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POPULATION VARIABILITIES OF BIRD GUILDS IN KANSAS DURING FALL AND WINTER: WEEKLY CENSUSES VERSUS CHRISTMAS BIRD COUNTS[1]

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Abstract. Fall and winter (September through March) weekly census data from 1978 through 1992 were examined for 18 species of birds in forests and cultivated fields near Manhattan, Kansas. The 18 species were grouped into five feeding guilds: frugivores; granivores on the ground; acorn cachers; leaf, bud, and twig gleaners; and trunk and branch gleaners. Frugivores exhibited the most variable populations, both within years and between consecutive years. Granivores on the ground exhibited the second most within-year population variability. Among the remaining guilds, there were no statistically significant differences among either the within- or between-year variabilities. Although data were limited, there were significant correlations between the mean numbers in some species of frugivores, granivores, and acorn cachers and relative annual fruit or seed crop size in the area. The size and mobility of feeding flocks, the annual variability of food crops, and the manner of food exploitation all influenced the between-year variability of winter bird species population density. The rank order of between-year variability for species populations censused on Christmas Bird Counts in the same area correlated significantly with between-year variability of our weekly censuses. The within-year nomadic tendencies of some of the species with the greatest between-year variability decreased the correlation between Christmas Bird Counts and mean weekly censuses for these species.

Key words: *Guilds; winter bird censuses; population variability; Kansas.*

INTRODUCTION

Long-term population studies of birds (e.g., Brennan and Morrison 1991) often include data from the Christmas Bird Counts (CBC) or Breeding Bird Surveys (BBS) (Robbins et al. 1986). Because of temporal and budgetary constraints, the data from these studies are nearly always collected from an area or a route on only one day per year, rather than weekly or monthly (but see Loery and Nichols 1985). An underlying assumption for these methods has been that the bird population numbers and species composition on the day of the census are typical for that year. The CBC and BBS provide no estimate of the variance of the number of individuals of a species during the winter and spring, respectively. Here we used a 14-year, weekly bird census taken within the confines of the Manhattan, Kansas CBC area to determine how closely between-year variability in CBC corresponded to the same variability of weekly bird censuses averaged over the period of September to March.

The objectives of this study were (1) to quantify within- and between-year variabilities for 18 bird species belonging to five guilds, (2) to identify differences in within- and between-year variabilities for species belonging to the same guild, (3) to identify relationships between fall and winter population sizes of birds and the relative sizes of the annual wild fruit and seed crops, and (4) to analyze how food supply and avian social behavior may influence within- and between-year variation in bird populations in ways that would limit the accuracy of an annual census in measuring between-year variation in bird populations. Fall and winter data from our censuses were compared to CBC instead of comparing our

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breeding season data to BBS because the former involved fewer species, belonging to more easily distinguishable guilds. Moreover, the winter food in temperate regions is a nonrenewed resource on an annual basis and is easier to quantify than summer resources which are being renewed in patterns that are difficult to measure. Acorns from trees have a between-year pattern of abundance that differs from the pattern for seeds from native perennial forbs and grasses (Briggs et al. 1989). Tree crops are often affected by conditions in late winter and early spring when the flowers are pollinated, while in prairie regions summer moisture should be the main determinant of seed production by annual weeds and crops and perennial prairie grasses.

METHODS

CENSUS ROUTE AND SELECTION OF GUILDS

Birds were counted with a modified BBS procedure (Robbins and Van Velzen 1967, Stapanian 1982) along a regular route in Riley County, Kansas. The route consisted of 16 stations selected to be representative of forests bordering cultivated fields and pastures. A detailed study of the vegetation in these wooded sections of the Kansas Flint Hills Prairies can be found elsewhere (Bragg 1974). Of the 16 stations, nine were along one road and seven were along another. These roads approximated a NE-SW transect through the Manhattan, Kansas, CBC area (Zimmerman 1974). Unlike those used in the BBS, the stations along the transects were not separated by 0.81-km intervals. Instead, stations were selected to represent typical upland and riparian forests in proportion to their presence in the Flint Hills area. Distances between stations on the same road ranged from 0.3 to 1.6 km. The nearest stations on the two roads were separated by 13 km. There were eight practical sequences in which the stations could be visited, due to road access and distance covered. Unlike BBS, each of the eight possible sequences was followed over an eight-week period before initiating a new rotation of sequences. In this manner, station differences would not be the result of consistent time differences. Birds were identified to species, and the number of individuals was counted for 3 min at each station. Censuses were conducted at approximately weekly intervals. Each census began within 1 hr after sunrise and required approximately 2 hr to complete. Censuses were canceled or discontinued when (1) wind speed exceeded approximately 40 km/hr, (2) rain intensity exceeded a light drizzle, or (3) access roads were impassable. A total of 299 censuses was used in our calculations.

In this study, fall and winter data (i.e., 1 September through 31 March) from 1978 through 1992 are considered. Data for January through October 1982 are missing, so we did not include data for fall–winter 1981–1982 in the statistical analysis. We selected 18 bird species that are common in the area in fall and winter, and organized then into five guilds based on similarities in diet and feeding behavior (Beal 1915; Bent 1939, 1953, 1964, 1968; Martin et al. 1951; Bossema 1979; Thompson and Willson 1979; Darley-Hill and Johnson 1981) (Table 1). European Starlings are included in the frugivore guild rather than the granivore guild because they feed in large flocks in native fruit trees and eat seeds mainly in cattle feed lots where the food supply is less likely to follow natural variation. The number of individuals in a guild was the sum of the number of individuals observed for the member species.

Clearly, the number of individuals in a guild was not independent of the number of individuals in any of its member species. Therefore, statistical relationships between a guild and fruit or seed crop size were not independent of those involving member species and fruit or seed crop size.

FRUIT AND SEED CROPS

With the exceptions of hackberry (*Celtis occidentalis*), corn (*Zea mays*), and soybeans (*Glycine max*), all of the fruit and seed crop data were collected on Konza Prairie Research Natural Area (KPRNA), within 9 km of any point on the bird census route. Data for hackberries were collected from trees on a farm in Geary County, Kansas 29 km from the census route and the corn and soybean crops are for a broad area of NE Kansas. We made the simplifying assumption that the annual seed crops of big bluestem (*Andropogon gerardii*), corn, and soybeans would be representative of the size of the seed crops from herbs and grasses in the area. In prairies, average evapotranspiration exceeds precipitation and plant productivity is very sensitive to water supply. Data for the annual seed crops of *A. gerardii* for 1982 through 1990 were obtained from Knapp et al. (1992), in which the seed crop was esti-

TABLE 1. Species composition of the guilds examined in this study. Abbreviations are used in Figure 2.

Frugivores
American Robin (*Turdus migratorius*)—AMRO
Cedar Waxwing (*Bombycilla cedrorum*)—CEWW
Eastern Bluebird (*Sialia sialis*)—EABL
European Starling (*Sturnus vulgaris*)—EUST
Ground granivores
Northern Cardinal (*Cardinalis cardinalis*)—CARD
Dark-eyed Junco (*Junco hyemalis*)—DEJU
Harris' Sparrow (*Zonotrichia querula*)—HASP
American Tree Sparrow (*Spizella arborea*)—TRSP
Acorn cachers
Blue Jay (*Cyanocitta cristata*)—BLJA
Red-bellied Woodpecker (*Melanerpes carolinus*)—RBWP
Red-headed Woodpecker (*Melanerpes erythrocephalus*)—RHWP
Leaf gleaners
Black-capped Chickadee (*Parus atricapillus*)—BCCH
Tufted Titmouse (*Parus bicolor*)—TUTI
Golden-crowned Kinglet (*Regulus satrapa*)—GCKI
Trunk gleaners
Downy Woodpecker (*Picoides pubescens*)—DOWP
Hairy Woodpecker (*Picoides villosus*)—HAWP
White-breasted Nuthatch (*Sitta carolinensis*)—WBNH
Brown Creeper (*Certhia americana*)—BRCR

mated by counting the number of fruiting heads of *A. gerardii* in 0.25-m^2 plots. The means of 25 plots in each of six burning and soil type categories were averaged to give one value for density of *A. gerardii* fruiting heads per m^2. Data for corn and soybeans for 1978 through 1984 in northeastern Kansas were obtained from Williams et al. (1989). We calculated the means of the annual yields of corn and soybeans from six experimental tillage treatments. From the three years of overlap in these two data sets, we were able to estimate the seed crop size, on a scale of 1 (lowest) to 4, of herbs and grasses for all study years except 1991. Due to a late summer drought, 1991 was recorded as crop size 1, although it is not part of either published seed crop data set.

Annual fruit or seed crops were estimated for juniper (*Juniperus virginiana*), hackberry, ash (*Fraxinus pennsylvanica*), and chinquapin oak (*Quercus muehlenbergii*) by counting the number of propagules from the same two branches beyond a given branch diameter on each of 10 trees every year. These data were collected for fall 1987 through fall 1991. Annual seed crop of bur oak (*Quercus macrocarpa*) from 1981 through 1989 was estimated by calculating the mean weight of acorns in 60 litter traps each 0.25 m^2 placed on the floor of the gallery forest in KPRNA. Relative annual seed crop for each of the tree species was estimated by dividing the annual crop by the smallest nonzero annual crop.

STATISTICAL ANALYSES

Classical methods and estimators in statistics assume sample independence. Therefore, the issue of time-dependency of the bird populations had to be addressed before other tests of hypotheses could be performed. We could not use classical time-series (Box and Jenkins 1976) methods because they require equally spaced time intervals. In this study censuses were sometimes two or three weeks apart. We did not pool the observations over a month because that would result in only seven observations per year, thus giving poor estimates of parameters. We performed an informal test of independence by examining autocorrelations with lags (m) of one, two, and three censuses for each species by station and by year. Let $n_{i,j,k,p}$ equal the number of individuals of species i seen at station j on the kth census of year p.

Lag = 0	Lag = 1	Lag = 2	Lag = 3
$n_{i,j,1,p}$	$n_{i,j,2,p}$	$n_{i,j,3,p}$	$n_{i,j,4,p}$
$n_{i,j,2,p}$	$n_{i,j,3,p}$	$n_{i,j,4,p}$	$n_{i,j,5,p}$
·	·	·	·
·	·	·	·
$n_{i,j,k-m,p}$	$n_{i,j,k,p}$	$n_{i,j,k,p}$	$n_{i,j,k,p}$

We examined the data for each year as follows:

Step 1: For each species, we first found the correlation at a station between the number of individuals originally observed (i.e., Lag = 0) and Lag = 1, then Lag = 2, then Lag = 3 for all possible census data.

Step 2: We repeated Step 1 for the remaining stations.

Step 3: We calculated the mean of the correlation coefficients found for the 16 stations for that species. Undefined correlation coefficients (i.e., when zero individuals of that species were observed at a station in a particular year) were not included in the calculation of the mean.

Step 4: We repeated Steps 1 through 3 for the remaining species.

Steps 1 through 4 were repeated for each year. Bar charts of the means of the correlation coefficients are shown in Figure 1. Clearly, the majority of these means are low, between −0.1 and 0.1 for all lags. The distribution of correlation coefficients is similar for each of the lag times. The maximum mean correlation coefficients were 0.455 for Lag = 1 (Brown Creeper in 1984–1985), 0.481 for Lag = 2, and 0.461 for Lag = 3 (both for Red-headed Woodpeckers in 1984–1985). From these results, we made the simplifying assumption for each species that the number of individuals observed on a particular date at a particular site was independent of the number observed on another date. A shortcoming of this method is that nonlinear relationships between number of individuals of a species and census number in a particular year are not considered.

We used the coefficient of variation (CV) of the total number of individuals observed on each census as a measure of within-year population variability for each species and guild. Relatively low values of the CV for a species or guild indicated a stable (i.e., less variable) population; relatively high values indicated an unstable (i.e., more variable) population. A plot of CV against mean showed that species that averaged less than one individual per census had an inflated CV. Thus, if a species had a mean of less than one individual per census in a year, that species was not included in the statistical analysis of population variability among species for that year. The Friedman's nonparametric analysis of variance for randomized blocks (Sokal and Rohlf 1981) was used to test the null hypothesis of no difference in within-year variabilities among guilds or species.

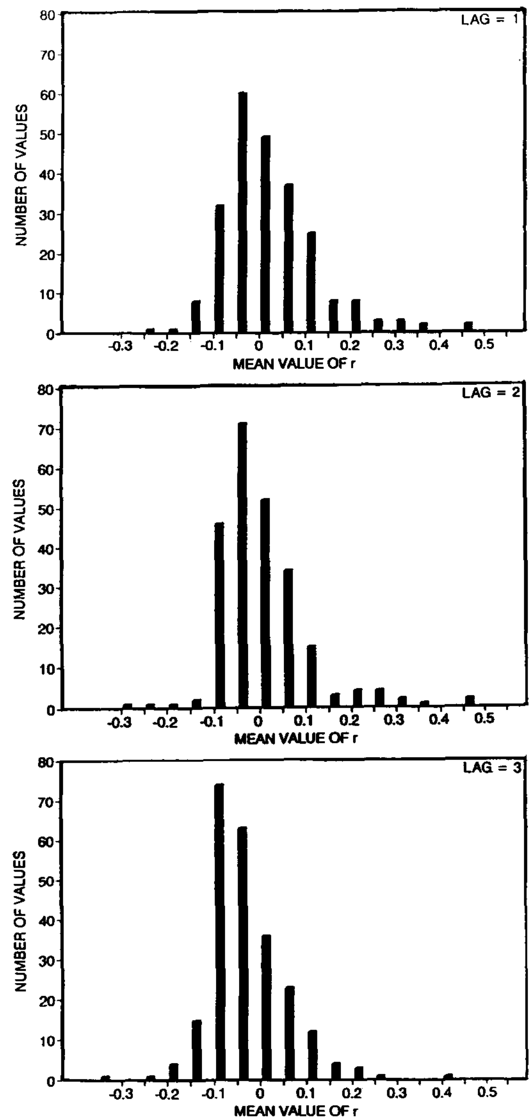

FIGURE 1. Mean autocorrelation coefficients for Lag = 1, Lag = 2, and Lag = 3. Each bar represents the number of coefficients in the 0.05 range between hash marks on the abscissa.

Population variability between two consecutive years for our weekly censuses was calculated as:

$$WC_{i:p+1,p} = (X_{i,p+1} - X_{i,p})/[(X_{i,p+1} + X_{i,p})/2]$$

where $X_{i,p}$ represents the mean of species or guild i in year p. Low absolute values of $WC_{i:p+1,p}$ indicate a stable population between consecutive years; high absolute values indicate an unstable population. If a species had a mean of less than one individual per census in year p and in year

TABLE 2. Average ranks of within- and between-year variabilities. A rank value of 1.0 indicates highest variability. Chi-square values are for Friedman's tests.

Within-year variability		Between-year variability	
Guild	Mean rank	Guild	Mean rank
Frugivores	1.0	Frugivores	1.2
Ground granivores	2.5	Leaf gleaners	3.0
Acorn cachers	3.5	Trunk gleaners	3.3
Leaf gleaners	3.8	Acorn cachers	3.7
Trunk gleaners	4.3	Ground granivores	3.8
$\chi^2_4 = 35.38$, $P < 0.01$		$\chi^2_4 = 20.15$, $P < 0.01$	

Within-year variability		Between-year variability	
Species	Mean rank	Species	Mean rank
European Starling	2.0	Cedar Waxwing	2.6
American Tree Sparrow	2.2	American Robin	3.6
Harris' Sparrow	2.9	Red-headed Woodpecker	4.1
American Robin	3.5	Harris' Sparrow	4.6
Tufted Titmouse	5.2	European Starling	6.1
Northern Cardinal	6.8	American Tree Sparrow	6.7
Dark-eyed Junco	6.9	Downy Woodpecker	8.4
Red-bellied Woodpecker	8.5	Tufted Titmouse	9.3
Blue Jay	9.0	Dark-eyed Junco	9.6
White-breasted Nuthatch	9.1	Hairy Woodpecker	9.8
Black-capped Chickadee	9.9	White-breasted Nuthatch	9.9
$\chi^2_{10} = 103.14$, $P < 0.01$		Black-capped Chickadee	10.6
		Red-bellied Woodpecker	11.0
		Blue Jay	11.6
		Northern Cardinal	12.1
		$\chi^2_{14} = 75.35$, $P < 0.01$	

p + 1, then that species was not included in the analysis of between-year variabilities among species for those years. The Friedman rank sum test was used to test the null hypothesis of no difference in the absolute values of $WC_{i:p+1,p}$ among the guilds.

The annual means for each species (i.e., the $X_{i,p}$) were paired with the number of individuals observed per party hour in the CBC for Manhattan, Kansas, of the corresponding years. The correlation between the results for our censuses and the CBC was then calculated for each species. Next, the between-year variabilities of the species in this study were compared with those from the CBC data for the same years. Let $N_{i,p}$ equal the number of individuals of species or guild i seen per party-hour in the CBC of year p. Population variability between two consecutive years for the CBC data can be represented by

$$CBC_{i:p+1,p} = (N_{i,p+1} - N_{i,p})/[(N_{i,p+1} + N_{i,p})/2].$$

The values of $WC_{i:p+1,p}$ and $CBC_{i:p+1,p}$ were calculated for species that had means of greater than one individual per census in at least one of every pair of consecutive years (intervals) studied. The absolute values of $WC_{i:p+1,p}$ and $CBC_{i:p+1,p}$ were then ranked separately, within each interval. The sums of the ranks of $WC_{i:p+1,p}$ and $CBC_{i:p+1,p}$ over all intervals were then calculated and ranked, resulting in an ordering of the species according to their relative between-year population variabilities in the two data sets. The relationship between the rankings of species in the data sets was then investigated.

Correlations were calculated for each bird species or guild and each set of crop measurements for the number of years in which both data sets are available. Correlations among annual means of species populations were generally low. Univariate statistics were, therefore, sufficient in testing the relationship between food crops and bird populations.

RESULTS

WITHIN-YEAR VARIABILITY

The within-year variabilities of the guilds were significantly different (Table 2). Among the guilds, the frugivores had the greatest within-year variability (i.e., largest values of the CV), followed by the granivores (sign test, number of like signs = 2, $P < 0.05$). The within-year variabilities for the remaining guilds were not significantly different from one another.

We included only the 11 species for which the annual mean was always greater than one individual per census in the statistical analysis of within-year variability by species. There was a significant difference in within-year variabilities among the species. However, there was considerable overlap in the rank sums of the members of the guilds, particularly in the frugivore and granivore guilds (Table 2). European Starlings and American Robins, both members of the frugivore guild, ranked first and fourth in within-year variability, respectively. American Tree Sparrows and Harris' Sparrows, both members of the granivore guild, ranked second and third. The remaining two species in the granivore guild, Northern Cardinals and Dark-eyed Juncos, ranked sixth and seventh, respectively. Of the nine years in which their annual mean was greater than one individual per census, Cedar Waxwings ranked first in within-year variability in seven years and second in two. Black-capped Chickadees, White-breasted Nuthatches, Blue Jays, and Red-bellied Woodpeckers exhibited the least within-year variabilities.

BETWEEN-YEAR VARIABILITY

The values of $WC_{i:p+1,p}$ for the 11 intervals are shown in Table 3. Because the 1981–1982 data are missing, we were unable to calculate $WC_{i:p+1,p}$ for intervals 3 and 4. The between-year variabilities among the guilds differed significantly (Table 2). The frugivore guild had significantly greater values of $WC_{i:p+1,p}$ than the other guilds (sign test, number of like signs = 2, $P < 0.05$). Differences among the values of $WC_{i:p+1,p}$ for the remaining guilds were not significantly different. Fifteen species satisfied the requirement stated above for inclusion in the statistical analysis of between-year variability. There was a significant difference in the absolute values of $WC_{i:p+1,p}$ for these species. Northern Cardinals had the least variable between-year populations, and Cedar Waxwings had the most, based on the sums of the ranks of the absolute values of $WC_{i:p+1,p}$ (Table 2). The three frugivore species considered in the statistical analysis were among the five species that had the greatest between-year variability. Unlike the other frugivores, however, Eastern Bluebirds (which did not meet the acceptance criterion for inclusion in the statistical analysis) exhibited absolute values of $WC_{i:p+1,p}$ that were generally intermediate when included in the analysis.

The relationship between population variability and guild is less clear in the acorn cachers and ground granivores. Red-headed Woodpeckers had the third most variable populations between years. The other members of its guild, Blue Jays and Red-bellied Woodpeckers, had the thirteenth and fourteenth most variable populations, respectively, between years. Two members of the ground granivore guild (Harris' Sparrows and American Tree Sparrows) had relatively variable between-year populations (ranking fourth and sixth most variable, respectively). However, one member (Northern Cardinal) had the least variable population of all species considered. The remaining member, Dark-eyed Junco, had an intermediate between-year variability.

The species belonging to the leaf gleaner and trunk gleaner guilds were less sharply divided in their between-year variabilities. Two leaf gleaner species satisfied the requirement for inclusion in the statistical analysis of between-year variability. Black-capped Chickadee and Tufted Titmouse had relatively intermediate variabilities (i.e., they ranked 12th and 8th most variable, respectively). As a group, the trunk gleaner species had relatively low variability between years. The three trunk gleaner species that were included in the analysis ranked seventh, tenth, and eleventh least variable (Table 2).

COMPARISON TO CBC

For the majority of species, the correlations between the annual means from this study and the number observed per party hour in the Manhattan, Kansas CBC were not significant (Table 4). Exceptions were Cedar Waxwings, Eastern Bluebirds, the frugivore guild, Red-headed Woodpeckers, and Golden-crowned Kinglets.

In general, there was close agreement between the ranks of the 15 species in terms of their relative population variabilities (Spearman rank correlation $r_s = 0.67$, $P < 0.05$, Fig. 2). Each point in Figure 2, represented by the species' abbreviation, corresponds to the rank of the rank sums of the absolute values of $WC_{i:p+1,p}$ (x-axis) and $CBC_{i:p+1,p}$ (y-axis) for a species. If a single species (Northern Cardinal) were excluded, this relationship would improve considerably.

TABLE 3. Values of WC, where $WC_{i;p+1,p} = (X_{i,p+1} - X_{i,p})/[(X_{i,p+1} + X_{i,p})/2]$. No value of WC was zero when expressed to infinite significant digits. Because data for 1981–1982 and 1982–1983 are missing, intervals 3 and 4 are omitted.

Guild or species	Interval 1 1978–1979 to 1979–1980	2 1979–1980 to 1980–1981	5 1982–1983 to 1983–1984	6 1983–1984 to 1984–1985	7 1984–1985 to 1985–1986	8 1985–1986 to 1986–1987	9 1986–1987 to 1987–1988	10 1987–1988 to 1988–1989	11 1988–1989 to 1989–1990	12 1989–1990 to 1990–1991	13 1990–1991 to 1991–1992
Frugivore Guild	1.2	−0.8	−1.3	0.3	0.8	−1.5	0.9	1.5	−1.4	1.3	1.5
American Robin	1.3	−0.9	−1.6	0.8	0.9	−1.6	0.6	0.6	−0.9	1.4	1.5
Cedar Waxwing	2.0	−1.1	−0.5	−0.7	1.3	−1.9	1.8	0.9	−1.7	1.1	2.0
Eastern Bluebird	−0.1#	1.8	0.8	−0.2	0.5	−0.3	0.4	0.3	−0.2	0.2	0.8
European Starling	−0.3	−0.3	−0.7	−0.4	0.0	−1.5	1.6	1.7	−1.6	1.3	1.6
Ground Granivore Guild	0.5	0.0	−0.9	0.2	0.2	0.0	−0.1	−0.1	0.2	0.1	0.8
Northern Cardinal	0.1	0.5	−0.4	0.1	0.2	−0.1	0.0	−0.1	0.3	−0.1	0.3
American Tree Sparrow	1.3	−0.4	−1.1	0.4	−0.2	−0.9	−0.2	0.8	−0.6	1.0	1.2
Harris' Sparrow	1.1	0.7	−1.3	0.8	0.5	−1.6	−0.6	1.3	1.1	0.1	1.6
Dark-eyed Junco	0.4	−0.1	−0.9	−0.1	0.4	0.7	−0.1	−0.4	0.2	−0.2	0.6
Acorn Cacher Guild	−0.2	−0.3	0.4	−0.0	0.1	−0.2	0.3	−0.1	−0.2	0.2	1.0
Red-bellied Woodpecker	−0.0	0.5	−0.4	0.5	−0.1	−0.4	0.5	−0.1	0.3	−0.0	0.3
Red-headed Woodpecker	−0.3	−1.6	1.7	−1.1	1.1	−0.3	0.7	−0.2	−1.4	1.0	2.0
Blue Jay	−0.1	−0.3	0.4	−0.0	0.1	−0.2	0.3	−0.1	−0.2	0.2	1.1
Leaf Gleaner Guild	0.1	0.4	−0.6	−1.4	4.5	0.2	0.1	−0.2	0.3	−0.2	0.5
Black-capped Chickadee	0.0	0.5	−0.4	−0.3	0.3	0.3	0.0	−0.3	0.3	−0.2	0.4
Tufted Titmouse	0.2	0.4	−1.0	0.4	0.2	−0.2	0.5	0.2	0.3	−0.2	0.5
Golden-crowned Kinglet	2.0#	1.1#	−2.0	2.0#	0.3#	0.7	−0.6	0.6	−0.1	0.2	1.9
Trunk Gleaner Guild	0.5	0.7	−0.3	−0.1	0.3	−0.1	0.3	−0.2	0.4	−0.7	0.1
Downy Woodpecker	1.2	0.9	−0.5	0.2	0.4	−1.0	1.0	−0.1	0.2	−0.5	0.0
Hairy Woodpecker	−0.1	−0.6	0.7	−0.5	0.6	0.5	−0.2	−0.0	−0.0	−0.4	0.2
White-breasted Nuthatch	0.2	0.8	−0.3	−0.2	0.1	0.3	0.3	−0.4	0.5	−0.9	0.1
Brown Creeper	1.5#	0.4#	2.0#	2.0#	1.4#	−0.3#	−0.1#	1.2	1.1	−1.4	1.2#

Mean < 1 bird/census in both comparison years.

TABLE 4. Correlations between our censuses (ann. means) and CBC (individ./party hr) for Manhattan, KS. $n = 13$ years.

Guild or species	r	$P > F$
Frugivores	0.64	0.02
American Robin	0.35	0.24
Cedar Waxwing	0.96	0.00
Eastern Bluebird	0.66	0.02
European Starling	0.45	0.12
Ground granivores	−0.27	0.37
Northern Cardinal	0.13	0.66
American Tree Sparrow	−0.06	0.86
Harris' Sparrow	0.34	0.26
Dark-eyed Junco	0.37	0.22
Acorn cachers	0.53	0.06
Red-bellied Woodpecker	0.16	0.60
Red-headed Woodpecker	0.85	0.00
Blue Jay	0.44	0.14
Leaf gleaners	0.24	0.42
Black-capped Chickadee	0.09	0.78
Tufted Titmouse	0.29	0.33
Golden-crowned Kinglet	0.76	0.00
Trunk gleaners	0.44	0.13
Downy Woodpecker	0.29	0.33
Hairy Woodpecker	−0.08	0.79
White-breasted Nuthatch	0.48	0.10
Brown Creeper	0.53	0.06

FRUIT AND SEED CROP SIZE

Relative fruit and seed crop sizes are given in Table 5. There were only two of five years in which the relative fruit crop size for hackberry was nonzero. Correlations between annual fruit or seed crop size and annual mean of individual birds per census for the bird species and guilds are shown in Table 6. Due to the relatively few years ($n = 5$) of data for four tree species, caution should be exercised when interpreting these correlations, particularly for hackberry.

Of all bird species, a granivore (Dark-eyed Juncos) had the highest correlation with weed seed crop. As expected, correlations between bur oak seed crop size and Red-headed Woodpeckers, Blue Jays and the acorn cacher guild were strongly positive. However, poor correlation existed between seed crop size of bur oak and Red-bellied Woodpeckers, the remaining member of the guild. Correlation coefficients for three frugivore species and for the frugivore guild with bur oak seed crop size were statistically or marginally significant. However, plots of the data suggest that the correlations between European Starlings and bur oak and between the frugivore

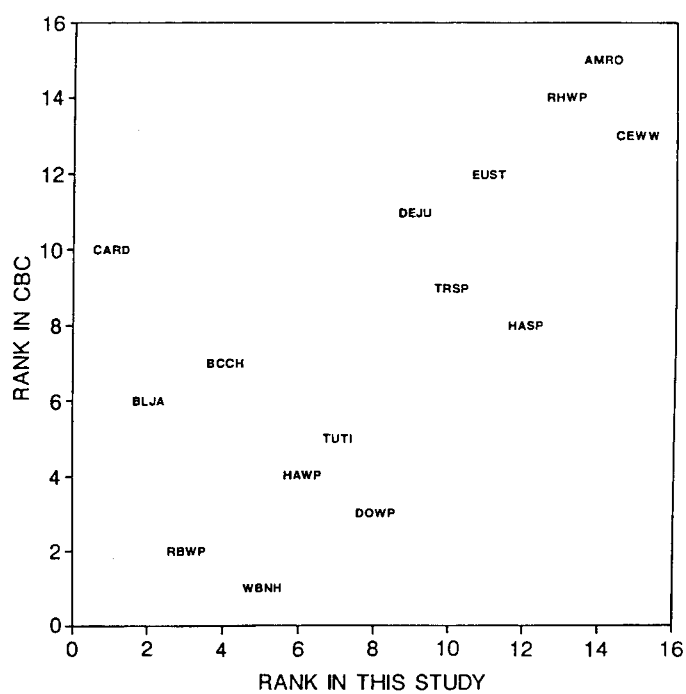

FIGURE 2. Ranks of the sums of ranks for the between-year variabilities in the CBC versus the present study. Each point corresponds to the ranks found for an individual species. Abbreviations are in Table 1.

TABLE 5. Estimates of sizes of fruit or seed crops from selected species in Kansas. Relative crop sizes are unitless.

Year	Big bluestem (flowering stems/m²)	Corn (bu/acre)	Soybeans (bu/acre)	Relative weed crop estimate	Bur oak	Chinquapin oak	Juniper	Hackberry	Ash
1978–1979	—	86.4	21.4	2	—	—	—	—	—
1979–1980	—	142.6	36.2	4	—	—	—	—	—
1980–1981	—	16.6	26.9	1	—	—	—	—	—
1981–1982	—	125.8	41.5	4	—	—	—	—	—
1982–1983	6.0	108.5	40.0	4	240	—	—	—	—
1983–1984	0.6	28.6	13.1	1	400	—	—	—	—
1984–1985	0.4	54.6	19.7	1	1	—	—	—	—
1985–1986	2.6	—	—	2	540	—	—	—	—
1986–1987	3.6	—	—	3	64	—	—	—	—
1987–1988	4.8	—	—	4	760	1.0	3.0	0.0	3.6
1988–1989	2.0	—	—	2	1,040	3.7	4.6	6.6	52.1
1989–1990	2.3	—	—	2	260	2.5	1.3	0.0	14.8
1990–1991	3.9	—	—	3	—	6.0	5.1	1.0	23.2
1991–1992	—	—	—	1	—	2.8	1.0	0.0	1.0

guild and bur oak may be spurious, due to one cluster of points and a single distant outlying point.

Statistical or marginal significance was observed in five out of eight correlations between the annual fruit crop sizes of juniper and hackberry and the mean annual population sizes of the frugivore species. Further, the correlation between the frugivore guild and the annual fruit crops of juniper and hackberry was marginally significant. In only one other species (and no other guilds), American Tree Sparrow, were the correlations with juniper and hackberry fruit crop at least marginally significant. The only species for which the correlation with chinquapin oak was at least marginally significant were American

TABLE 6. Correlation coefficients between bird species and relative sizes of fruit or seed crops.

Guild or species	Weeds $n = 13$	Bur oak $n = 8$	Chinquapin oak $n = 5$	Juniper $n = 5$	Hackberry $n = 5$	Ash $n = 5$
Frugivores	0.30	0.64+	0.68	0.87+	0.87+	0.94*
American Robin	0.51+	−0.03	0.88*	0.86+	0.25	0.44
Cedar Waxwing	0.37	0.76*	0.19	0.74	0.93*	0.88*
Eastern Bluebird	−0.08	0.77*	0.43	0.82+	0.64	0.81+
European Starling	−0.15	0.72*	0.58	0.79+	0.94*	0.97**
Ground granivores	0.60*	−0.23	0.37	0.50	−0.05	0.25
Northern Cardinal	0.13	−0.12	0.23	0.06	−0.30	0.01
American Tree Sparrow	0.37	−0.25	0.95*	0.81+	0.30	0.50
Harris' Sparrow	0.12	−0.29	0.64	0.23	−0.15	0.18
Dark-eyed Junco	0.80**	−0.04	−0.44	0.19	−0.08	−0.01
Acorn cachers	0.31	0.69+	0.05	0.71	0.31	0.42
Red-bellied Woodpecker	−0.09	0.19	0.36	0.19	−0.32	0.00
Red-headed Woodpecker	0.30	0.77*	−0.19	0.64	0.45	0.38
Blue Jay	0.28	0.61	0.07	0.72	0.31	0.43
Leaf gleaners	0.48	0.24	−0.11	0.11	−0.19	0.05
Black-capped Chickadee	0.45	−0.09	−0.36	0.05	−0.31	−0.16
Tufted Titmouse	0.24	0.30	0.34	0.17	0.06	0.36
Golden-crowned Kinglet	0.40	0.08	0.57	0.69	0.42	0.68
Trunk gleaners	0.07	0.31	−0.55	−0.26	−0.05	−0.04
Downy Woodpecker	−0.08	0.53	−0.61	−0.21	0.10	0.14
Hairy Woodpecker	0.21	0.32	−0.47	0.16	0.35	0.37
White-breasted Nuthatch	0.14	−0.04	−0.62	−0.33	−0.19	−0.11
Brown Creeper	−0.05	−0.00	−0.09	−0.33	−0.06	0.14

Symbols: + = $0.10 < P < 0.05$; * = $P < 0.05$; ** = $P < 0.01$.

Tree Sparrow ($P = 0.01$) and American Robin ($P = 0.05$).

The correlations between the populations of frugivores and acorn crops do not fit the feeding habits of those bird species. The correlations may be explained by seed and fruit crops over five years for four species of trees varying in phase (Table 5); large crops were produced during the falls of 1988 and 1990 and smaller crops in 1987, 1989, and 1991. Bur oak also fits that pattern in 1987–1989, for which records overlap the other four tree species. The crops of ash seeds, which are not eaten by any of the bird species studied, also correlate with population variation in frugivorous birds. These correlations would also seem to be a consequence of a common pattern of fruit production over five years by tree species pollinated in the spring. Correlations between weed seeds and American Robins and chinquapin oaks and American Tree Sparrows have no obvious causal explanation.

DISCUSSION

Within-year variability for guilds appeared to depend on the size and long-range mobility of the flocks they formed to exploit different winter resources. Frugivores in the Manhattan area tend to forage in large, mobile flocks. The more common species (European Starlings and American Robins) sometimes form even larger central roosts at night (pers. observ.). Frugivore numbers at any particular fruit producing area during the day are extremely variable (Stapanian 1982). Different species in the guild may group at rich food sources, but do not appear to move as mixed foraging flocks. Among the frugivorous species examined, Eastern Bluebirds were the least social and least dependent on fruit, foraging for insects from raised perches at all seasons.

Mixed foraging flocks of American Tree Sparrows, Harris' Sparrows and Dark-eyed Juncos are also large, but less mobile than frugivores. They are most common on the weedy borders between fields and forests where they are joined by Northern Cardinals, and also Black-capped Chickadees from the leaf gleaning guild. American Tree Sparrows predominate in flocks farther from forest edge. The leaf and trunk gleaning guilds form mixed foraging flocks in riparian forests where they are often joined by Northern Cardinals and Dark-eyed Juncos from the granivore guild and by Red-bellied Woodpeckers from the acorn caching guild. These tend to be smaller flocks than the predominantly granivore flocks of weedy fields.

In the acorn caching guild, Red-headed Woodpeckers defend small individual territories around one or two trees that hold their concentrated cache of acorn pieces during one winter (Stickel 1965) and are seminomadic in response to the location of acorn crops between years (Bock and Lepthien 1975). Red-bellied Woodpeckers scatterhoard acorns in the bark of trees over large individual territories, but cannot defend their caches (Kilham 1963). Blue Jays scatterhoard acorns in the ground over an even larger area (Darley-Hill and Johnson 1981).

The frugivore guild forms both the largest and most mobile flocks, which should be the cause of the high variability of their numbers in a weekly census run by one party over a relatively few sites. The larger flock size and migratory status of the most common members of the granivore guild seem to be enough to account for the greater variability of this guild compared to the variability of the remaining three.

Between-year variability for guilds should be more influenced by the annual variability of their food resource than by the manner in which it is exploited, although the latter factor appears to have an effect. Because of their size and abundance, juniper and hackberry trees are probably the most abundant fruit supply for wintering frugivores in the Manhattan area. Hackberry is sensitive to late spring frosts, which killed all of the flowers in four of the last six years. Therefore, hackberries were a very unpredictable food supply. Juniper is not sensitive to frost during flowering but varies in frequency of pollination and fruit abortion (Smith, unpubl. data). This variability in fruit production and the strong dependence of guild members on fruit during the winter should be the basis of the significantly greater variability of numbers in the frugivore guild between years, in comparison to other guilds.

The extreme variation in bur oak acorn crops should have a similar effect on the acorn caching guild. Acorns, however, have a much greater unitary nutritional value and ability to withstand decay, making them more economical for long-term caching than fleshy fruit (Smith and Reichman 1984). Red-headed Woodpeckers are the most aggressive members of the guild, allowing them to defend concentrated caches against other diurnal arboreal acorn feeders. They actually drive Red-bellied Woodpeckers out of the habitat where they form their concentrated caches (Kilham 1958, Moskovits 1978). This aggression may help to explain the negative, albeit statistically not significant, correlation ($r = -0.34$, $P = 0.26$) between Red-headed and Red-bellied Woodpecker populations in spite of their mutual dependence on stored acorns. Blue Jays are supposed to prefer small acorns, such as chinquapin oak, which they can carry in their esophagus to cache sites (Vander Wall 1990). The stronger correlation of Blue Jay populations with bur oak acorn crops would seem to belie this generality. Only the correlation between Red-headed Woodpeckers and bur oak acorn crops is statistically significant for members of the caching guild. The aggressive interaction between Red-headed and Red-bellied Woodpeckers and the more omnivorous diet of Blue Jays (Martin et al. 1951) may limit the effect of variation in acorn crops to Red-headed Woodpeckers and not the acorn caching guild as a whole (Table 5).

Granivores, feeding on small seeds, have not evolved caching economies. The individual species are likely to respond to seed crops in the same pattern as does the guild as a whole. The granivore guild correlates significantly with our estimate of the weed seed crop, although that correlation is mainly dependent on Dark-eyed Juncos, the dominant species in the guild. The fact that the granivore guild is significantly less variable than the frugivore guild is probably a result of the weed seed supply being less variable than the fruit crop between years. The difference between the two crops is not unexpected. Annual weeds will channel whatever reserves they accumulate during a growing season into seeds. Perennial plants producing fleshy fruits can withhold energy from reproduction without loss of a genetic line.

Leaf and trunk gleaning guilds feed on diapausing arthropods, most of which have an annual life cycle. These birds may have a food supply similar in variability to granivores. Nuthatches and parids make short-term caches of acorns and other seeds (Kilham 1974, Sherry 1984) and may decrease the between-year variability of their winter populations by this alternate food supply.

The order of variability among species on the CBC is significantly correlated with the order of variability for annual averages of weekly censuses. The evidence that the differences in annual variability between species is at least partly based on annual variation in food resources rather than simply daily weather patterns of bird activity gives a causal basis to the correlation. Two of the species that deviate most from the correlation, Northern Cardinals and Black-capped Chickadees, are resident species that form mixed foraging flocks with both granivores at forest edges and leaf and trunk gleaners in forests. Perhaps our census route included mainly preferred habitat for the species and was saturated with individuals each year. Overflow individuals in more marginal habitats would vary more between years and be more likely to be counted in CBC, in which all habitats are covered thoroughly.

The correlations for most species between the CBC and our averaged weekly censuses over 13 years were weak. This result supports the conclusion that our census is unable to test the repeatability of the much more thorough CBC for one given day. Lack of habitat balance between the two censuses is probably the cause for this inequality. With the exception of Golden Crowned Kinglets, the species that show strong correlations are those that feed on the most variable between-year food supply. American Robins and European Starlings among the frugivores probably have weaker correlations because their largest concentrations are not maintained all winter. In some years, tens of thousands of American Robins or European Starlings have formed roosts during the CBC, only to break up and disperse out of the area later in the winter. In other years, equally large groups of American Robins have first entered the area in March. In contrast, the territorial caches of Red-headed Woodpeckers insure that populations stay constant throughout the fall and winter insuring a close correlation between the CBC and our census. It is not clear why the correlation between the two censuses was stronger for Cedar Waxwings than for American Robins or European Starlings, but Cedar Waxwings have not been observed to form large communal roosts that break up during the winter.

In general, the accuracy of representing variability in local bird populations by single annual counts, such as the CBC, is greatest for species that exploit the most variable food supply. Among those species, those whose social behavior relating to food exploitation make them the least mobile are most accurately represented by single counts.

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