CLIMATIC INSTABILITY AND THE "ECOLOGICAL SATURATION" OF BIRD COMMUNITIES IN NORTH AMERICAN GRASSLANDS[1]

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Evolutionary ecologists have, in recent years, devoted considerable attention to the suggestion that many natural communities may be "saturated," i.e., they contain the maximum number of coexisting species that they are able to support. While observations of apparent saturation are few (e.g., Elton 1950, 1966; Cody 1966a; Patrick 1968), theoretical considerations of limits on diversity and species packing are profuse (e.g., MacArthur 1965, 1969, 1972; MacArthur and Levins 1967). In particular, Cody (1966a) has suggested that communities of breeding grassland birds are saturated, noting the remarkable constancy [3 to 4 breeding passerine species, bird species diversity (H') of 0.76 to 1.34] of censuses in North America, Iceland, Panamá, and Chile. If these habitats are in fact saturated, then one may infer perhaps that "the kinds of species occupying the habitat are those most appropriate, and hence are better adapted than an equal number of a rather different set of species, as well as better than a different number of species" (Cody 1966a:375).

My objectives in this paper are threefold. First, I wish to examine the degree of packing of breeding bird species in North American grasslands in somewhat more detail than did Cody. Then I will explore factors possibly underlying this limitation of avifaunal diversity. Finally, I will determine whether patterns of variation in community structure within the saturation limits may be discerned. Grasslands are especially well suited for this sort of analysis, since the number of breeding species is small, populations may be censused with relatively little difficulty, and the effects of abiotic factors should be only slightly buffered by the biotic community and thus be rather directly evidenced. In places my arguments are frankly speculative, but I believe such speculation is valuable, both by indicating gaps in our knowledge and by suggesting hypotheses which may be central to a good deal of avian community ecology.

GRASSLAND BIRD COMMUNITY STRUCTURE

STUDY AREAS AND CENSUS METHODS

From 1967 to 1971 I censused breeding bird populations on 10.6-ha sample plots located over a broad range of grassland conditions. In all, 33 plots at 13 sites in Texas, Oklahoma, Kansas, Colorado, Nebraska, South Dakota, Wyoming, Montana, Washington, and Oregon were studied. Detailed descriptions of the study sites and the census results are presented in an analysis of habitat heterogeneity and avian community structure (Wiens 1974). Here I consider the results in terms of several grassland types (fig. 1) as generalized from Küchler (1964). In addition to Great Plains grassland sites, plots in western Palouse prairie (Festuca-Agropyron dominated) and northern Great Basin (Artemisia) shrubsteppe are included since they have interesting relationships to the more typical prairies (see Mengel 1970). This survey is thus confined to temperate North American grasslands. Parallel studies in California annual grasslands and desert grasslands would be highly instructive.

Population densities of all species breeding on the study plots were estimated by mapping individual territories using the "territory-flush" procedure (Wiens 1969). A singing male was flushed from its display site, and its initial position, flight path, and landing position were plotted on a scaled field map. This procedure was repeated until a minimum of 20 consecutive flushes were mapped. A line enclosing the periphery of these movements was then drawn to delimit the territory boundary. Breeding individuals generally remained within clearly delimited areas during these flushes, and independent observations indicated a close agreement of these "flush areas" with breeding territories. After all the territories of a species were mapped, the total number of territories and portions of territories lying within the plot boundaries was determined and multiplied by a mating system conversion factor [2.0 for typically monogamous species, 2.5 for typically polygynous spe-
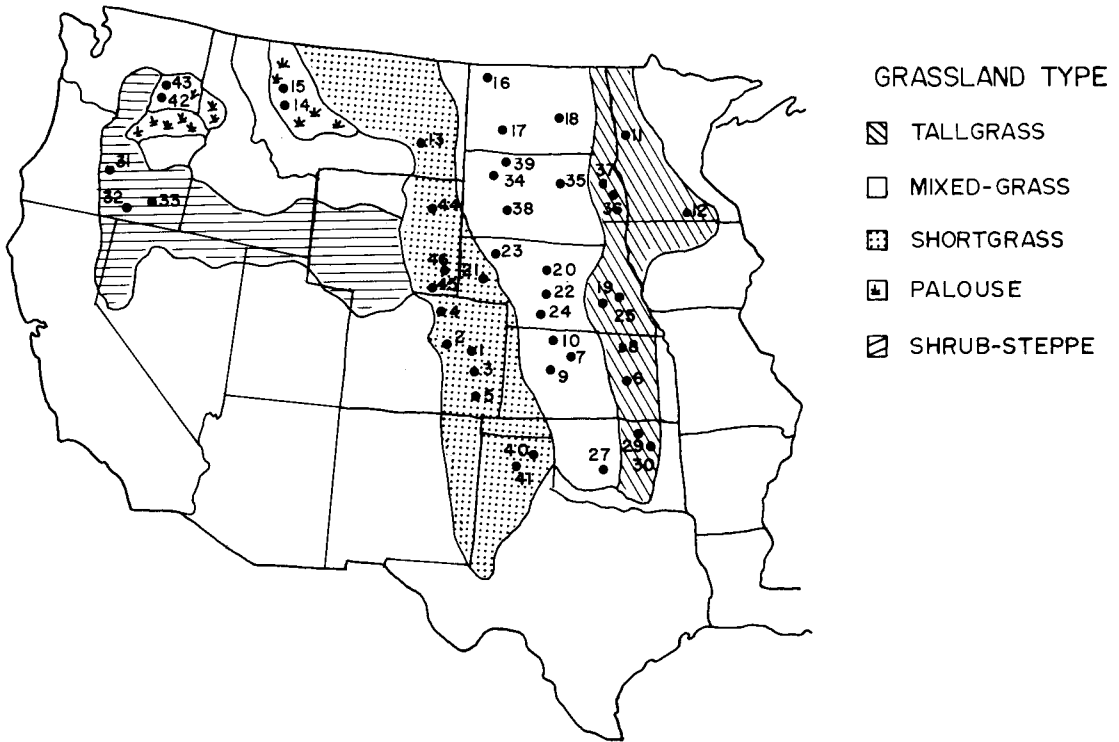
FIGURE 1. Locations of U.S. Weather Bureau climatological stations used to analyze patterns of precipitation variability. Grassland types are generalized from Küchler (1964). Avian study plots were located near stations 4, 6, 8, 14, 23, 29, 31, 32, 33, 38, 41, 42, and 46.

cies such as Eastern and Western Meadowlarks (*Sturnella magna* and *S. neglecta*) and Dickcissel (*Spiza americana*) (assuming that every other male has two mates)] to obtain the plot census. These values were then converted to total individuals per square kilometer. Standing crop biomass values for each species population on a plot were obtained by multiplying the population density estimate by the mean live body weight per individual, using weight values from specimens collected nearby.

RESULTS

The results of these censuses (table 1) confirm the general paucity of breeding bird species (2–6) in grasslands. Species diversity was also uniformly low and species equitability relatively high, relative to values recorded in other habitat-types (Wiens 1973). These results demonstrate the general similarity of species packing between the different grassland types. Especially intriguing is the finding that Palouse and shrubsteppe habitats, despite their greater structural development, seem to support no richer an avifauna than lawn-like shortgrass prairies. The species occurring in each of the grassland types are listed in appendix 1.

Cody (1966a) confined his analysis to species numbers and diversity, and my results provide a further, independent substantiation of his findings. The "saturation" of natural habitats, however, may involve additional features of community structure and merits more intensive consideration. For example, is the total number of individuals, or the biomass present during the breeding season, also uniformly limited across the spectrum of grassland types? The area-based plot samples taken in this study permit estimation of both density and standing crop biomass. Total breeding population densities, while variable from plot to plot, did not differ significantly between the grassland types (table 1), suggesting that the number of individuals as well as species numbers may have a generally similar upper limit not only in various "typical" grasslands but in Palouse and shrubsteppe habitats as well. Further, at the time of population censusing, individuals were packed to a similar degree in their spatial relationships within plots in the different grassland types. By superimposing maps of individual territory locations for the different species occupying a plot, the extent of spatial overlap between species could be measured. To allow comparisons of plots supporting different numbers of

TABLE 1. A. Means and standard deviations (in parentheses) for features of avian community structure from 10.6-ha census plots in North American grasslands.

Grassland type	No. of samples	No. of species	Species diversity[a]	Species equitability[b]	Density (individual/ km²)	Standing crop biomass (g/ha)[c]	Interspecific overlap index[d]
Tallgrass	5	3.6 (0.55)	1.11 (0.12)	0.88 (0.04)	251.0 (30.9)	123.6 (7.4)	0.33 (0.06)
Mixed-grass	8	4.1 (1.36)	1.05 (0.32)	0.78 (0.18)	212.9 (78.9)	124.8 (60.2)	0.35 (0.21)
Shortgrass	14	3.4 (1.28)	0.89 (0.32)	0.76 (0.17)	256.7 (64.6)	99.6 (23.4)	0.34 (0.18)
Palouse	3	3.3 (0.58)	0.98 (0.14)	0.82 (0.11)	216.0 (73.5)	95.7 (20.8)	0.37 (0.19)
Shrubsteppe	3	4.3 (0.58)	1.19 (0.14)	0.81 (0.09)	263.3 (171.5)	67.0 (11.4)	0.30 (0.04)

B. Matrix of significance of differences between grassland types (t-tests: NS $= P > 0.05$, * $= P < 0.05$, ** $= P < 0.01$).

Types compared	df	No. of species	Species diversity[a]	Species equitability[b]	Density (individual/ km²)	Standing crop biomass (g/ha)[c]	Interspecific overlap index[d]
Tall—Mixed	11	NS	NS	NS	NS	NS	NS
Tall—Short	17	NS	NS	NS	NS	*	NS
Tall—Palouse	6	NS	NS	NS	NS	*	NS
Tall—Shrub	6	NS	NS	NS	NS	**	NS
Mixed—Short	20	NS	NS	NS	NS	NS	NS
Mixed—Palouse	9	NS	NS	NS	NS	NS	NS
Mixed—Shrub	9	NS	NS	NS	NS	NS	NS
Short—Palouse	15	NS	NS	NS	NS	NS	NS
Short—Shrub	15	NS	NS	NS	NS	*	NS
Palouse—Shrub	4	NS	NS	NS	NS	*	NS

[a] Measured by $H' = -\Sigma\ p_i\ \log_e\ p_i$, where $p_i =$ proportion of individuals belonging to the ith species (MacArthur 1965).

[b] Equitability is the evenness of distribution of individuals among species, measured as H'/H'MAX, where H'MAX $= \log_e$ S, and S $=$ number of species.

[c] Standing crop biomass $= \Sigma\ (N_i W_i)$, where $N_i =$ density of ith species, and $W_i =$ mean body weight (g) per individual of ith species.

[d] See text.

breeding species and occupied to varying degrees, I used an Index of Interspecific Overlap (IO) (Wiens 1974) calculated by:

$$IO = \left[\frac{\Sigma\,[\,i(a_i/\Sigma a_i)\,]}{N} - M \right] \left[\frac{1}{1-M} \right]$$

where

$i = 1, 2, \ldots, N$ species

$a_i =$ area (ha) occupied by species i (i.e., by 1, 2, . . ., N species)

$N =$ total number of species present

$M =$ minimum value of $\dfrac{a_i}{\Sigma\ a_i}$ recorded

The value $\Sigma\ a_i \dfrac{a_i}{a_i}$ thus represents the percentage of the total occupied area of a plot in which i species occur. This index ranges in value from $\dfrac{1}{N}$ when there is no spatial overlap among the species present to one (1) when spatial overlap among all species is complete. [A revised form of this index is given in the appendix of Wiens (1974); the revision does not alter these conclusions.] The index values of the true grasslands, Palouse, and shrubsteppe plots are quite similar and rather low

(table 1). Thus, at the total density levels which appeared more or less standard for these plots, the plots were not maximally filled with individuals of all species present (see Wiens 1969, Fig. 17 for example). This apparent restriction of the degree of spatial packing of species may be at least partially a reflection of the fact that despite the high equitability of species, plots usually contained at least one locally rare or uncommon species. Further, if different species respond differently to the patchy mosaic of habitat structure present within a plot, or if behavioral interactions (e.g., interspecific territorialism) occur, species distribution in the plot may be largely complementary rather than coincidental.

While the number of species and the density and spatial dispersion of individuals were thus similar though the range of grassland types examined, the total standing crop biomass of breeding birds varied significantly between types (table 1). Tallgrass plots consistently supported greater standing crops than shortgrass, Palouse prairies, or shrubsteppe, while shortgrass and Palouse contained more biomass than shrubsteppe plots.

DETERMINANTS OF COMMUNITY LIMITS

Limitations on the structure and diversity of communities may be imposed by a variety of factors, most of which have been discussed by Pianka (1966, 1967). In grasslands, saturation levels of bird communities would probably be determined by food resource availability, and/or habitat physiognomy, and/or production-climatic patterns.

FOOD AVAILABILITY

Statements regarding the "food availability" of natural populations must be evaluated with due caution (see Watson 1970). Still, I consider it unlikely that food supplies during the breeding season act in a *consistently* limiting manner to determine the opportunities for niche diversification and species packing in grasslands, although food availability may at times be extremely important (see below). While grassland birds have generally similar diets during the breeding season (Wiens 1973), under most conditions food generally *appears* to be superabundant (Evans 1964; Wiens 1969, unpubl. observ.). While these admittedly qualitative observations must be substantiated with intensive, detailed studies of food availability and the time, energy, and spatial dimensions of food-selection behavior, some support for this contention can be gathered from other sources. Grassland ecosystems are characterized by a highly seasonal pattern of primary production, and the concentration of production into a relatively short growing season may result in a flush of available food which exceeds consumer demands (Boulière and Hadley 1970). Also, estimates based upon bioenergetic considerations (Wiens 1973; Wiens and Innis 1974) suggest that breeding bird populations may place extremely low energy intake demands upon the ecosystem, on the order of 1.0 to 2.5 kcal/m² for an entire breeding season (April–August) for all species populations on a plot, or peak demands of perhaps 0.02 to 0.03 kcal/m²/day. In an Oklahoma tallgrass prairie, for example, the estimated peak energy demand of breeding bird populations amounted to 0.0147 kcal/m²/day, only $0.6 \times 10^{-6}\%$ of the standing crop of above-ground plant biomass (of which an unknown fraction is seeds) and $1.9 \times 10^{-2}\%$ of the standing crop of arthropods. While most of these arthropods are *potentially* utilizable food sources, their availability or temporal-spatial accessibility to the birds is unknown. Determining this relationship between prey presence and prey accessibility is fundamental to evaluations of the effects of food supply on population dynamics, and begs close study. These arguments are perhaps not wholly convincing, but it is important to stress that I am not suggesting here that food resource supply is *never* low enough to produce competitive situations and thus influence community diversity and organization, but only that such food limitation is by no means an annual event.

HABITAT STRUCTURE

The physical structure of the habitat undoubtedly has important effects upon the relationships among grassland bird species, as several workers have shown (Cody 1968; Martin 1971; Wiens 1969, 1974; Zimmerman 1971). Cody's model (1968), for example, predicts species diversity in grassland communities from grass height, vertical habitat separation among species, and the relative degree of food specialization. Yet habitat structure may influence grassland bird populations primarily in a proximate manner through its direct, immediate effects on habitat selection (Hildén 1965) and activity patterns. As an ultimate (or evolutionary) factor, habitat physiognomy may contribute to the differences in avifaunal development between grasslands and more complexly structured habitat-types such as thickets or forests, but I suggest that it is not the major ultimate factor governing the evolution of diversity in grassland bird communities.

CLIMATE

Climate, particularly climatic instability, has also been suggested to limit opportunities for niche diversification and thus saturation levels. Grasslands especially are characterized by extremes of weather—droughts, blizzards, cloudbursts, tornados, bitter cold, intense heat, etc. While the severity of grassland weather is frequently exaggerated in the eyes of the layman, the climate does undergo strong seasonal shifts, and yearly differences are also frequently large. Further, in grasslands there is little biotic buffering of the environmental fluctuations by the community as occurs in a forest, and the ecosystem may thus be more directly affected by climatic variations.

While many climatic features may contribute to this general instability, variability in precipitation especially may act in a limiting manner through its direct effects on primary production (Rosenzweig 1968; Holdridge 1947) and thus on food supplies. Brown (1973), for example, has suggested that the species diversity of heteromyid rodents in Nevada and California deserts is greater where the rainfall is greater, even

though there are no conspicuous differences in vegetation in the rainier patches. In this situation rainfall may increase seed production, creating greater opportunities for niche diversification.

A dry year in grasslands not only has low precipitation, but is accompanied by higher than average temperatures and wind movements and, therefore, higher evapotranspiration rates, with the result that the need for water in the system is potentially highest during the years when it is least available (J. L. Rasmussen, pers. comm.). Because of its potential influence on avian community development in grasslands, it is prudent to consider more precisely the nature of "instability" in grassland precipitation regimes.

PRECIPITATION PATTERNS IN GRASSLANDS

ANALYTIC METHODS

To determine regional patterns of variation in precipitation, records from 46 U.S. Weather Bureau stations from the initiation of recording through 1960 were gathered from various summaries (U.S. Weather Bureau 1930, 1952, 1961). Stations were selected to characterize the major types of grassland and to provide a broad sampling of weather conditions within each type (fig. 1). Only annual precipitation patterns were analyzed. This certainly obscures much meaningful variation in monthly rainfall or in intensity of showers, factors which may have rather direct immediate effects on breeding phenology or reproductive success, for example. Annual patterns are much more amenable to analysis, however, and in the long run may be most important as ultimate factors in determining community composition and complexity.

Variability and/or predictability of annual rainfall were measured in the following ways:

1. The coefficient of variation (CV) of annual precipitation was calculated for each station, and a mean CV was derived from these for all stations within each grassland type. This provides a comparative index of the degree of variation of yearly rainfall amounts about the long-term average.

2. The extreme dry and wet years recorded for each station were determined, and the ratio of wet to dry values was calculated. These values were then combined to give a mean ratio for each grassland type. The measure is indicative of the magnitude of extreme variations in rainfall.

3. More important biologically, perhaps, than variation around a long-term mean, or

the extreme conditions, is the frequency of occurrence of years which deviate strongly from "average." From the standpoint of bird populations, the occurrence of unusually dry or wet years (with the attendant effects on production and food supplies) may impose crucial limitations. To measure this, I calculated for each station the percent of all years in which the yearly rainfall deviated from the long-term average by at least 0.25 of the long-term mean, and also by at least 0.50 of the long-term mean. As before, these values were summarized for each grassland type.

4. Variation in precipitation does not necessarily imply instability, for variations may be large but of a regular, predictable occurrence (e.g., seasonal patterns). To test the predictability of rainfall regimes, I used time-series analysis or "autocorrelation" (Kendall and Stuart 1967) to analyze the monthly precipitation records for each station. Autocorrelation is positive when values of monthly precipitation are positively correlated with monthly rainfall at some earlier time, and negative when the two values are inversely correlated. Autocorrelation values near zero indicate independence of the two rainfall values, and thus also indicate relative unpredictability. This sort of approach has previously been applied to an analysis of patterns of lizard diversity in North American deserts by Pianka (1967). In my analysis, the interval of time (or lag) between compared monthly precipitation values was varied from 1 to 12 months. In essence, then, I asked: Given the rainfall amount of any month, n, what is the likelihood that the rainfall of month $n + 1$, $n + 2$, . . ., $n + 12$ will be quite similar or quite dissimilar? This approach thus looks at climatic stability by examining the average correlation of rainfall both between and within seasons and from one year to the next.

RESULTS

Patterns of annual precipitation. It is no surprise that the series tallgrass—mixed-grass—shortgrass is paralleled by steadily decreasing mean annual precipitation (table 2). The tallgrass stations have a mean annual rainfall roughly 1.5 times that of the mixed-grass sites, which in turn average 1.25 times more precipitation than the shortgrass stations. All of these differences are significant. Palouse prairies and northern shrubsteppe are characterized by less yearly rainfall than any of the Great Plains grassland types, but are quite similar to each other.
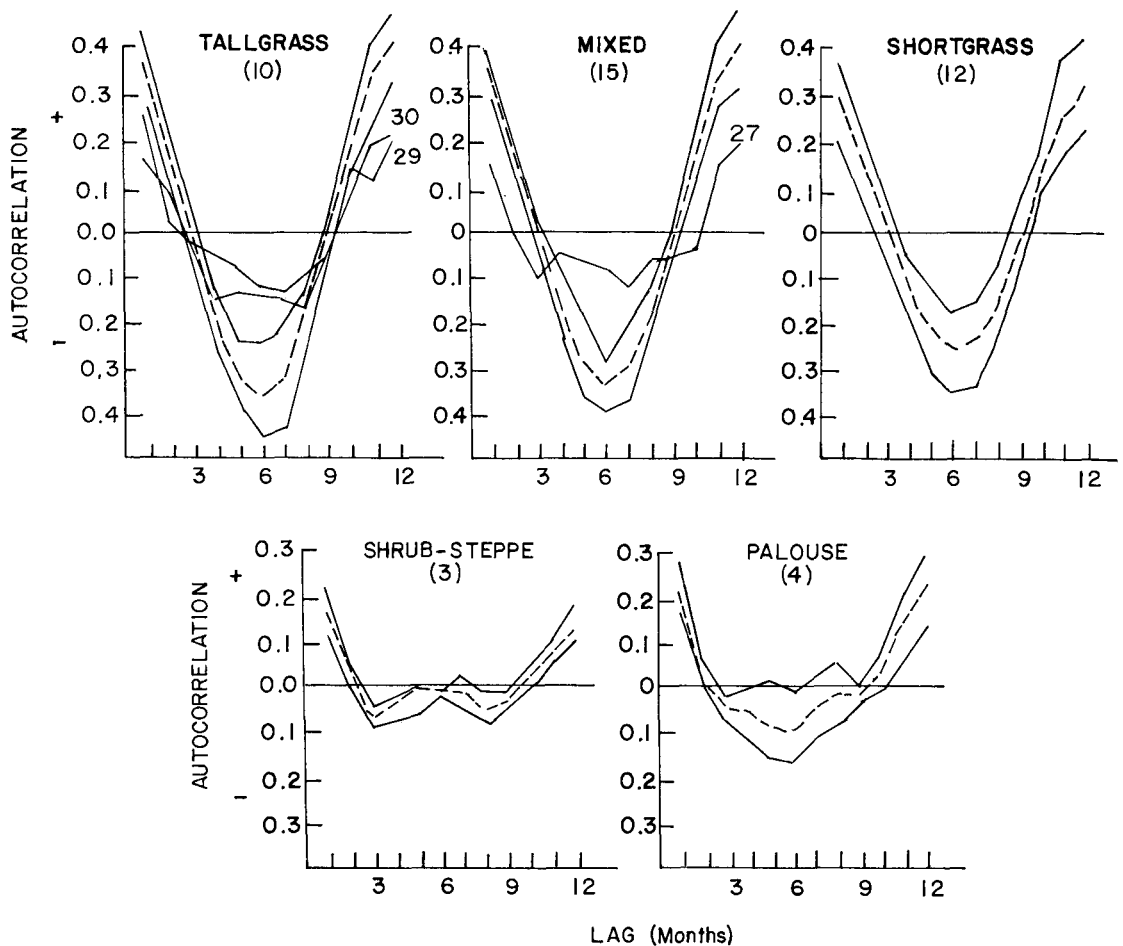
FIGURE 2. Autocovariances of monthly total precipitation for lags of 1–12 months and for stations in five grassland types. Points above the zero line indicate positive autocorrelation and mean that the precipitation for a given month is positively correlated with the precipitation for the month at a given lag period away. Points below the zero line indicate inverse autocorrelation, meaning that conditions may be expected to change during the given lag interval. Points near the zero line indicate that there is little autocorrelation and that precipitation is unpredictable. Solid lines enclose the range of autocorrelation curves for a given grassland type, while the dashed line indicates the mean autocovariance for all stations within a type (number is given in parentheses). The Oklahoma stations (no. 27, 29, 30) are considered separately.

Roughly three-fourths of the yearly rainfall in the Great Plains grasslands occurs in summer, while both Palouse and shrubsteppe types occupy the rain shadow of the intermontane western regions (Trewartha 1961) and are dominated by winter-season precipitation.

Predictability of precipitation. The autocorrelation analysis (fig. 2) allows an evaluation of the relative predictability of rainfall patterns over a 12-month period regardless of total annual precipitation differences or differences in variability. The strong seasonality of rainfall in tallgrass, mixed-grass, and shortgrass areas is apparent. In each there is a strong positive autocovariance with a 12-month lag [i.e., if it is wet (dry) now, it is highly likely that it will be dry (wet) in 5–7 months and wet (dry) again at the same

time next year]. The seasonal predictability of tallgrass prairies is slightly greater than that of mixed-grass types, which in turn are somewhat more predictable than shortgrass prairies. The three Oklahoma stations (two tallgrass, one mixed-grass) deviate markedly from these autocorrelation patterns (fig. 2), and for that reason have not been included in the general analyses for these grassland types (table 2); these differences may be largely due to the effects of Gulf coastal weather systems (Trewartha 1961).

Palouse and shrubsteppe are much less predictable in the seasonal distribution of their rainfall than the Great Plains grasslands. Given a time lag of roughly 2–10 months, autocovariance values are relatively close to zero, indicating the unpredictability of

TABLE 2. A. Precipitation characteristics (means, with standard deviation in parentheses) of grassland types. See text for further explanation of measures. The Oklahoma Stations (no. 27, 29, 30 in fig. 1) are omitted from this analysis.

Grassland type	No. of stations	Mean length of record (years)	Annual precipitation Mean (cm)	CV[a]	Annual precipitation in summer[b] (%)	Frequency of deviation[c] 0.5 x̄	0.25 x̄	Max/Min annual precipitation[d]
Tallgrass	8	59.3	72.4 (13.82)	0.233 (0.031)	76.1 (2.85)	2.4 (2.72)	24.5 (5.50)	3.04 (0.56)
Mixed-grass	14	58.5	49.5 (11.48)	0.258 (0.025)	77.2 (1.58)	4.8 (2.76)	34.1 (7.33)	3.97 (0.62)
Shortgrass	12	54.5	39.4 (8.03)	0.285 (0.038)	74.5 (3.53)	8.0 (1.28)	40.5 (9.89)	3.75 (0.62)
Palouse	4	52.0	27.7 (11.32)	0.247 (0.035)	45.0 (16.37)	3.0 (1.41)	24.0 (4.20)	3.35 (0.42)
Shrubsteppe	3	41.7	26.9 (2.90)	0.271 (0.028)	41.3 (3.51)	5.7 (4.04)	37.7 (8.02)	3.57 (0.78)

B. Matrix of significance of differences between grassland types (t-tests: NS = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$).

Types compared	df	Annual precipitation Mean (cm)	CV[a]	Annual precipitation in summer[b] (%)	Frequency of deviation[c] 0.5 x̄	0.25 x̄	Max/Min annual precipitation[d]
Tall—Mixed	20	**	*	NS	NS	**	**
Tall—Short	18	**	**	NS	**	**	*
Tall—Palouse	10	**	NS	**	NS	NS	NS
Tall—Shrub	9	**	NS	**	NS	**	NS
Mixed—Short	24	*	*	*	**	NS	NS
Mixed—Palouse	16	**	NS	**	NS	*	NS
Mixed—Shrub	15	**	NS	**	NS	NS	NS
Short—Palouse	14	*	NS	**	**	**	NS
Short—Shrub	13	*	NS	**	NS	NS	NS
Palouse—Shrub	5	NS	NS	NS	NS	**	NS

[a] Coefficient of variation.
[b] April to September.
[c] Percent of years when annual precipitation deviates from the long-term average (x̄) by at least the indicated amount.
[d] Maximum recorded annual precipitation ÷ minimum recorded annual rainfall.

monthly rainfall. There is a yearly (12-month lag) pattern, but here also the predictability is less than in the "true" grasslands.. The shrubsteppe stations especially lack well-defined, repetitive precipitation patterns.

Variability of precipitation. As suggested above, long-term variability in precipitation may have more important influences on the biotic composition of grassland than seasonal or year-to-year variations. When the magnitude of difference between extreme wet and dry years is considered (table 2), shortgrass and mixed-grass prairies have a significantly greater range between extremes than tallgrass prairies, substantiating in a general way the observation of J. L. Rasmussen (pers. comm.) that as mean annual precipitation decreases, the rainfall becomes more variable from year to year. Palouse and shrubsteppe types are intermediate in the magnitude of variation between extreme years, but do not differ significantly from any of the other grassland types in this respect nor from each other.

The coefficient of variation of mean annual precipitation indicates a similar pattern of variability. Shortgrass stations have a significantly higher CV than mixed-grass stations, which in turn are significantly more variable

than tallgrass stations (table 2). Again, the intermediate condition of Palouse and shrubsteppe types is indicated.

Finally, we may examine the frequency of occurrence of years which deviate markedly from the long-term average in their precipitation. In shortgrass areas roughly 1 out of every 12 years can be expected to differ from the long-term average by at least half that average (i.e., be half again as wet, or have only half the "normal" precipitation) while 1 of every 2.5 years deviates from "normal" by at least one-quarter of the mean (table 2). In mixed-grass prairies, on the other hand, extremely wet or dry years (those which deviate by ± 0.50 x̄) are only 60% as frequent as in shortgrass areas, and unusually wet or dry years (those which deviate by ± 0.25 x̄) are also less frequent, although not significantly so. In tallgrass prairies extremely wet or dry years occur only once in every 42 years on the average, and unusually wet or dry years occur roughly 1 in every 4 years. Palouse and shrubsteppe types are intermediate although unusually wet or dry years are significantly more frequent in shrubsteppe than Palouse areas. Significance levels for all of these comparisons are given in table 2.

CLIMATIC IRREGULARITY AND COMMUNITY "SATURATION"

Community structure may be affected by both seasonal and long-term irregularity of precipitation. In highly seasonal climates the availability of resources may undergo large seasonal variations. Resident populations may be restricted by the scarcity of food during the seasonal "lows" and thus be unable to utilize the "excess" food produced at other times (e.g., during the wet season) (Willis 1966; Boulière and Hadley 1970; Eadie 1970). Seasonally varying resources may thus be less finely subdivided than constant resources, limiting the number of coexisting resident species (MacArthur 1969, 1971). Grassland habitats, especially the "true" grasslands, are characterized by a highly seasonal distribution of precipitation and production. While this may influence the number of resident species or the size of resident populations, it may not determine the limitation of total breeding species numbers and densities. The seasonality of precipitation in the Great Plains, at least, is relatively predictable (fig. 2), and thus the production flush during the breeding season should be open to exploitation by seasonal residents.

Grasslands are also typified by long-term, largely stochastic irregularities in total yearly rainfall, the frequency and intensity of which vary regionally (table 2). These patterns of irregularity may be major determinants of breeding community structure, acting in the following way.

Successful exploitation of grassland or shrubsteppe as a breeding habitat may be expected to require a complex of rather distinctive adaptations: ground nesting, well-defined diversionary displays, flight song, cryptic coloration, relatively short incubation and nestling periods, perhaps physiological abilities to withstand water stress, and so on. If this is so, then the "appropriateness" of species (in Cody's sense) should be most rigorously tested at times of breeding season resource limitation, and relatively few species may be able to coexist in grasslands at such production lows. The evolution of a larger number of well-adapted or "appropriate" species may thus be limited by the frequent but irregular recurrence of climate-production bottlenecks. At other points along the climate-production spectrum, resources may be abundant, but few additional species may be able to exploit grasslands during such "good" years. This is so partially because the pool of grassland-adapted species is small but, perhaps

more importantly, because of the geographic distribution of grasslands. True grasslands in North America cover large, relatively unbroken expanses (fig. 1) which are frequently subject to similar climatic events over wide areas (Borchert 1950). Thus, in a drought year, for example, it is unlikely that more favorable grassland conditions will be available nearby. Further, there are few patches or "refugia" of different habitat-types (e.g., woods and thickets) available in this expanse which are large enough to shelter populations of species less well-adapted to grasslands and thus capable of opportunistically exploiting favorable climatic-production conditions. And the relatively small number of species per genus in grasslands (1.1) suggests that only rarely has this environment been fragmented for periods long enough to permit speciation among isolated populations (Mengel 1970). For these reasons, grassland habitats may be "saturated" by a relatively small number of breeding bird species when apparently greater opportunities for resource partitioning frequently exist.

These comments apply most directly to shortgrass prairies, which are climatically the most irregular and distributionally the most continuous of the North American grasslands. Tallgrass prairies, on the other hand, are not only less irregular and more productive, but are frequently interspersed in a broken patchwork with other habitat-types. While the number of breeding species and breeding densities I recorded in tallgrass plots were no greater nor more diverse than in shortgrass plots (table 1), variation between nearby plots (beta diversity of Whittaker 1965) was greater in tallgrass areas (unpubl. data), suggesting that a wider variety of species may exploit such areas. Further indication of the greater local availability of species "inappropriate" to grasslands in tallgrass areas comes from examination of the results of roadside censuses conducted as part of the U.S. IBP Grassland Biome program. In these censuses individuals observed within 0.8 km of points along a roadside route in grassland-dominated areas were counted following standard procedures (Robbins and Van Velzen 1967). The data (table 3) show that the tallgrass censuses recorded more species and individuals and had a greater diversity and equitability than shortgrass censuses, and that a larger proportion of the species recorded could be characterized as "inappropriate" grassland species. The censuses taken at the mixed-grass site were generally intermediate.

TABLE 3. Analysis of results of roadside counts taken at three U.S. IBP Grassland Biome Sites, 1970, 1971. Species were considered grassland or nongrassland by virtue of the degree of development of the various adaptations mentioned in the text.

Grassland type	Site		Year	No. of species	Individuals per sample stop	Species diversity	Species equitability	Proportion of species "appropriate" to grasslands
	State	Name						
Tallgrass	Oklahoma	Osage (29)	1970	28	27.2	2.04	0.73	39
			1971	25	34.8	2.26	0.70	40
Mixed-grass	South Dakota	Cottonwood (38)	1970	25	19.5	2.10	0.65	44
			1971	25	26.0	2.22	0.69	52
Shortgrass	Texas	Pantex (41)	1970	22	14.7	1.73	0.56	59
			1971	18	19.1	1.80	0.62	50

The number in parentheses indicates the weather station closest to the site (fig. 1).

COMMUNITY PATTERNS

This suggested limitation of breeding species numbers in grasslands by recurrent but unpredictable climatic "catastrophes" need not imply a lack of community patterns. Thus, while opportunities for regular exploitation of seasonal resource "excesses" by seasonally resident species may be reduced, at least in shortgrass and mixed-grass areas, by the absence of suitable "refugia" for inappropriate species, migration may still be an important part of the exploitation strategy of the more narrowly defined true grassland species. On this basis, one should expect seasonal rather than permanent residency to be most strongly expressed in communities inhabiting highly seasonal habitats or, more specifically, in areas where low winter food supplies preclude long-term residency to most species (MacArthur 1959). At first glance the data (table 4) would seem to contradict this, since seasonal residency is only moderately expressed in seasonal tallgrass areas but is nearly complete in the avifaunas of less seasonal shrubsteppe habitats. The pattern is more subtle, however. Since arthropods are scarce in all grasslands in winter, residency in any area must be largely dependent upon winter seed availability, which in turn is a function of the rate of seed production by the vegetation. Quantitative estimates of seed production in various

TABLE 4. A. Migratory tendencies, dietary characteristics, and body-size frequencies in breeding bird populations in North American grasslands. Values are mean percentages of species (migration) or individuals (diet, body size), with standard deviations in parentheses.

Grassland type	Residency		Dietary type[b]		Body size[c]		
	Seasonal[a]	Permanent	Omnivore	Carnivore	Small	Medium	Large
Tallgrass	66.4 (7.3)	33.6 (7.3)	64.6 (7.3)	35.4 (7.3)	34.6 (10.2)	29.8 (7.2)	35.6 (7.3)
Mixed-grass	65.4 (29.5)	34.6 (29.5)	70.0 (12.8)	30.0 (12.8)	32.4 (23.4)	37.8 (27.7)	30.0 (13.2)
Shortgrass	42.3 (30.2)	57.7 (30.2)	83.6 (13.1)	16.4 (13.1)	5.9 (8.6)	82.6 (14.1)	11.4 (11.8)
Palouse	61.3 (34.9)	38.7 (34.9)	73.7 (15.4)	26.3 (15.4)	45.7 (12.3)	27.3 (25.3)	27.0 (14.7)
Shrubsteppe	95.3 (8.1)	4.7 (8.1)	47.3 (17.3)	52.7 (17.3)	70.3 (23.4)	15.3 (5.1)	14.0 (18.5)

B. Matrix of significance of differences between grassland types (t-tests: NS = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$). Sample sizes as in table 1.

Types compared	Residency		Dietary type[b]		Body size[c]		
	Seasonal[a]	Permanent	Omnivore	Carnivore	Small	Medium	Large
Tall—Mixed	NS	NS	NS	NS	NS	NS	NS
Tall—Short	*	NS	**	**	**	**	**
Tall—Palouse	NS	NS	NS	NS	NS	NS	NS
Tall—Shrub	**	**	*	*	*	*	*
Mixed—Short	*	NS	*	*	**	**	**
Mixed—Palouse	NS	NS	NS	NS	NS	NS	NS
Mixed—Shrub	NS	NS	*	NS	*	NS	NS
Short—Palouse	NS	NS	NS	NS	**	**	*
Short—Shrub	**	**	**	**	**	**	NS
Palouse—Shrub	NS	NS	NS	NS	NS	NS	NS

[a] Wintering range separated by at least 200 km from breeding area.
[b] Omnivore = animal food types comprise < 75% of diet by dry weight.
[c] Small = ≤ 25 g/individual, medium = 26–80 g/individual, large = > 80 g/individual.

grassland types are lacking, and generalizations must be equivocal. Qualitative impressions, however, suggest that the highest rates of seed production may occur in shortgrass prairies; intermediate production, in mixed-grass, tallgrass, and Palouse; and certainly the least production, in shrubsteppe. In addition, the seed supply may be more readily available in winter in shortgrass than in tallgrass habitats, partly because the lower stature of the vegetation may permit more efficient foraging and partly because winter snows in shortgrass areas are usually associated with high winds. Thus, bare areas may be present on wind-swept ridges, while in tallgrass habitats even a light snowfall may completely cover the seed supplies. Permanent residency is, in fact, most strongly expressed among the breeding birds of shortgrass communities (table 4), while tallgrass, mixed-grass, and Palouse types are intermediate, and the shrubsteppe breeding avifauna is almost entirely migratory. Dietary habits parallel these relationships. During the breeding season, omnivory is significantly greater in shortgrass bird populations than those elsewhere in the grasslands, while most of the individuals in shrubsteppe habitats are carnivorous (table 4). A more detailed analysis of estimated energy intake and dietary composition of breeding bird populations at the IBP Grassland Biome sites (Wiens 1973) suggests that both the proportional and the absolute consumption rates of seeds are greatest in shortgrass areas, less in mixed-grass, and even less at tallgrass sites.

The results presented earlier (table 1) indicated that while species numbers, diversity, and total density of breeding bird populations appeared to be generally similar over a wide range of grassland and even shrubsteppe conditions, standing crop biomass decreased from tallgrass to shortgrass to shrubsteppe. This implies that there may be basic differences in the way biomass is partitioned among different-sized species in these areas. The data (table 4) reveal that in tallgrass and mixed-grass types there are roughly equal densities of small, medium, and large-sized species, but that in shortgrass, medium-sized species predominate. In shrubsteppe the lower total standing crop biomass is a result of the abundance of small species in the breeding avifauna. Thus, the changes in standing crop biomass from shrubsteppe through shortgrass to tallgrass areas apparently stem from shifts in dominance among different-sized species rather than changes in total numbers of individuals of all species. Cody (1971) has suggested that birds of larger body size, with a lower metabolic rate per gram body weight, should be able to survive longer periods of energy deprivation and thus might be more successful in occupying a variable environment. Yet, while larger birds do incur lower energy costs per unit of body weight, their metabolic demands per individual are greater than those of a smaller bird, since there is more biomass to support. In the grasslands larger species are most numerous in the relatively productive and relatively stable tallgrass prairies and are nearly absent from the more variable shortgrass sites. The relative equitability of distribution of individuals among different-sized species in tallgrass and mixed-grass areas may suggest a greater degree of niche diversification (e.g., MacArthur 1971). In these areas the more equable climate, coupled with the greater availability of marginally adapted species, might permit a fuller degree of exploitation of food resources and lead to divergences in food types or sizes or in patterns of habitat utilization associated with body-size differences. In shortgrass areas, on the other hand, the greater irregularity of precipitation and production and the lower abundance of "inappropriate" species may result in frequent "excesses" in food resources. Under these conditions, selection for body-size differences among coexisting species may be weak or absent, and the relative uniformity of body sizes may reflect adaptation to some noncompetitive niche dimension (e.g., thermal or water stress). Data on food habits gathered at several IBP Grassland Biome sites revealed a slightly greater divergence in dietary composition and food-item sizes among breeding species in tallgrass and mixed-grass plots than in shortgrass situations, but the similarities in diet were generally more impressive than the differences. Incomplete behavioral observations indicate that subdivision of habitat structure in accordance with body-size differences may be somewhat greater in tallgrass than in shortgrass sites, as Cody's studies (1968) also suggested. These arguments are discouragingly unsubstantiated, and attest to the need for careful comparative community studies.

POPULATION GROWTH AND LIMITATION

If, in fact, grassland breeding bird faunas are limited in the way I have suggested, then resources should frequently (but not consistently) be "superabundant." One might thus expect various life-history adaptations of grassland birds to promote rapid population

growth during these intervals of relative resource abundance (i.e., they should be subjected to "r-selection"). Increases in population growth rates should be most directly affected by alterations in clutch size or number of broods.

Unfortunately, there have been few careful studies of clutch size in the various grassland types. In a shortgrass area in Colorado, Strong (1971) recorded clutch sizes of 2–6 with means of 3.0–4.9 for six grassland species, and values recorded elsewhere in grasslands are similar. It appears that clutch sizes of grassland-nesting passerines generally approximate those of similar species nesting in other temperate North American habitats (Ricklefs 1970), although in some groups (e.g., Icteridae) the grassland species may average larger clutches than forest or parkland species (Cody 1971) (but this may be more a reflection of body-size differences than habitat differences). In any case, interpretation of clutch-size variations within grasslands, or between grasslands and other habitat-types, must be somewhat ambiguous. Virtually all grassland species are ground-nesters, and trends toward increasing clutch size in response to food availability may thus be compromised by responses to the relatively high nest predation suffered by ground-nesters (Ricklefs 1969). Further, as Cody (1966b) has observed, changes in clutch size in a species must be considered in terms of its overall time-energy allocation strategy. Among most grassland species, considerable time may need to be allocated to shading the young as a result of the high midday temperatures and the general scarcity of dense, sheltering vegetation. Exposed nest sites of Dickcissels in Kansas tallgrass prairies, for example, have a more severe microclimate than sites sheltered by dense vegetation, especially with regard to temperature (Blankespoor 1970). Blankespoor demonstrated a significant inverse relationship between light intensity at nest sites (a measure of exposure) and the growth rate of nestlings, and his behavioral observations suggested that this was because females nesting in exposed situations left the nests to gather food less often and spent less time gathering when they were off the nest. In addition, Martin (1971, 1974) has suggested that asynchronous hatching of clutches, with subsequent possibilities for reduction in brood size during the nestling stage by starvation of the "runts," might be more fully developed in grassland birds than in species characteristic of other habitats, since brood reduction may permit a direct and immediate adjustment of brood size to variations in food availability or demands of the activity budget.

Even in the absence of alterations in clutch size, however, grassland birds might still capitalize on the frequent abundance of food resources by increasing the number of broods attempted per season. While there is evidence that some grassland species are in fact double-brooded (Strong 1971), this habit is apparently not widespread. Multiple-broodedness is a distinctly limited option in most temperate grasslands since most species (especially migrants) cannot initiate nesting until late April or early May, and there is little nesting activity after the onset of high daytime temperatures in late June (Strong 1971; pers. observ.). One solution to this problem might be to accelerate the growth rate of nestlings, but this would incur the cost of increasing the rate of delivery of food to the nest (which may already be limited), thereby increasing the risks of predation through increasing the frequency of conspicuous activities about the nest. In fact, growth rates of those grassland species which have been examined (Strong 1971; Maher 1972) seem to differ little from those reported by Ricklefs (1968) for passerines breeding in other temperate habitats.

These points suggest that recruitment rates may be distinctly limited in breeding bird populations in grasslands, but the final determination of population growth potential or breeding densities may also depend strongly upon winter mortality. Most species nesting in temperate North American grasslands winter in similar habitat-types (pastures, old fields, grain croplands, grasslands) from the southern United States into México, with a few species wintering as far south as Bolivia or Argentina. While these wintering populations have received far too little study, it is apparent that they are primarily granivorous and that they may frequently share a wintering habitat with migrant species from other breeding habitat-types [e.g., Swamp Sparrows (*Melospiza georgiana*), or Song Sparrows (*Melospiza melodia*) from shrubby forest edges, or various marsh-nesting passerines]. Thus, there may be considerable pressure placed upon food resources (seeds) which are nonrenewing during the wintering period and are depleted at a constant rate. Under these conditions, Fretwell (1972) has suggested that an increase in breeding recruitment rates might reduce the equilibrium breeding population since the more birds that were recruited in the summer, the faster the seeds would be depleted, and fewer birds would survive the

winter. While it is difficult to imagine how such winter mortality could select for reduced individual recruitment potential by means other than group selection, winter mortality may play a potentially important role in the determination of breeding population densities in grassland birds. If bird populations are reduced by overwinter mortality, they should encounter proportionately higher food densities in summer (Ashmole 1963). In grassland nesting birds, then, winter mortality, coupled with restrictions on clutch-size enlargement and multiple-broodedness during the breeding season, may restrict breeding populations to relatively low levels with limited potential for rapid increase. The results are relatively low and generally similar total breeding densities over a range of grassland conditions, and incomplete spatial packing (table 1). Again, these arguments lack the data base one might wish for and point up the need for intensive field studies.

AVIAN COMMUNITY STABILITY IN GRASSLANDS

Given these limitations on species numbers, diversity, and populations in grassland avifaunas, it is appropriate to ask how stable these communities may be from year to year. A certain degree of climatic instability is characteristic of all grasslands (table 2), and on this basis one might expect faunal instability as well. But the effects of climatic instability may not be equally expressed everywhere. In Palouse prairies and shrubsteppe, for example, precipitation occurs predominately in the winter rather than in the summer as is typical in the Great Plains. Thus, in the western habitat-types there may be a time lag between precipitation and production, with the result that variations in rainfall may be "damped out" by this time interval and have less severe manifestations during the avian breeding season. In shortgrass areas where no time lag exists, resource levels should be much more directly affected by rainfall and thus be more sensitive to rainfall variations. On this basis, one might predict greater avifaunal stability in shrubsteppe and Palouse sites than in shortgrass sites with roughly the same annual precipitation.

Greater avifaunal stability should also result from the greater structural stability of the western habitats. In arid shrubsteppe, for example, the vegetation is dominated by woody plants such as sagebrush (*Artemisia*) and rabbitbrush (*Chrysothamnus*), and much of the annual primary production is realized as incremental addition of new material to existing structure. Local areas may thus have an essentially unchanging habitat structure over a number of years despite variations in precipitation. The same is true, to a lesser extent, of Palouse prairies where plant growth and habitat structure are dictated by the dispersion of perennial clump bases. By contrast, in "true" grasslands each year's production determines the habitat structure, since most of the plant material is reduced to litter or humus each winter. Thus, variations in rainfall will likely be directly manifested as variations in habitat physiognomy. This in turn may influence populations of creatures which orient strongly to habitat structure, such as birds.

In tallgrass areas, on the other hand, yearly variation in precipitation is relatively small (table 2), and there should thus be somewhat greater stability of both production and structure than in shortgrass prairies. The greater climatic stability and higher net production rates lead to longer and more well-defined successional patterns in tallgrass than in shortgrass prairies. If successional sequences in the tallgrass prairies are predictable enough, some species may become adapted to exploit successionally predictable but spatially transient seral stages. Schartz and Zimmerman (1971) and Zimmerman (1971) have documented a series of behavioral adaptations for sere exploitation in Dickcissels, and Martin (1971) has discovered some parallels in Bobolinks (*Dolichonyx oryzivorus*). Lark Sparrows (*Chondestes grammacus*) might also be expected to be such a serally adapted species. All of these are essentially tallgrass inhabitants, and similar distinctive adaptations in behavior are apparently lacking in the more typically shortgrass species.

The stability of local breeding communities may also be related to the opportunism of grassland species. Given the above arguments, one would predict that philopatry (site tenacity) should be poorly developed in grassland birds. If conditions in any local breeding area were unpredictable during the life span of an individual, close attachment to a specific breeding location during successive years would be a poor strategy; individuals able to move some distance to exploit favorable conditions or avoid marginal situations would have higher fitness prospects. While field data on philopatry in grassland birds are few, the observations of Creighton (pers. comm.) in a Colorado shortgrass prairie suggest the habit is not strongly expressed.

Unfortunately, few studies in grasslands have continued long enough to provide tests

of these predictions about relative community stability. Censuses at the Pawnee National Grassland in Colorado from 1968–71 (unpublished) revealed annual variations of 4–44% in total densities of breeding bird populations, and the relative densities of the breeding species varied comparably. Species composition, however, remained relatively stable. Most enlightening, perhaps, are observations made at the shortgrass Pantex Site in the IBP Grassland Biome (station 41 in fig. 1). In this area 1970 was an unusually dry year and plot counts recorded relatively high densities of Horned Larks (*Eremophila alpestris*), and intermediate densities of Western Meadowlarks, with Lark Buntings (*Calamospiza melanocorys*) and Grasshopper Sparrows (*Ammodramus savannarum*) present but rare. The drought was more severe and widespread in 1971; the density of Horned Larks almost doubled, while the density of meadowlarks decreased by roughly one-half, and the latter two species were entirely absent. In late 1971 and early 1972, however, the area received several rains of 6 cm or more, and above-ground primary production increased accordingly. In the 1972 census, density of Horned Larks dropped to one-third the 1971 level, while density of meadowlarks tripled, and Grasshopper Sparrows were abundant. The effects of increasing precipitation in addition to altering the relative densities of species were to produce shifts toward greater standing crop biomass, a more equitable distribution of individuals among species size categories, and a greater degree of carnivory, all organizational traits of avian communities in mixed or tallgrass situations. Further, the ability of Grasshopper Sparrows to invade the area in high densities following their absence in the previous year attests to their opportunism and adds strength to the suggestion that philopatry is poorly developed.

SUMMARY

The prospect that grassland breeding bird communities may be ecologically "saturated" was examined using data from 33 plots at 13 sites distributed through five types of temperate North American grasslands. Tallgrass, mixed-grass, shortgrass, and Palouse prairies and northern shrubsteppe were all characterized by a similarly low number of breeding species, low species diversities, relatively uniform total breeding population densities, and a similar degree of spatial packing of species. Standing crop biomass, however, was highest in the more productive tallgrass sites, intermediate in shortgrass and Palouse areas, and low in shrubsteppe. Closer study showed that small-sized species predominated in shrubsteppe; medium-sized species, in shortgrass prairies; and the avifauna of tallgrass sites was equally divided between small, medium, and large species.

Analysis of records from 46 weather bureau stations distributed over these grassland types showed that yearly rainfall fluctuated considerably throughout the grasslands, but was most variable in shortgrass areas; intermediate in shrubsteppe, Palouse, and mixed-grass prairies; and least variable in tallgrass. I suggest that the number of breeding bird species which can successfully and persistently exploit grassland habitats is limited by recurrent but unpredictable large magnitude variations in climate and thus production, coupled with the absence of suitable "refugia" which could harbor suboptimally adapted populations during such periods of resource stress. These effects may be most pronounced in shortgrass, with the greater stability of production in tallgrass areas facilitating the development of succession-based exploitation strategies by some species. Migration is most completely expressed in shrubsteppe avifaunas and is least in shortgrass areas. These patterns appear to be related to rates of seed production and relative availability of seeds during winter, which may not be direct functions of total primary production rates.

The argument suggests that food should frequently be "superabundant" in grasslands during the breeding season. Bird populations, however, seem unable to effect rapid population growth to exploit these "excesses." This may be due to limitations placed on clutch-size enlargement by the need to allocate considerable time to brooding at relatively unsheltered nest sites during midday heat, and limitations on multiple-broodedness imposed by the relatively short intervals between the initiation of production in spring and the onset of high summer temperatures. Winter mortality may also contribute to the determination of the relatively low breeding densities. The argument also suggests that breeding bird communities should be expected to exhibit greater year-to-year stability in western shrubsteppe and Palouse and in eastern tallgrass prairies, with shortgrass avifaunas the least stable.

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APPENDIX 1. Bird species recorded in censuses of grassland types.

Grassland type	Number of censuses	Species Recorded	Frequency[a]
Tallgrass	5	*Bartramia longicauda* Upland Sandpiper	0.60
		Sturnella magna Eastern Meadowlark	1.00
		Spiza americana Dickcissel	1.00
		Ammodramus savannarum Grasshopper Sparrow	1.00
Mixed-grass	8	*Numenius americanus* Long-billed Curlew	0.25
		Bartramia longicauda Upland Sandpiper	0.25
		Eremophila alpestris Horned Lark	1.00
		Sturnella neglecta Western Meadowlark	1.00
		Calamospiza melanocorys Lark Bunting	0.12
		Ammodramus savannarum Grasshopper Sparrow	0.75
		Calcarius ornatus Chestnut-collared Longspur	0.50
Shortgrass	14	*Charadrius montanus* Mountain Plover	0.14
		Chordeiles minor Common Nighthawk	0.14
		Eremophila alpestris Horned Lark	1.00
		Sturnella neglecta Western Meadowlark	0.71
		Calamospiza melanocorys Lark Bunting	0.57
		Ammodramus savannarum Grasshopper Sparrow	0.21
		Spizella breweri Brewer's Sparrow	0.29
		Calcarius mccowni McCown's Longspur	0.36
Palouse	3	*Zenaida macroura* Mourning Dove	0.33
		Eremophila alpestris Horned Lark	0.67
		Sturnella neglecta Western Meadowlark	1.00
		Ammodramus savannarum Grasshopper Sparrow	0.33
		Pooecetes gramineus Vesper Sparrow	0.33
		Amphispiza belli Sage Sparrow	0.67

[a] Percent of censuses in which species was recorded.

APPENDIX 1. *Continued.*

Grassland type	Number of censuses	Species Recorded	Frequency[a]
Shrubsteppe	3	*Eremophila alpestris* Horned Lark	0.33
		Salpinctes obsoletus Rock Wren	0.33
		Oreoscoptes montanus Sage Thrasher	0.67
		Lanius ludovicianus Loggerhead Shrike	0.33
		Sturnella neglecta Western Meadowlark	0.67
		Pooecetes gramineus Vesper Sparrow	0.67
		Amphispiza belli Sage Sparrow	0.67
		Spizella breweri Brewer's Sparrow	0.67

[a] Percent of censuses in which species was recorded.