and desert habitat were combined to calculate the percentage of arid habitat within each census area.

Location	Latitude/longitude	Years of census	Arid habitat (%)	\bar{x} summer precipitation (mm)	\bar{x} total birds/party-hour
Portal	31°55'N/109°08'W	8	50	287.9	43.02
Patagonia	31°29'N/110°55'W	17	30	277.7	39.84
Nogales	31°23'N/110°12'W	20	35	273.1	69.20
Ramsey Canyon	31°29'N/110°12'W	11	42	224.2	27.91
Tucson Valley	32°18'N/110°58'W	21	35	143.3	49.93

Parker (1979) suggest that the density and distribution of wintering sparrows in the southwestern United States and northern Mexico reflect facultative migrations in which birds select wintering sites on the basis of seed availability, which in turn is dependent upon rainfall during the previous growing season. They supported this concept with data showing a positive correlation between local rainfall levels and the numbers of a single species, *Spizella passerina*, in different parts of its wintering range. The generality of this relationship remains to be tested.

The present study is an independent, a priori test of the hypothesis that available food resources limit local population densities of wintering sparrows in southeastern Arizona. This test rests on one critical assumption: that food resources available to wintering sparrows are closely and positively correlated with the quantity of precipitation during the previous summer. The validity of this assumption is supported by data demonstrating a direct relationship between seed production and summer rainfall in one arid grassland in southeastern Arizona (Pulliam and Brand 1975, Pulliam and Parker 1979). In addition, there is abundant evidence that seed production is closely coupled with precipitation in arid and semiarid habitats throughout the southwestern United States (Brown et al. 1979). On the basis of these studies, we make three predictions: (1) If food limits sparrow populations in winter, then we predict a positive correlation between summer precipitation and unbiased estimates of sparrow densities the following winter. (2) Because variations in total sparrow densities could be the result of wide fluctuations in one or a few abundant species, an additional test is required to determine the generality of the above prediction. If all sparrow

species are food-limited, good years for one sparrow species should be good years for most other species. Therefore, we predict that population densities of individual species should be positively correlated with densities of all other sparrows. (3) There are theoretical reasons to expect that consumer species diversity should increase with increasing productivity (MacArthur 1972). In seed-eating rodents and ants there appears to be a positive relationship between granivore species diversity and seed availability among sites of different productivity (Brown 1973, Brown et al. 1979). Granivorous birds might show similar responses from year to year, because sparrow species that are usually absent or rare in poor years might be present in increased numbers when more seeds are available. Therefore, we predict a positive correlation between summer precipitation and sparrow species diversity recorded on counts the following winter. We tested all three predictions using estimates of sparrow densities from Christmas Bird Counts and data on summer precipitation for the U.S. Weather Bureau.

METHODS

Christmas Bird Counts published by the National Audubon Society (Audubon Field Notes 1958–1970, American Birds 1971–1979) were used to estimate local sparrow abundance in southeastern Arizona. Counts from five census localities (Table 1) were selected for analysis on three bases: numerous annual censuses were available, a large proportion of arid grassland and desert habitats were included in the census area, and large numbers of many species of sparrows were counted. Christmas Bird Counts provide standardized censuses of wintering birds within a constant area (a circle of 12 km radius). In addition to the number of birds seen of each species, counts provide data on the proportion of different kinds of habitat in the census area and descriptive

TABLE 2. Correlation coefficients for regressions of numbers of sparrows on rainfall for all combinations of species and localities, including total birds of each species summed over all localities and birds of all species summed for each locality. Results of least squares regression analyses using both untransformed (above) and log₁₀ transformed (below) data are shown. Dashes indicate species that were not recorded in enough years for analysis.^a

Location	<i>C. melano-</i> <i>corys</i>	<i>P. sand-</i> <i>wichensis</i>	<i>P. grami-</i> <i>neus</i>	<i>C. gram-</i> <i>macus</i>	<i>J. hyemalis</i>	<i>S. passerina</i>	<i>S. breweri</i>	<i>Z. leuc-</i> <i>ophrys</i>	<i>M. lincolni</i>	<i>C. ornatus</i>	All species
Nogales	0.609** 0.418	0.457* 0.512*	0.665** 0.548**	0.758** 0.594**	0.076 0.183	0.473* 0.468*	0.431 0.462	0.362 0.293	0.262 0.196	0.057 0.101	0.652** 0.522*
Patagonia	0.739** 0.467	— —	0.027 0.131	-0.335 -0.465	-0.245 -0.159	0.719** 0.636**	0.273 0.355	-0.166 -0.194	0.552* 0.501*	0.640** 0.452	0.640** 0.507*
Portal	0.071 0.551	0.832* 0.808*	0.225 0.529	— —	0.514 0.536	0.486 0.716	-0.044 0.411	0.580 0.664	0.785* 0.559	0.400 0.615	0.460 0.710
Ramsey Canyon	0.100 0.323	0.756* 0.740*	0.410 0.444	0.690* 0.470	0.300 0.041	0.361 0.780**	0.413 0.502	0.220 0.400	-0.094 -0.059	0.119 0.512	0.519 0.637*
Tucson Valley	-0.030 0.010	0.498* 0.217	-0.495 0.259	-0.036 0.061	— —	0.194 0.189	0.426 0.489*	0.022 0.086	-0.313 0.060	— —	0.590** 0.131
All sites	0.607** 0.789**	0.071 0.560*	0.650** 0.821**	0.409 0.678**	0.651** 0.525*	0.721** 0.795**	0.538* 0.560**	0.544* 0.607**	0.308 0.715*	0.647** 0.771*	0.635** 0.766**

^a * = $P < 0.05$; ** = $P < 0.01$.

data of the census itself (weather statistics, number of participants, etc.). Because the amount of time and effort put into each census varies both from year to year and from count to count, each count also records the number of party-hours, the total time spent afield by each group doing the censusing, as a measure of census effort.

Christmas Bird Counts are subject to sampling errors resulting from data collection by nonscientific amateurs (Stewart 1954), but they provide relatively unbiased estimates of winter bird distribution and abundance. They have proven valuable in several recent quantitative studies (DeHaven 1973; Bock and Lepthian 1974, 1976; Tramer 1974; Anderson and Anderson 1976; Bonney 1979). To minimize errors owing to variation in sampling effort, data were normalized by calculating the number of each species reported per party-hour. This method was criticized by Stewart (1954), but its validity has been established by several recent studies (e.g. Bock and Smith 1971, Raynor 1975).

For each species of finch in the subfamily Emberrizinae reported in the counts, we calculated means and variance/mean ratios for the number of birds counted per party-hour. Using these statistics we selected for analysis 10 species [*Calamospiza melanocorys*, *Passerculus sandwichensis*, *Poocetes gramineus*, *Chondestes grammacus*, *Junco hyemalis* (including related *J. caniceps*), *Spizella passerina*, *Spizella breweri*, *Zonotrichia leucophrys*, *Melospiza lincolni*, and *Calcarius ornatus*] that were reasonably abundant at all sites during at least some winters and had high variance/mean ratios, indicative of a variable winter population density. This effectively eliminated from the analysis nonmigratory resident species and very rare species. Total sparrow densities for each site in each year were calculated by summing the reported numbers of each of the 10 common species and dividing by party-hours. To indicate relative abundances of each species, the total number of individuals reported, summed over all available years, is given in Table 4.

Data on precipitation for the summer months (June–September) were compiled from the U.S. Environmental Data Service's monthly reports of weather statistics for U.S. Weather Bureau stations in Arizona. Data were taken from stations within each count circle. Southeastern Arizona typically has two rainy seasons per year, in summer and winter; the intervening fall and spring are dry. Total summer precipitation was calculated by summing the monthly totals from June to September, the normal season of summer rains in the census areas.

RESULTS

We first test the prediction that densities of wintering sparrows should be positively correlated with the quantity of precipitation re-

TABLE 3. Spearman's coefficients of rank correlation for either numbers of all species summed for each locality or total numbers of each species summed over all localities correlated with summer rainfall.^a

A. All species, by locality				
Nogales	Patagonia	Portal	Ramsey Canyon	Tucson Valley
0.734**	0.555*	0.833*	0.382	0.483*

B. All localities, by species									
<i>C. melanocorys</i>	<i>P. sandwichensis</i>	<i>P. gramineus</i>	<i>C. grammacus</i>	<i>J. hyemalis</i>	<i>S. passerina</i>	<i>S. breweri</i>	<i>Z. leucophrys</i>	<i>M. lincolni</i>	<i>C. ornatus</i>
0.302	0.619**	0.545*	0.737**	0.734**	0.796**	0.674**	0.579**	0.632**	0.801**

^a * = $P < 0.05$; ** $P < 0.01$.

ceived during the previous summer. Because we had no a priori reason to assume a particular form for the assumed relationship between rainfall and seed production and because some data suggest that it is nonlinear (Pulliam and Parker 1979), we performed least squares regression analysis using both untransformed and \log_{10} transformed data from counts published between 1958 and 1977, inclusive. Results of the analysis (Table 2) show a high frequency of significant positive correlations. Twenty-seven of 66 correlations between numbers of individual species and summer precipitation totals at particular localities were positively significant at the 0.05 level using untransformed data, whereas 24 of the 66 correlations using \log_{10} transformed data were positive and significant. Only 12 correlations of untransformed data and 6 of transformed were negative, and only 1 of these was statistically significant. Most important is the observation that total numbers of sparrows of all 10 species were significantly correlated with summer precipitation for 4 of the 5 census localities in either linear or \log_{10} transformed analyses. The other site, Portal, had the fewest years of census data available at the time of the study. Subsequent calculations show that, with the addition of 2 more years of data (1978 and 1979), the correlation with \log_{10} transformed data from Portal was significant ($r = 0.782$, $P < 0.05$, $df = 7$). All 10 finch species showed significant positive correlations with summer precipitation summed over all localities combined, in one of the two analyses. There was no clear pattern that regressions using either untransformed or \log_{10} transformed data fitted the observed values better. Sites or species for which fewer observations were

available tended to be significant only with \log_{10} transformation. The probabilities of finding this many positive correlations strictly by random chance is extremely small. These results strongly support the first prediction, although correlation coefficients usually were less than 0.70, indicating that precipitation accounted for less than half of the variance in sparrow densities.

For statistical clarity, we also performed a more general, conservative analysis using Spearman's coefficient of rank correlation (r_s). Data published from 1958 through 1979, inclusive, were analyzed. The results are summarized in Table 3. Total numbers of all sparrows were significantly correlated with summer precipitation for four of the five sites. Correlations of each species summed over all localities with summer precipitation were significant for 9 of the 10 species. Again, these results strongly support the first prediction.

We now use Spearman's coefficient of rank correlation to test the second prediction: that densities of individual species of wintering sparrows should be positively correlated with densities of all other species. Table 4 shows that this prediction is sustained for all 10 species studied. It is noteworthy that the highest correlations were for *Passerculus sandwichensis*, *Chondestes grammacus*, *Spizella breweri*, and *Calcarius ornatus*, which are highly mobile, flocking species that winter primarily in desert and grassland habitats. The least significant correlations were found for the *Junco hyemalis* species complex and for *Calamospiza melanocorys*. Juncos characteristically winter in more wooded habitats at higher elevations than the grasslands. *C. melanocorys* winters primarily on the southern Great Plains and the

TABLE 4. Results of Spearman's rank correlation analysis, in which, for each species, number of birds/party-hour was correlated with the combined totals of all other species.

Species	Total number of birds/party-hour	r_s^a
<i>Calamospiza melanocorys</i>	722.90	0.504*
<i>Passerculus sandwichensis</i>	67.94	0.762**
<i>Poocetes gramineus</i>	236.30	0.788**
<i>Chondestes grammacus</i>	198.30	0.933**
<i>Junco hyemalis</i>	171.23	0.508*
<i>Spizella passerina</i>	867.68	0.738**
<i>Spizella breweri</i>	332.29	0.832**
<i>Zonotrichia leucophrys</i>	1,153.27	0.598**
<i>Melospiza lincolni</i>	37.17	0.626**
<i>Calcarius ornatus</i>	150.95	0.808**

** = $P < 0.05$; * = $P < 0.01$.

uplands of the Chihuahuan desert, well to the east of our study area. While *C. melanocorys* does occur in relatively high densities in southeastern Arizona in some winters, it is likely that its appearance is more related to poor conditions on its normal winter range than to good food supplies in Arizona. This hypothesis might be tested using other Christmas Bird Count data. In general, the data strongly support the second prediction.

Finally, we correlated summer precipitation with species diversity as measured by the Shannon-Wiener information index. Numbers of all emberizine sparrows reported on the Christmas Counts were used in calculating the indices. Results are summarized in Table 5. Only the Nogales correlation was significant. The number of sparrow species reported on the counts does not vary widely from year to year, and this may be responsible, in part, for the lack of correlation in this analysis. The data, at best, only weakly support the third prediction.

DISCUSSION

We have conducted a quantitative, a priori test of the hypothesis that winter sparrow populations in southeastern Arizona are limited by food resources. Three specific predictions from the hypothesis were tested using quantitative, apparently unbiased data available in the literature. Predicted positive correlations between the number of sparrows recorded per party-hour on Christmas Bird Counts and the total quantity of precipitation during the preceding summer were obtained. In addition,

TABLE 5. Results of Spearman's rank correlation analysis of species diversity on rainfall for each locality. Species diversity was estimated using the Shannon-Wiener information index ($H' = -\sum p_i \log p_i$).^a

Nogales	Patagonia	Portal	Ramsey Canyon	Tucson Valley
0.541*	-0.100	0.286	0.673	-0.270

** = $P < 0.05$.

expected positive correlations between abundance of individual sparrow species and total abundance of all other species also were obtained. A third prediction, that species diversity should be positively correlated with summer precipitation, was not strongly supported. Our test of the first prediction assumes a positive relationship between summer rainfall and the production of food (primarily seeds) available to wintering sparrows. This assumption is supported by several studies of seed production in arid and semiarid habitats (cited in the introduction) and does not require further justification. There remains the possibility that the correlation between summer rainfall and winter sparrow densities reflects some causal process other than food limitation. The most likely candidate is cover, which probably increases, particularly at ground level, in response to summer precipitation and which might be conducive to high bird densities. We think precipitation-mediated changes in cover are unlikely to account for the patterns reported above, however, because some of the sparrow species (most notably *Calcarius ornatus*) that responded positively to increased rainfall characteristically forage in open areas and do not seem to rely on cover for protection from predators or for other vital functions (Pulliam and Mills 1977). Our analysis provides strong support for the proposition that the local abundance and distribution of seed-eating birds, at least of sparrows in southeastern Arizona, are regulated primarily by the availability of food resources (Pulliam 1975, Pulliam and Brand 1975, Raitt and Pimm 1976, Pulliam and Parker 1979). The mechanism of this regulation is not apparent from our data, but facultative migration, as proposed by Pulliam and Parker, is consistent with our results.

While our analyses do not provide any direct evidence on the extent of interspecific competition for food among wintering sparrows or

the importance of such competition in structuring winter finch communities, our results do have significant implications for evaluating the role of competition. First, they suggest the potential importance of competition. If, as our results suggest, winter sparrow populations are food-limited, then it is only necessary for different species to overlap significantly in their utilization of food for interspecific competition to occur. To the extent that purported demonstrations of interspecific overlap in food utilization (Pulliam and Enders 1971, Fretwell 1972, Pulliam 1975, Pulliam and Parker 1979) are correct, then our analyses support the interpretation that competition is important in determining population densities and community structure in wintering sparrows. Our data do not enable us to evaluate how food limitation varies with seed production, however, because we have no direct information on the relationship between summer rainfall and seed availability to sparrows the following winter. Thus, we cannot refute the contention (Pulliam and Brand 1975, Pulliam and Parker 1979) that seed availability may be severely limiting to wintering finch populations only in winters following summers of exceptionally low rainfall and seed production. This problem warrants further study. The conclusions of Pulliam and his coworkers are based on estimates of sparrow energy requirements in relation to measured seed production and assume that all seeds produced are equally available for sparrow consumption. This may not be true if, in years of high rainfall and heavy seed crops, an increasing proportion of the seeds are harvested by other granivores (e.g. ants and rodents) or hidden in the denser vegetation and litter.

A second implication of our results is that resource-limited, potentially competing species often may show positive correlations in their population densities over time if the limiting resource that they share is subject to wide annual variation. Negative correlations in densities are often presented as evidence for competition. Some authors have even suggested that such relationships, corrected for differences between species in habitat utilization, can be used to calculate the intensity of competition interaction (Hallett and Pimm 1979, see also Crowell and Pimm 1976). Such inferences are questionable, because positive correlations in population density, even among

intensely competing species, are likely whenever there are significant fluctuations in the availability of shared limiting resources. We submit that it is hazardous to conclude anything about competition from temporal patterns of fluctuation in natural populations unless a great deal is known about levels of resource availability and mechanisms of resource utilization.

ACKNOWLEDGMENTS

This study was supported in part by NSF Grant DEB 76-83858 to J. H. Brown and an NSF Predoctoral Fellowship to J. B. Dunning.

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