DYNAMICS OF BIRD COMMUNITIES IN THE CHIHUAHUAN DESERT, NEW MEXICO

RALPH J. RAITT

AND

STUART L. PIMM

To say that communities of organisms are dynamic entities is a truism. Communities of birds—in common with those of other organisms—are in a perpetual state of flux, changing from day to day, season to season, and year to year in a number of properties: overall abundance, species composition, relative abundance of species, and impact on other components of the ecosystem, among others. It is also obvious that a fruitful approach for ecologists seeking to understand factors influencing properties of bird communities might be to follow different ones through time, comparing different properties as they change, while simultaneously following potential causative factors such as climate and food supply. In spite of the logic arguing for such an approach we can find little evidence of attempts to employ it, though many investigations have been made of both short-term and long-term changes in individual species populations (the more significant of these are summarized by Lack 1966). We know of only two published studies of temporal changes in a grassland or desert bird community (Finzel 1964, Webster 1964). Recent, largely unpublished studies made in connection with the International Biological Program will be discussed below.

The initiation in 1971 of regular, year-round bird censuses and reproductive studies on three sites of the Analysis of Ecosystems, U.S. International Biological Program (IBP) provided the means and incentive to overcome the disadvantages of studying temporal changes as just outlined. All three sites are in portions of typical ecosystems of the northern portion of the Chihuahuan Desert. The fact that the Chihuahuan Desert experiences relatively minor seasonal changes in climate and is a wintering ground for more northern bird populations gave strong incentive for obtaining data for all seasons. Concurrently with bird studies, other aspects of the same ecosystems have been measured; parameters especially relevant to our study include air temperature, precipitation, various parameters of the vegetation, and insect densities.

The data thus gathered provide a basis for discussion of both within- and between-community variation in a number of community characteristics. In this paper we will stress overall levels of numbers and biomass, temporal changes in them, and the factors that might be responsible for them. Subsequent papers will deal with the trophic impact of the bird communities on the ecosystems of which they are part (Pimm and Raitt, unpubl.), and species diversity (Pimm, unpubl.).

STUDY AREAS

The three field sites of this study lie near the southern end of the Jornada del Muerto plain (32° 30′ N, 106° 45′ W) in Doña Ana County, New Mexico (fig. 1). Buffington and Herbel (1965) described its topography, soils, climate, land use history, and vegetation, but we will briefly characterize the setting again, giving details for specific sites in subsequent sections. The level or gently rolling Jornada plain is from 15 to 30 km wide in the region of the sites, at elevations of about 1300 m, bounded on the east by the San Andres Mountains (2100 to 2500 m at their summits) and on the west by the Doña Ana Mountains (1700 m) and the valley of the Rio Grande. The substrate is alluvial fill occupying a deep structural basin (Gile et al. 1970); soils generally are sandy, with loams in interior drainage basins (playas). At the bases of mountains the plain slopes up across alluvial fans (bajadas) containing coarser soils cut by narrow ephemeral water courses (arroyos) whose bottoms are usually of coarse sand.

The climate of the region can best be understood by examining table 1 and figure 2. Temperatures are typical of regions of moderate elevation in the Southwest; the region is arid with a long-term mean annual precipitation of 228 mm, most of which falls in local summer rainstorms. Main vegetation types of the Jornada are either desert scrub, dominated by various combinations of creosotebush (*Larrea divaricata* Cav.), mesquite (*Prosopis juliflora* (Sw.) DC.), and tarbush (*Flourensia cernua* DC.), or yucca-grasslands, dominated by *Yucca elata* Engelm., black grama (*Bouteloua eriopoda* (Torr.) Torr.), mesa dropseed (*Sporobolus flexuosus* (Thurb.) Rybd.), and/or tobosa grass (*Hilaria mutica* (Buckl.) Benth.). Available water for birds is found permanently at several wells scattered across the plain (fig. 1) and temporarily in playas after heavy rains. The entire southern portion of the plain is included in either the Jornada Experimental Range administered by the U.S. Department of Agriculture or the New Mexico State University (NMSU) Ranch administered by the NMSU Department of Animal, Range, and Wildlife Sciences. Both agencies manage their units for sound livestock grazing (primarily by cattle).
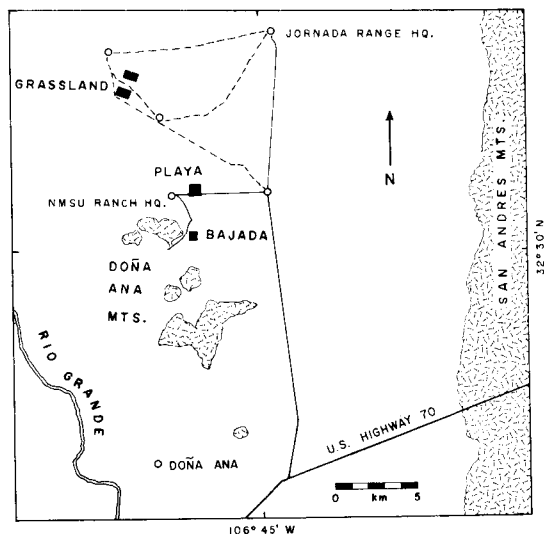
FIGURE 1. Map of study region. Solid lines indicate roads (all unpaved except U.S. 70); dashed lines show route of roadside census. Solid rectangles are study plots. Circles mark settlements and principal water sources.

FIGURE 2. Monthly means of daily maximum, mean, and minimum air temperatures (in shade) for the Playa, 1971–1972.

Of the three specific sites on which this study is based, one (hereinafter called the "Grassland site") is a portion of the US/IBP Grassland Biome comprehensive network of sites; it is on the Jornada Experimental Range. The other two, the Bajada and Playa sites, are US/IBP Desert Biome validation sites, on the NMSU Ranch.

GRASSLAND SITE

This site is on the Jornada plain proper, in Sections 4 and 9, Range 1 East, Township 20 South, within several meters of the fenced ungrazed enclosure on which much of the Grassland Biome data for the area have been collected since its establishment in 1970. Our work was carried out on two plots, each 1600 × 2400 ft (488 × 732 m) and each demarcated by a grid of wooden stakes placed at 200-ft (61-m) intervals. Soils of the site are sandy with a well developed caliche layer; fragments of caliche have been mixed with surface sand by rodents in many spots. The vegetation consists of low grasses and forbs, with scattered *Yucca elata* (0.5 to 5 m tall) and a few low mesquite bushes and other shrubs. The half-shrub *Gutierrezia sarothrae* (Pursh.) Britt & Rusby attains moderate density and high frequency. Black grama is the principal grass, followed by mesa dropseed. Although the site is within more or less typical black grama grassland, the actual density of grass is low, with a basal cover of less than 1%. Most of the forbs are low annuals whose density and species composition vary considerably from year to year; common species are *Croton pottsii* (Klotsch) Muell.-Arg. (perennial), *Salsola Kali* L., *Dithyraea wislizeni* Engelm., and *Cryptantha crassisepala* (T. & G.) Greene.

Annual precipitation measured at the site was 103 mm in 1970, 206 mm in 1971, and 325 mm in 1972 (54-year mean at Jornada headquarters: 228 mm). Details of the timing of precipitation for 1971–1972 are given in table 1. Temperatures recorded at the site indicate levels and annual march similar to those given for the
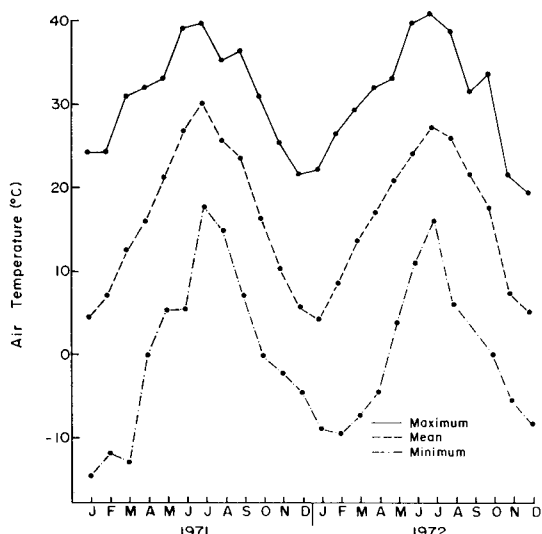
Playa site in figure 2. (Data on vegetation and climate were provided by R. D. Pieper.)

PLAYA SITE

Both Playa and Bajada are portions of a single restricted watershed that originates on the south slopes of Mt. Summerford, the northernmost portion of the Doña Ana range. The Playa site includes the termination of this watershed; it lies about 8 km SE of the Grassland site and 1 km E of the NMSU Ranch Headquarters, in Sections 25 and 36, Range 1 East, Township 20 South. The common plot for Desert Biome validation studies is a square, 600 m on a side (36 ha). It includes the open playa bottom, consisting of 12.6 ha, and a bordering fringe of shrubby vegetation, portions of which are obviously strongly influenced by the more mesic conditions obtaining in the playa.

Vegetation of this site is more heterogeneous than that of the others. The major portion of the playa bottom bears dense low herbaceous cover dominated by vine-mesquite grass (*Panicum obtusum* H.B.K.) and cocklebur (*Xanthium strumarium* L.). Lesser areas at the edge of the playa proper are dominated by tobosa grass. Playa bottom soils are predominantly clay. Most of the immediate fringe of the playa is occupied by dense, tall thickets of mesquite. The mean height of these mesquite bushes is 0.66 m and the mean canopy volume is 3.6 m³. This fringe of mesquite is narrow; beyond 100 m from the bottom it gives way to a more xeric, open community characterized by mormon tea (*Ephedra trifurca* Torr.), snakeweed (*Gutierrezia sarothrae* (Pursh.) Britt. & Rusby), and fluff grass (*Erioneuron pulchellum* (H.B.K.) Tateoka), with some *Yucca elata*. Clay soils of the bottom are replaced in the fringe by the sandy ones typical of the area generally. Both the playa and its fringe produce large and varied crops of herbaceous plants in wet years.

Variation in weather at the Playa during 1971 and 1972 is illustrated in figure 2 and table 1. The total annual rainfall was 197 mm in 1971 and 395 mm in 1972. Precipitation was measured for only a few

TABLE 1. Monthly rainfall (mm) on the Playa (P), Bajada (B), and Grassland (G) of the Jornada, 1971–1972.

| Year | Sites | Month | | | | | | | | | | | | Total |
		J	F	M	A	M	J	J	A	S	O	N	D	
1971	P	4.6	0.0	0.0	3.8	0.0	7.4	25.9	43.9	31.5	40.4	15.8	23.6	196.9
	B	N[a]	N	N	N	N	3.6	36.6	25.5	32.8	40.9	17.5	23.1	—
	G	0.8	0.0	0.0	7.9	0.0	8.1	27.8	48.8	19.6	50.6	23.3	19.3	206.1
1972	P	7.1	0.0	0.0	0.0	14.0	59.7	55.4	61.0	77.5	86.9	15.0	18.8	395.2
	B	4.6	0.0	0.0	0.0	18.0	43.4	34.3	71.1	30.2	85.1	13.5	16.5	316.7
	G	2.0	0.0	0.0	0.0	6.6	51.3	36.5	77.5	34.5	76.5	25.3	14.8	325.0

[a] No measurement taken.

months in 1970, but the total was almost certainly low, as it was on the Grassland site.

In the summers of 1970 and 1972, but not in 1971, the playa received sufficient runoff to retain standing water for some days. Heavy rains in late July 1970 resulted in flooding with water which remained for 3 weeks. In 1972 the playa flooded three times; for about 3 weeks following 19 July, for approximately 1 month beginning 1 September, and from 19 October through November. Flooding has been shown to have profound effects on plant productivity, and the standing water affects birds directly as well.

BAJADA SITE

Bajadas are sloping alluvial fans at the bases of mountains in arid regions, and this site occupies such a slope. The plot is 500 × 700 m and is subdivided by marked posts at 100-m intervals. A sizable arroyo bisects the area as it drains the slopes of Mt. Summerford into the playa about 2 km to the north. The vegetation is typical Chihuahuan Desert scrub with sparse low cover of creosotebush (23% total cover) and other shrubs such as mesquite (1% cover), tarbush, *Gutierrezia sarothrae, Parthenium incanum* H.B.K., *Yucca elata,* and *Yucca baccata* Torr. (each of the latter five species contributes less than 1% total cover). The main arroyo and its larger tributaries contain shrubs of these species along their edges, where they are larger and denser than elsewhere on the site. In addition, the arroyo contains several hackberry trees (*Celtis reticulata* Torr.) and desert willows (*Chilopsis linearis* (Cav.) Sweet) and dense clumps of the shrub, apache plume (*Fallugia paradoxa* (D. Don) Endl.). The substrate on this site is desert pavement underlain by sand and a well-developed caliche layer. Rainfall records are shown in table 1. Temperature records are only slightly different from comparable ones from the Playa station; morning temperatures are lower on the Playa since cold air accumulates there during the night; this cold air may take several hours to dissipate.

METHODS

This study required data on the absolute numbers of all species occurring in three very different areas and on how these numbers changed through time. Emlen (1971) proposed a method that is suitable year-round for a variety of habitats and, therefore, was used on censuses on all sites. In addition, a "roadside" census devised and employed in 1970 by J. A. Wiens was used in the grassland on two consecutive days each month to obtain better data on the spatial distribution of birds and to obtain a better picture of the numbers and activities of the highly mobile birds, such as raptors and flocks of seed-eating species, whose presence on the sites is brief and irregular.

EMLEN CENSUS

All birds seen along a prescribed route were counted and the lateral distance of birds from the line estimated. Each Grassland plot was covered by a route 4800 ft (1463 m) long; all birds were recorded within 400 ft (120 m) of the route, making the area of the transects 88.15 acres (35.7 ha). The Bajada was censused using three transects, two in the creosotebush-desert pavement portions, each 200 m wide (100 m on either side of the route) by 700 m, and one along the main arroyo, 100 m by 700 m (thus, 35 ha total). The Playa transect was an average of 225 m wide and 1600 m long (36 ha), with the route describing a square around the perimeter of the playa bottom. The Grassland sites were gridded with posts every 200 ft (61 m), and the other sites by posts every 100 m, to facilitate the estimation of distances.

In the Emlen method secretive species are seen only close to the line of transect and conspicuous species are seen at distances out to the limit of the transect width. From the distances of detection one may derive a coefficient of detectability (CD) to correct the initial census observations and obtain an estimate of the absolute number of each species on the plots. Each CD was calculated by plotting the frequency of observations against distance in 8-m increments. Peak frequency, which should be close to the line of transect, was extrapolated out to the transect width and an estimate of the number under this line calculated. The CD is the observed number divided by the expected number. Coefficients were calculated for each species and each site. Within these groupings CD's were calculated for: (1) each observer; (2) summer (April to July inclusive); (3) winter; (4) whether the bird was singing or not; and (5) whether the bird was in a flock or not. The frequency-distance plots were then tested using a χ^2 statistic with 10% of the level of rejection of the null hypothesis that they should be considered similar. This process produced as many as six CD values for each site for each species, though for most species only one CD was retained. A complication arose from the distribution of the distances of detection; most species showed a peak frequency some distance from the line of transect. This was due to the birds' moving laterally to the line of transect when they had seen the observer but he had not seen them. All of the observations as close or closer to the line of transect than the peak frequency were averaged and this new value was assigned the peak frequency. With many species, values were missing in the distance-

frequency plots. Values were substituted equal to the next observation further from the line of transect. The calculations were completed using a computer program, which can be provided on request.

The CD's obtained were checked against the criteria of personal intuition, values from other sites, and values for similar species. Density estimates obtained using CD's were checked against density estimates obtained by other techniques used in the breeding season (e.g., spot-map censuses). A small number of suspect CD's were examined; if there were few observations, the value was replaced by a more suitable value based on the criteria mentioned. Thus, the CD for the Ferruginous Hawk (see Appendix for scientific names) for the Grassland plots, based on less than 10 sightings, was 0.8. This is a conspicuous species, and the CD for the Swainson's Hawk for all the other sites was 1.0, so the latter value was substituted. When no CD was obtained, one was estimated on the criteria mentioned. Most of the CD's obtained fell in the range 0.4 to 0.7.

With a few exceptions each plot has been censused at least once a month, and often on a weekly schedule. In all cases the results are presented as monthly means.

Weights for estimates of live biomass were obtained from three sources. Common species were collected or mist-netted and weighed in the field. Data for rarer species were obtained from the literature or museum specimens.

ROADSIDE COUNTS

In roadside counts a standard route was driven through grassland portions of the Jornada (fig. 1). Thirty stops were made at standardized points, no closer together than 0.4 miles (0.6 km). At each stop observers (usually two) counted all birds detected within a radius of 300 m of the vehicles within four observer-minutes. These counts were all made in early hours of the day and on days without high winds or heavy precipitation. Results presented are all combined numbers of the two counts for each month.

RESULTS

Species were grouped into assemblages which would be expected to respond to similar environmental influences and in turn to exert similar effects on the ecosystems of which they are a portion. The seven categories based on trophic position and seasonal status are: (1) breeding species (BS); (2) doves and quail (DQ); (3) nonbreeding insectivorous passerines (OI); (4) nonbreeding, mainly wintering, seed-eaters (WS); (5) raptors (RA); (6) aquatic and semiaquatic species (AQ); and (7) a residuum of miscellaneous species (MS). A complete list of species in each category is included in the Appendix.

Breeding species in our classification included only passerines; most are insectivorous and all are in the breeding season. Some are permanent residents (e.g., Loggerhead Shrike, Cactus Wren, Verdin) and some are strictly

summer residents (e.g., Western Kingbird, Mockingbird, Scott's Oriole). The dove and quail category included three species, *Zenaida asiatica*, *Z. macroura*, and *Callipepla squamata*. The latter two breed in the area, but they were included with the other rare dove because of their large body size and because they are primarily granivorous. Although the quail are permanent residents, they were relatively unimportant during this study, probably because their numbers fell to very low levels during the dry conditions of 1970 and 1971. Some doves were present in the area in all months of the year, but migrants and winter residents augmented or replaced breeding individuals. In most months on all sites figures for doves dominated those for the DQ category as a whole.

Nonbreeding insectivorous species were principally passerine migrants, especially warblers and flycatchers. Winter seed-eaters included primarily emberizines such as Lark Buntings, Brewer's Sparrows, Sage Sparrows, and longspurs, but also some members of other groups, notably Horned Larks. Some members of this category spent most of the winter months in the area, others were present only during migratory periods, but none bred on the study plots and most not even in the general vicinity.

Raptors included breeding, migrant, and wintering species, mainly hawks. The aquatic category included waterfowl and shorebirds which appeared on the Playa when it contained a substantial amount of standing water. Miscellaneous species included birds of omnivorous or unknown feeding habits. None was of much importance over any period of longer than 1 month.

Preliminary analysis revealed that the DQ and WS categories underwent similar temporal changes, and so for some further analyses we combined them into a single category of seed-eating birds. The logic of this combination was confirmed by the fact that diversity of the combined group remained within narrow limits throughout the period of the study, indicating that the several species were, to a degree, responding as a single unit to environmental variables. With similar justification insectivores of breeding and nonbreeding species were combined into a single category.

Mean estimates of density by month for each site are given in numbers of birds in tables 2 to 4 and in live biomass in tables 5 to 7. Total numbers detected on the 2-day monthly roadside counts are summarized in table 8.

TABLE 2. Monthly mean numbers of birds per 100 km² on the Bajada.

Year	Species group[a]	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
1971	BS			47.9	18.8	42.6	76.1	52.5		30.1	34.6	21.5	
	DQ			0.0	0.0	0.0	0.0	2.2		0.0	27.1	23.2	
	MS			4.3	0.0	1.4	0.8	6.6		0.0	1.1	0.7	
	OI			8.6	0.0	5.7	17.9	5.3		1.7	11.9	0.0	
	RA			0.0	0.0	0.0	0.0	0.0		1.4	5.4	6.4	
	WS			0.0	0.0	2.4	0.7	2.1		3.2	51.3	77.7	
	Total			60.3	18.8	52.1	95.5	68.7		36.4	131.4	129.5	
1972	BS		18.3	36.3	64.7	130.2	130.3	130.3	89.8	116.9	65.3	31.0	50.8
	DQ		0.0	1.6	6.5	13.6	2.2	3.2	112.0	24.4	0.0	6.5	17.9
	MS		0.8	0.0	12.9	10.2	2.2	0.0	9.7	136.4	20.0	15.2	4.3
	OI		0.0	0.0	0.0	53.4	3.4	2.3	10.3	8.3	16.2	12.7	14.3
	RA		0.0	0.0	0.0	4.6	0.0	0.0	0.0	4.3	28.6	14.3	0.0
	WS		19.6	2.0	12.2	7.1	0.0	5.7	51.9	18.6	97.7	59.8	26.5
	Total		38.7	39.9	96.3	219.1	138.1	141.5	273.7	308.9	227.8	139.5	113.8
1973	BS	41.9	23.9	61.5		60.4							
	DQ	0.0	3.2	39.6		69.2							
	MS	10.0	10.7	7.1		1.0							
	OI	0.0	9.5	9.5		36.6							
	RA	0.0	0.0	0.0		0.0							
	WS	111.3	167.3	163.9		46.2							
	Total	163.2	214.6	281.6		213.4							

[a] BS = breeding species, DQ = doves and quail, MS = miscellaneous species, OI = nonbreeding insectivores, RA = raptors, WS = nonbreeding seed-eaters. See Appendix for species allocations.

ANNUAL DIFFERENCES

Probably the most striking, best documented temporal change exhibited by the densities was the increase from 1971 to 1972 and into 1973. When comparing total numbers in a given month in 1971 with the total for the same month in 1972 on the same site, there were 16 increases in 1972 and only 2 decreases. For 1973 versus 1972 there were 11 increases and 2 decreases. These year-to-year increases occurred on all three sites and in virtually all categories (in fact, for most species), but not equally in all. With a few exceptions densities of breeding species and of other insectivores appeared to increase modestly in both years. Seemingly large increases in insectivorous migrants on the Bajada in May 1972 and on the Playa in August–September 1972 were perhaps exaggerated by sampling, which coincided with the height of a short-term wave of migrants. Decreases in May 1973 levels of breeding species on both Playa and Bajada were probably caused either by sampling errors or, more likely, by delay of the season as a result of an exceptionally cool spring; breeding densities in June and July of 1973 (data not included herein) appear to have been even higher than in 1972.

Censusing of raptors afoot, even in relatively large plots such as ours, is likely to involve large sampling errors; so for considerations of temporal changes we believe that the roadside counts giving relative numbers provided the most reliable data. Since the roadside census route was chosen to be representative of Jornada grasslands rather than of desert scrub, the results are biased toward grassland birds. However, for raptors this bias is probably minimal because most are wide-ranging and readily cross vegetation types in their foraging. In seeking explanations of the changes in densities of raptors we discovered that three subgroups of raptors behaved differently. Summer residents (Swainson's Hawk, Turkey Vulture) showed the usual pattern of progressive increase from 1971 to 1973, but mammal-eating winter residents (other buteos, Golden Eagles) decreased while other winter residents (Marsh Hawks and Prairie Falcons) increased (table 9).

By far the largest annual increases occurred in seed-eating birds. Great influxes of winter seed-eaters and of Mourning Doves occurred in late summer of 1972, and numbers and biomass remained generally high into the spring of 1973. These high levels of seed-eaters were especially notable on the Playa (fig. 3).

SEASONAL VARIATION

Attempts to discern seasonal patterns are somewhat confounded by year-to-year changes

TABLE 3. Monthly mean numbers of birds per 100 km² on the Playa.

Year	Species group[a]	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
1971	AQ					0.0		0.0	0.0				0.0
	BS					64.1		51.9	49.1				4.6
	DQ					4.5		39.9	62.0				1.8
	MS					2.1		2.9	0.0				0.0
	OI					23.7		0.0	5.7				0.0
	RA					0.0		0.0	2.9				2.9
	WS					11.3		14.4	0.0				95.9
	Total					104.8		109.1	119.7				105.2
1972	AQ	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	181.4	0.0	0.0	0.0
	BS	19.7	17.0	31.9	14.3	88.5	71.4	75.5	48.4	14.9	11.0	14.5	3.7
	DQ	0.0	0.0	0.0	3.7	7.3	25.3	20.9	427.6	533.3	210.2	260.8	125.8
	MS	0.0	4.8	3.1	9.5	6.9	1.9	0.0	19.0	27.9	7.0	0.0	0.0
	OI	0.0	0.0	1.5	7.1	11.3	2.9	6.8	34.2	40.9	9.5	0.0	0.0
	RA	0.0	0.0	0.7	2.9	7.4	0.0	0.0	1.9	4.3	0.0	7.1	3.8
	WS	19.3	33.4	20.9	22.0	0.0	13.9	14.8	191.0	704.7	755.7	543.5	860.9
	Total	39.0	55.2	58.1	59.5	121.4	115.4	118.0	722.1	1507.4	993.5	825.9	994.2
1973	AQ	17.1	0.0	0.0	0.0	0.0							
	BS	0.0	1.8	30.2	99.8	49.3							
	DQ	1035.4	109.0	155.7	38.1	136.9							
	MS	0.0	0.0	9.5	0.0	1.1							
	OI	0.0	25.0	0.0	9.6	16.7							
	RA	8.6	2.9	5.7	0.0	1.7							
	WS	209.2	303.3	34.6	385.4	121.4							
	Total	1270.3	442.0	235.7	532.9	327.1							

[a] AQ = aquatic and semiaquatic species, BS = breeding species, DQ = doves and quail, MS = miscellaneous species, OI = nonbreeding insectivores, RA = raptors, WS = nonbreeding seed-eaters. See Appendix for species allocations.

already described, but some consistent patterns are apparent (bottom rows of tables 2–8). The Grassland contained higher overall densities in the nonbreeding season than in the breeding season. (The roadside counts showed this pattern for Jornada grasslands more obviously than did the plot censuses, probably because they are less subject to large variations in numbers due to large and highly mobile flocks which are common in winter.) The contrast between autumn and winter densities and those of the breeding seasons was especially marked in 1972–1973. In those years the Playa also had much higher densities in the nonbreeding season. For both areas the large numbers of the nonbreeding season were accounted for by seed-eating birds such as Mourning Doves, Horned Larks, Lark Buntings, Brewer's Sparrows, and Sage Sparrows. Influxes of nonbreeding insectivores occurred in migratory periods in spring and autumn, but their effects on overall totals were swamped by the seed-eaters. Contributions by breeding species that are resident were similarly negligible in the nonbreeding season. Raptors followed a peculiar pattern that will be discussed beyond; their effects on overall totals were mainly to obscure consistencies evident in other groups.

Seasonal variations on the Bajada and on the Playa until autumn 1972 were much narrower. Winter densities were low relative to those of breeding seasons; large flocks of seed-eaters did not appear. As with the Grassland area, migrant insectivores played minor roles. Minor peaks in the autumn (October–November 1971; August–October 1972) were in part due to influxes of seed-eaters at the end of the breeding season, but these birds did not persist through the winter. On the Bajada, resident members of the breeding avifauna were relatively important in winter.

In summary, the general seasonal changes on the Grassland site and on the Playa in the last two-thirds of the study were similar, with markedly higher densities in autumn and winter, whereas those of the Bajada and of the Playa in the first year were weak and different in timing. The overriding influence on the patterns seems to have been the degree to which a given area contained numbers of seed-eating birds in the nonbreeding season.

COMPARISONS OF SITES

Except in the winter of 1971, for most groups for most seasons the Playa supported highest numbers and biomass, although differences between Playa and Bajada insectivores were not

TABLE 4. Monthly mean numbers of birds per 100 km² on the Grassland.

Year	Species group[a]	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
1971	BS					14.9	5.0	8.9	0.0	11.8	4.5	10.3	
	DQ					0.5	0.0	0.0	0.0	0.0	0.0	0.0	
	MS					0.0	0.0	0.0	0.0	0.0	0.0	0.0	
	OI					0.0	0.0	0.0	0.0	0.0	0.0	0.0	
	RA					0.0	0.0	0.7	0.0	1.4	2.5	2.2	
	WS					0.0	0.0	0.0	0.0	796.3	46.0	207.5	
	Total					15.4	5.0	9.6	0.0	809.5	52.0	220.0	
1972	BS		4.3	3.3	5.2	12.1	14.6	19.0	9.7	8.8		7.3	3.3
	DQ		0.0	0.0	3.8	25.8	20.5	8.9	0.0	2.4		0.0	8.5
	MS		0.0	0.0	0.5	0.0	1.2	0.0	3.5	21.0		0.0	0.0
	OI		1.2	4.8	2.4	0.7	0.0	0.5	3.5	3.5		0.0	0.0
	RA		0.7	0.0	1.4	0.3	1.5	0.0	2.8	5.6		1.0	0.4
	WS		234.4	4.8	0.0	0.0	0.0	0.0	37.5	155.7		459.5	254.8
	Total		240.6	12.9	13.3	38.9	37.8	28.4	57.0	197.0		467.8	267.0
1973	BS	2.7	3.4	0.0	3.9	8.9							
	DQ	15.8	0.0	2.8	4.8	6.1							
	MS	0.0	0.0	0.0	0.0	0.0							
	OI	0.0	11.2	0.0	5.6	0.0							
	RA	1.4	8.4	5.6	2.8	0.0							
	WS	550.3	427.0	182.0	132.2	65.5							
	Total	570.2	450.0	190.4	149.3	80.5							

[a] See table 2 for abbreviations.

great (fig. 4). Grassland and Bajada sites exhibited some interesting differences. Insectivores were never abundant on the Grassland, but they were relatively dense on the Bajada in summer and autumn (fig. 4). Conversely, seed-eaters were denser on the Grassland than on the Bajada in winter (fig. 3).

DISCUSSION

Our primary goal here is to explain three sorts of variations in density: (1) among sites representing different types of ecosystems, (2) among years, and (3) among seasons. In order to approach these three, we must also explain a fourth: variation among general ecological subgroups comprising the overall bird communities. Complex interactions exist among these different sorts of variation.

Variations in densities did exhibit some important consistencies: (1) the Playa exhibited the highest densities in most groups in most seasons (except winter 1971), but Playa and Bajada insectivores did not differ greatly; (2) insectivores were more important and denser on the Bajada than on the Grassland site, while the seed-eaters were denser on the Playa and Grassland; (3) the Grassland supported higher densities in the nonbreeding season than in the breeding season, the higher densities being accounted for by wintering seed-eaters; the Playa exhibited a similar pattern in 1972–73;

prior to autumn 1972 the Bajada and the Playa showed little seasonal variation in overall density; (4) densities generally increased from 1971 through 1972 and into 1973; and (5) raptors varied in a complex pattern comprehensible only by subdividing them into three groups of species.

COMPARISONS WITH OTHER AREAS

There are few year-round investigations of densities in grassland or desert bird communities. Finzel (1964) censused birds on two 20-acre (8.1-ha) plots in each of four grassland types in Wyoming (41°N, 105°W) in three breeding seasons and the intervening months. Nonbreeding periods were divided into "postbreeding season" and "winter." Densities dropped strikingly from the breeding season to winter. In five out of seven cases postbreeding density was intermediate between those of the preceding breeding season and the following winter. Breeding season densities on the shortgrass and mixed-grass prairie sites varied from 308 to 574 birds per km², while those of the winter were 10 to 19 birds per km². Variation among the three consecutive breeding seasons was slight. The high breeding season densities, the consistency and regularity of temporal changes, and the great contrast between summer and winter densities may well be typical of north temperate grass-

TABLE 5.   Monthly mean standing crop biomass (g live weight · ha⁻¹) of birds on the Bajada.

Year	Species group[a]	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
1971	BS			5.5	2.0	8.9	16.3	6.6		3.3	7.9	2.4	
	DQ			0.0	0.0	0.0	0.0	2.6		0.0	53.7	46.0	
	MS			3.9	0.0	0.1	0.3	2.6		0.0	1.2	0.7	
	OI			0.9	0.0	1.0	6.0	1.9		0.9	3.1	0.0	
	RA			0.0	0.0	0.0	0.0	0.0		2.2	14.5	21.7	
	WS			0.0	0.0	0.7	0.3	0.4		0.7	11.7	16.4	
	Total			10.3	2.0	10.7	22.9	14.1		7.1	92.1	87.2	
1972	BS		3.5	4.7	6.1	22.1	22.1	18.1	13.1	28.0	19.9	8.4	15.1
	DQ		0.0	1.9	7.7	21.8	2.6	3.8	132.2	28.7	0.0	7.7	21.1
	MS		0.3	0.0	7.2	3.2	0.9	0.0	4.8	150.8	8.6	1.9	4.3
	OI		0.0	0.0	0.0	9.3	1.7	1.1	1.7	0.7	5.5	0.8	0.9
	RA		0.0	0.0	0.0	7.0	0.0	0.0	0.0	6.6	43.7	21.9	0.0
	WS		3.9	0.4	2.6	1.3	0.0	2.1	13.5	5.3	33.2	15.1	5.4
	Total		7.7	7.0	23.6	64.7	27.3	25.1	165.3	220.1	110.9	55.8	46.8
1973	BS	14.2	5.2	7.7		13.8							
	DQ	0.0	3.8	52.4		85.1							
	MS	4.3	2.1	1.4		0.3							
	OI	0.0	0.6	0.6		4.4							
	RA	0.0	0.0	0.0		0.0							
	WS	15.4	28.1	30.3		8.9							
	Total	33.9	39.8	92.4		112.5							

[a] See table 2 for abbreviations.

land bird communities; certainly they are characteristics not exhibited on our study areas.

Southeast of Finzel's study areas is the Pawnee shortgrass prairie study area (41°N, 104°W) of the US/IBP Grassland Biome. From 1968–71 Ryder (1972) made counts in six 20-acre (8.1-ha) plots and on a roadside route similar to ours; these counts were made weekly in the late spring and summer and biweekly or monthly during the remainder of the year. The pattern for overall numbers (= total individuals of all species) roughly parallels that of the Wyoming grasslands, but with some important variations. In addition to the peaks in the breeding seasons (May–July), in 3 of the 4 years peaks occurred in February due to high numbers of Horned Larks. A similar situation prevailed in relative numbers in autumn; during years in which the usual autumn peaks of Horned Lark numbers were unusually high, the overall numbers showed secondary peaks at that season. In 1969 the overall numbers were unusually high in May, July, and August. Likewise, in 1969 unusually high densities of Western Meadowlarks in September prolonged the summer period of high total numbers. These changes present some parallels with those on the Jornada—particularly the Playa and Grassland sites—as follows: (1) some striking changes from year to year in both actual levels of density and seasonal pattern and (2) high densities in at least some periods of the nonbreeding season. On the other hand, whereas the high nonbreeding densities on the Pawnee reached only moderate levels (relative to those of breeding season), did not occur every year, and were of short duration, those on the Jornada sites were on the average very high relative to breeding season densities, more frequent, and longer in duration. Horned Larks and Lark Buntings were at times important members of the nonbreeding season communities in both areas, but other species were also important on the Jornada. Comparative data on absolute (vs. relative) densities are available only for the breeding season. On two Pawnee study areas during 4 years the breeding density varied between 185 and 393 birds per km². These figures are somewhat lower than those reported by Finzel (1964) for Wyoming grasslands, but are much higher than those for the Jornada, where breeding densities on the Grassland site did not exceed 40 birds per km², the range for the Playa was 105–121 birds per km², and that for the Bajada was about 52 birds per km².

Other comparative data are available for the Santa Rita and Silverbell Sites (32°N, 111°W) of the US/IBP Desert Biome in the Sonoran Desert near Tucson, Arizona (Russell et al. 1972, Russell et al. 1973, S. M. Russell,

TABLE 6. Monthly mean standing crop biomass (g live weight · ha^{-1}) of birds on the Playa.

Year	Species group[a]	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
1971	AQ					0.0		0.0	0.0				0.0
	BS					19.5		20.4	26.1				3.3
	DQ					7.5		59.9	78.9				2.2
	MS					0.4		1.1	0.0				0.0
	OI					2.7		0.0	0.6				0.0
	RA					0.0		0.0	8.3				122.9
	WS					2.5		1.1	2.8				19.9
	Total					32.6		82.5	116.7				148.3
1972	AQ	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	546.1	0.0	0.0	0.0
	BS	11.1	5.2	16.9	7.1	38.0	27.7	33.9	18.0	5.7	3.5	6.2	1.4
	DQ	0.0	0.0	0.0	4.3	12.1	43.1	25.4	516.0	629.3	248.0	307.7	149.4
	MS	0.0	1.2	1.4	1.9	2.7	0.7	0.0	7.4	15.1	5.1	0.0	0.0
	OI	0.0	0.0	0.4	1.3	1.3	1.3	2.9	5.9	6.4	0.6	0.0	0.0
	RA	0.0	0.0	3.7	3.3	95.3	0.0	0.0	24.7	18.0	0.0	14.4	16.2
	WS	4.1	6.7	2.5	2.6	0.0	5.0	2.8	62.3	216.7	243.8	146.5	259.5
	Total	15.2	13.1	24.9	20.5	149.4	77.8	65.0	634.3	1437.3	501.0	474.8	426.5
1973	AQ	48.7	0.0	0.0	0.0	0.0							
	BS	0.0	0.0	11.8	42.7	22.3							
	DQ	1221.8	128.6	183.7	50.8	162.6							
	MS	0.0	0.0	1.9	0.0	0.4							
	OI	0.0	7.8	0.0	0.7	2.4							
	RA	44.7	9.4	6.6	0.0	7.2							
	WS	42.3	88.2	6.1	122.1	49.4							
	Total	1357.5	234.0	210.1	216.3	244.3							

[a] See table 3 for abbreviations.

pers. comm.). For the Santa Rita Site total census results are available from April–November 1970, January–September 1971, and February–December 1972. In 1970 and 1971 lowest densities were in May–July; in 1972 they were in February–April. Highest densities were in winter in 1971 and in fall in 1970 and 1972. Winter densities were several times higher than those of breeding seasons (1751 birds per km^2 in January 1971 vs. 289 in July 1971). As on the Jornada sites, the high nonbreeding densities were largely accounted for by seed-eaters. Differences between years were considerable; in both absolute levels and in timing of changes. For the Silverbell Site results are available for a shorter period (June 1971–November 1972). Much less variation occurred, both between seasons and between years, and levels were lower than on the Santa Rita Site. Highest densities occurred in autumn and winter, but the seasonal trend was not as striking as on the Santa Rita. The highest total monthly density on the Santa Rita Site was very little higher than the maximum on the Jornada Playa, but the lowest on the Tucson sites (148 birds per km^2, June 1971, Silverbell) was higher than most monthly site totals for the Jornada; in general, densities on

both Tucson sites were higher than those on all three Jordana sites.

Webster (1964) censused birds in two plots in the southern Chihuahuan Desert in Zacatecas, México, both in the winter and the breeding season of 1964. One of the plots was in a desert scrub community, and the other grassland. Overall densities were as follows: scrub breeding season, 578 per km^2; scrub winter, 247 per km^2; grassland breeding season, 65 per km^2; and grassland winter, 578 per km^2.

Comparisons among all five areas—Wyoming, Pawnee, Jornada, Tucson, and Zacatecas—reveal some trends. From Wyoming through Pawnee to Jornada and Tucson there was a progressive decrease in relative magnitude of breeding season densities and an increase in autumn and winter densities. The Santa Rita densities were much higher in the nonbreeding months, as they were in the Zacatecas grassland and those of the Jornada Grassland and the Playa in 1972–73. The Tucson Silverbell Site, the Jornada Bajada, and the Jornada Playa in 1971–72 exhibited an essentially nonseasonal pattern of variation in total numbers. The overall seasonal trend is obviously correlated with latitude and severity

TABLE 7.   Monthly mean standing crop biomass (g live weight · ha^{-1}) of birds on the Grassland.

Year	Species group[a]	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
1971	BS					4.4	2.2	3.7	0.0	5.8	2.2	6.3	
	DQ					0.6	0.0	0.0	0.0	0.0	0.0	0.0	
	MS					0.0	0.0	0.0	0.0	0.0	0.0	0.0	
	OI					0.0	0.0	0.0	0.0	0.0	0.0	0.0	
	RA					0.0	0.0	7.2	0.0	2.2	11.0	2.4	
	WS					0.0	0.0	0.0	0.0	264.7	14.3	58.7	
	Total					5.0	2.2	10.9	0.0	272.7	27.5	67.4	
1972	BS		2.3	1.3	2.6	5.2	6.6	8.4	4.2	4.3		1.9	0.6
	DQ		0.0	0.0	4.3	28.9	23.0	10.0	0.0	2.7		0.0	9.5
	MS		0.0	0.0	3.5	0.0	0.1	0.0	0.2	16.8		0.0	0.0
	OI		0.5	1.7	0.5	0.2	0.0	0.3	0.7	0.7		0.0	0.0
	RA		3.7	0.0	1.6	2.9	14.4	0.0	28.2	6.5		3.1	3.5
	WS		71.8	0.6	0.0	0.0	0.0	0.0	7.5	31.2		160.1	90.4
	Total		78.3	3.6	12.5	37.2	44.1	18.7	40.8	62.2		165.1	104.0
1973	BS	1.4	0.0	0.0	3.9	4.0							
	DQ	17.6	0.0	3.1	5.4	6.8							
	MS	0.0	0.0	0.0	0.0	0.0							
	OI	0.0	3.2	0.0	1.0	0.0							
	RA	9.0	163.1	31.9	14.6	0.0							
	WS	166.3	168.9	21.9	24.0	23.1							
	Total	194.3	335.2	56.9	49.0	33.9							

[a] See table 2 for abbreviations.

of winter climate, and its underlying cause is related to this climatic trend. This trend may be reversed in the case of Zacatecas desert scrub, where in 1964 the breeding season density was twice as high as that in the winter. A combination of mild, dry winter and summer rains is perhaps the cause of this variation.

Differences between years appear to have been greater at Tucson and Jornada than at the two northern two areas. This difference between the two desert areas on the one hand and the two grasslands on the other may be related to the high variation in productivity of desert ecosystems in response to variations in rainfall (Noy-Meir 1973).

Another difference among areas is that between the Jornada and the other areas in overall levels of total density. The ecosystems of the Jornada are more arid and almost certainly less productive than those of the other areas, and we probably need search no further than this difference for a first-order explanation for the difference in levels of bird density.

FOOD AS A CAUSATIVE FACTOR

Although some of the spatial and temporal variation is obviously related to climate, it is unlikely that climatic factors exerted manifold direct effects on bird populations. Food is likely to be the most important direct governing factor. To analyze the influence of food,

we treat the following bird trophic categories separately: raptors, seed-eaters, and insectivores.

Raptors. The raptors of the Jornada fall into several categories. In the winter they include predominantly mammal-eating eagles and buteos (Red-tailed and Ferruginous hawks), plus Prairie Falcons and Marsh Hawks, which our observations and Bent (1937) suggest are significant bird predators. During the summer the commonest raptor was the Swainson's Hawk, which our observations suggest preys heavily on lizards. Mammal densities crashed during December and January of 1971–72 on the Playa and the Bajada sites and probably on the Grassland site. In the subsequent winter the density of mammals was considerably reduced from the pre-crash period (Pimm and Whitford 1973, Ludwig and Whitford 1974). This was undoubtedly the cause of the reduction in the mammal-eating raptors. Infrequent mammal sampling and the low monthly totals of buteos and eagles make it impossible to compute a meaningful statistical correlation. Bird numbers, however, were higher in the winter of 1972–73 (table 9), and this was reflected in an increase in Prairie Falcons and Marsh Hawks as well as in our increased observations of Cooper's and Sharp-shinned hawks off the study areas. Swainson's Hawk numbers during the summer months were con-
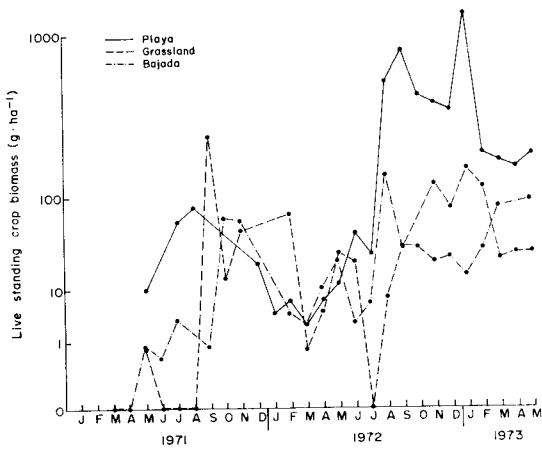
FIGURE 3. Changes in biomass of seed-eating birds on the three Jornada sites, 1971–1973. Biomass data have been transformed by a quartic root in order to more clearly show changes over several orders of magnitude.
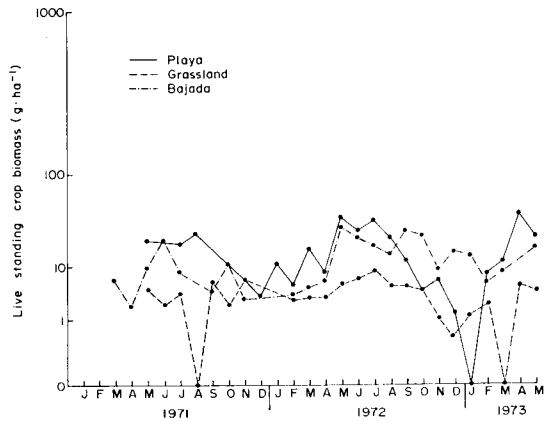

FIGURE 4. Changes in biomass of insectivorous birds on the three Jornada sites, 1971–1973. Biomass data have been transformed by a quartic root in order to more clearly show changes over several orders of magnitude.

stant in all years, but during the autumn of 1972 large numbers passed through the area, suggesting that the breeding season had been unusually successful. The greater abundance of lizards in 1972 on our sites is consistent with this observation.

Seed-eaters. Though seed-eating birds showed the most marked changes, the difference in seed production on the three areas between 1971 and 1972 (table 10) was not so dramatic. In table 10 the numbers refer to kg of total reproductive material rather than just seeds; thus in species like *Cryptantha crassisepala* much of the high production in 1972 on the Grassland was not seeds. The seeds of *Xanthium strumarium* and *Gutierrezia sarothrae*, which were so abundant, are not a resource for birds because they are extremely small. Less easily explained is the fact that despite the abundance of *Larrea* seed on the Bajada, seed-eating birds were least abundant there. Birds apparently cannot use *Larrea* even when the seeds are numerous; creosotebush bajadas are well-known for their depauperate bird faunas (Dixon 1959, Raitt and Maze 1968, Austin 1970).

With these provisions the Grassland site produced more seeds than the other sites, and this was reflected in the number of seed-eating birds there during the winter. Seed production was greater on the Grassland in 1972 than in 1971; though peak seed-eating bird numbers were not higher in 1972 than in 1971, seed-eating birds were present for a much longer period of time. Seed production on the Bajada both years—if *Larrea* is excluded—

was low, as were the numbers of seed-eating birds.

At the Playa site in 1972, a great many seed-eating birds were present, but seed production was no higher than in 1971. Rodent populations declined drastically during late winter 1971–72 (Pimm and Whitford 1973) and consumption of seeds by rodents was reduced at least one-half during the winter of 1972–73 as compared with the previous winter (Ludwig and Whitford, in press). More seeds were thus available to the birds. Of more significance was the flooding of the Playa during the autumn of 1972. Although this resulted in only a small input of seeds into the Playa system as a whole, the distribution of seeds was changed drastically. Measurements of seed density on the ground showed that nearly all the seeds produced on the playa fringe were washed down toward the playa bottom, resulting in large piles of seed. These local concentrations of seeds were readily and rapidly exploited by Mourning Doves, Lark Buntings, and other migrant buntings. It seems likely that in desert systems where seeds are widely dispersed and of relatively low density, the cost to a bird of acquiring a seed is close to the energy content of that seed. In many cases it must be uneconomical for a bird to exploit seed resources unless the distribution of the seeds is markedly changed by such factors as sheet flow during heavy rains. This suggests that the seed-eating birds should be highly clumped, reflecting the distribution of their food supply. Analysis of the 30 roadside stops does indicate clumping, which changed from year to year. Areas heavily utilized in the winter of 1971–72 were not utilized in the winter

TABLE 8. Monthly total numbers of birds counted on 2-day roadside censuses.

Year	Species group[a]	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
1971	BS					52	46	14	64	16	28	32	14
	DQ					4	3	23	5	0	21	0	0
	MS					0	0	1	2	0	33	0	
	OI					0	0	2	0	2	0	1	0
	RA					3	6	3	5	8	12	17	10
	WS					0	0	4	88	59	566	411	1841
	Total					59	55	47	164	85	660	461	1864
1972	BS	9	12	6	12	43	66	61		34	23	7	14
	DQ	4	0	0	2	17	20	45		84	27	16	112
	MS			3		0	0	4		12	2	1	0
	OI	2	18	2	14	9	0	0		4	0	1	8
	RA	5	9	5	3	1	2	9		29	11	6	4
	WS	587	535	26	46	1	0	20		1029	1328	1392	828
	Total	607	574	39	80	71	88	139		1192	1391	1423	966
1973	BS	15	15	20	54	74							
	DQ	49	10	2	26	99							
	MS	0	1	0	0	2							
	OI	0	8	34	0	0							
	RA	6	3	11	4	3							
	WS	1113	371	353	609	0							
	Total	1183	408	420	693	178							

[a] See table 2 for abbreviations.

of 1972–73. Counts of annuals at various sites in the spring of 1973 suggested that in areas where birds had been present there were fewer annuals. We suggest that birds respond only to dense aggregations of seeds and that they feed on these in a density-dependent manner. This leads to a pattern of over-dispersion of the annuals.

Insectivores. The insectivorous birds were less clearly related to their food supply. Figures 5, 6, and 7 show the density of insects sampled by a D-vac technique (Southwood 1966) from the three sites and the corresponding numbers of breeding birds (Pimm et al., unpubl. data; Ellstrom 1973). Only breeding bird species were considered; the migrant insectivores contributed little to the totals other than at migration periods when the presence of individuals on the site was probably brief and of little importance.

Insect and bird numbers on the Playa were clearly correlated (fig. 5). Numbers of insects and birds on the Grassland were not correlated (fig. 7); insect numbers remained rather constant throughout. The data for the Bajada show a negative correlation (fig. 6).

The relationships for the Playa and the Grassland may be spurious. The numerically dominant insects there were small forms such as ants and homopterans, whereas our studies of the food supplied to young Western Kingbirds, Loggerhead Shrikes, Crissal Thrashers, and Cactus Wrens suggested that by far the most important food source was grasshoppers.

TABLE 9. Annual differences in raptor populations (mean number seen per roadside census ± SE) and their food supply.

Species or Group	May–October 1971	October–March 1971–1972	May–October 1972	October–March 1972–1973
Raptors				
Swainson's Hawk	3.0 ± 0.20		7.6 ± 1.88	
Prairie Falcon		1.0 ± 0.20		1.4 ± 0.23
Marsh Hawk				
Buteo spp.		5.7 ± 0.97		3.2 ± 0.36
Golden Eagle				
Prey animals				
Lizards	317 g · ha⁻¹		431 g · ha⁻¹	
Birds		390 g · km⁻²		1170 g · km⁻²

TABLE 10. Biomass (kg · ha^{-1} dry weight) of plant reproductive parts in 1971 and 1972.

Species	Grassland		Playa		Bajada	
	1971	1972	1971	1972	1971	1972
Grasses						
Bouteloua barbata Lag.	3.04	1.31	0.01	0.74	0.00	0.00
Erioneuron pulchellum (H.B.K.) Tateoka	0.25	5.10	0.01	0.42	0.00	0.17
Hilaria mutica (Buckl.) Benth.	0.00	0.00	7.82	2.35	0.00	0.00
Panicum obtusum H.B.K.	0.00	0.00	10.00	5.00	0.00	0.00
Sporobolus flexuosus (Thurb.) Rydb.	0.94	10.45	0.00	0.00	0.00	0.00
Others	5.29	5.54	0.04	0.10	0.01	0.01
Shrubs						
Gutierrezia sarothrae (Pursh.) Britt. & Rusby	0.43	0.64	6.66	5.74	42.00	35.00
Larrea divaricata Cav.					160.00	55.00
Xanthium strumarium L.	0.00	0.00	94.50	0.30	0.00	0.00
Others	0.00	0.00	0.00	0.00	0.10	0.10
Forbs						
Allionia incarnata L.	0.97	11.64	0.01	8.21	0.00	0.00
Amaranthus spp.	0.00	0.12	0.04	2.08	0.00	0.00
Aphanostephus ramossissimus DC.	0.00	8.71	0.00	0.00	0.00	0.00
Baileya multiradiata Harv. & Gray	0.00	3.64	0.00	0.00	0.00	0.00
Cassia bauhinioides Gray	2.25	10.34	0.00	0.00	0.00	0.00
Chenopodium incanum (S. Wats.) Heller	0.00	1.63	0.00	0.24	0.00	0.00
Croton pottsii (Klotsch) Muell.-Arg.	1.02	2.93	0.00	0.04	0.00	0.00
Cryptantha crassisepala (T. & G.) Greene	9.23	176.10	0.00	0.00	0.00	0.00
Dithyraea wislizeni Engelm.	0.00	6.22	0.00	0.00	0.00	0.00
Eriogonum spp.	0.00	8.25	0.00	3.13	0.00	0.38
Euphorbia serrula Engelm.	0.00	0.00	0.01	1.18	0.01	0.00
Hoffmanseggia spp.	0.62	2.00	0.00	0.00	0.00	0.00
Hymenoxys odorata DC.	0.00	0.00	3.67	4.40	0.00	0.00
Kallstroemia hirsutissima Vail	3.63	0.76	0.00	0.00	0.00	0.00
Krameria lanceolata Torr.	0.00	1.50	0.00	0.00	0.00	0.00
Lepidium eastwoodiae Woot.	0.00	1.27	0.00	0.00	0.00	0.00
Mentzelia albicaulis Dougl.	0.00	1.06	0.00	0.00	0.00	0.00
Oenothera runcinata (Engelm.) Munz	0.00	2.49	0.00	0.00	0.00	0.00
Pectis papposa Harv. & Gray	3.62	8.40	0.00	0.00	0.00	0.00
Portulaca spp.	3.29	0.34	0.01	0.28	0.00	0.00
Psilostrophe tagetina (Nutt.) Greene	0.02	2.70	0.00	0.00	0.00	0.00
Salsola kali L.	0.30	3.26	0.00	0.01	0.00	0.00
Sida leprosa (Ort.) K. Shum.	0.00	0.00	1.70	0.00	0.00	0.00
Sphaeralcea coccinea (Pursh.) Rydb.	3.40	0.75	0.00	0.00	0.00	0.00
Tidestromia lanuginosa (Nutt.) Standl.	8.64	7.30	0.01	1.45	0.01	0.00
Others	10.92	7.55	0.01	7.55	0.01	1.43
Total	57.86	292.00	124.50	43.22	202.14	92.10
Total available[a]	48.20	115.26	23.34	37.18	0.14	2.09

[a] See text (subtract *Larrea*, *Gutierrezia*, *Xanthium*, and *Cryptantha*).

The only birds found feeding on smaller insects were Verdins, gnatcatchers, and Black-throated Sparrows—species dominant on the Bajada where they tended to nest early in the year (April and May), coincident with the peak of the smaller insects there. Grasshopper numbers, estimated by other techniques (Pimm et al., unpubl.) and not included in figures 5, 6, and 7, were smaller on the Bajada (where there were fewer of the larger insectivores) than on the Playa; in both places they tended to peak during July and August, coincident with the height of the breeding season of the larger species. Numbers of grasshoppers
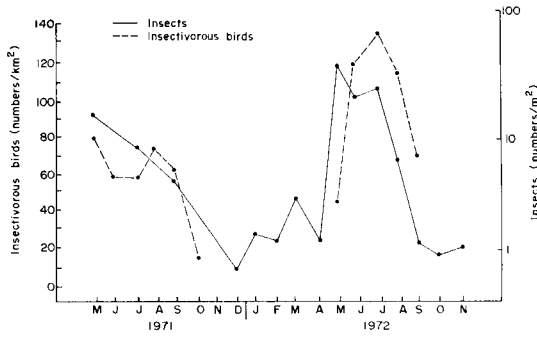
FIGURE 5. Insectivorous birds and insects on the Playa site, May 1971–November 1972.

FIGURE 6. Insectivorous birds and insects on the Bajada site, May 1971–November 1972.

were not independently estimated on the Grassland site. The bird × small insect correlations observed for the Playa and the Grassland sites may reflect the synchrony on these two sites between the various groups of insects. On the Playa, independently censused ground arthropods, grass arthropods, shrub arthropods, and the larger insects such as grasshoppers all peaked at the same time. The peak densities of grasshoppers on the Playa reached only about 0.1 per m², a density too low to be detected by D-vac sampling. However, at this density their standing crop biomass was considerably greater than the numerically more abundant ants and homopterans. Clearly any analysis of the insect-bird interaction must take into account the energy content of the insect food, as well as the increased demand on the food supply by the young in the nest.

Though simple relations cannot be drawn, there are interesting parallels with the raptors and seed-eaters and their food supplies discussed above. First, the insectivorous bird species must be grouped by the food selected before correlations can be expected. Second, the availability of food is determined by the density of sufficiently worthwhile items to make exploitation of the resource economically possible. Small insects and seeds may be economically unfeasible at low densities due to their small energy content per individual. Thus, the bird-insect and bird-seed interactions are probably characterized by a marked threshold effect. In view of these strong indications that food supply was responsible for most of the variation within and among the Jornada sites, the differences between bird communities of the Jornada and other desert and grassland regions are probably at least partially under the control of food supplies and their variation.

In conclusion, it appears that although food may be crucially important in determining the
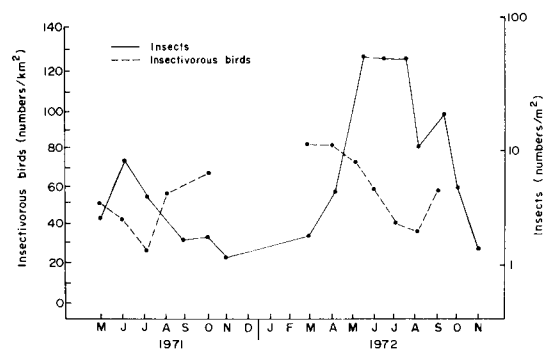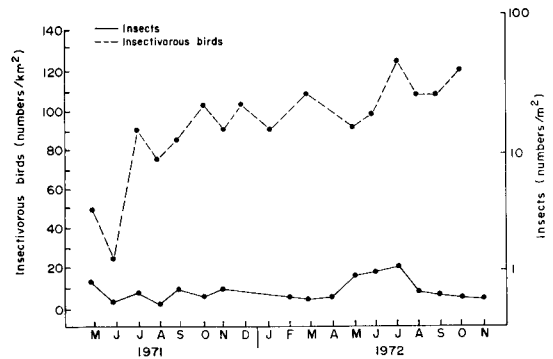

FIGURE 7. Insectivorous birds and insects on the Grassland site, May 1971–November 1972.

number of birds in desert and grassland communities, its availability is modified by a variety of factors. These include: (1) competition from other taxonomic groups at a similar trophic level; (2) insufficient density of the food items to make exploitation economical; and (3) unknown or poorly understood factors such as the failure of birds to exploit creosotebush seeds.

SUMMARY

This paper presents a summary of monthly census data for all the avian species occurring on three desert and grassland sites in southern New Mexico. To obtain absolute density estimates of birds, raw data were corrected using a coefficient of detection. To simplify interpretation, the data were grouped into ecologically similar groups of species. Trends within and between years are discussed. The Grassland showed considerably more birds, principally seed-eaters, in the winter than in the breeding season. These remained longer in 1972–73 than in the previous year. The Playa had more insectivores in the summer, but its flooding in the autumn of 1972 caused

a considerable increase in doves and other seed-eaters which persisted through the winter. The Bajada had its peak numbers during the breeding season, but the insectivores present were many fewer than the numbers of seed-eaters present at the other sites during the winter. Comparison of these areas with other grassland and desert data show an increasing dominance of winter numbers in the southern sites.

The number of birds was related to food supply but the relationship was complicated by three factors. (1) The availability of food may be modified by the presence of competitive groups, such as rodents, for seeds. (2) The distribution of food items may be such that it may be uneconomical to exploit these resources unless the items achieve sufficient densities (e.g., flash flooding in autumn can dramatically change the distribution of seeds). (3) Certain items may be unexploitable because of their size (e.g., small insects) or for unknown reasons (in the case of creosotebush seeds).

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Department of Biology, New Mexico State University, Las Cruces, New Mexico 88003. Present address of second author: Department of Biological Sciences, Texas Tech University, Lubbock, Texas 79409. Accepted for publication 22 April 1975.

APPENDIX. Systematic list of species with ecological category designations[a].

Scientific Name	Common Name	Category
Accipiter cooperii	Cooper's Hawk	RA
A. striatus	Sharp-shinned Hawk	RA
Actitis macularia	Spotted Sandpiper	AQ
Aeronautes saxatalis	White-throated Swift	OI
Aimophila cassinii	Cassin's Sparrow	BS
Amphispiza belli	Sage Sparrow	WS
A. bilineata	Black-throated Sparrow	BS[b]
Anas acuta	Pintail	AQ
A. americana	American Wigeon	AQ
A. crecca	Green-winged Teal	AQ
A. discors	Blue-winged Teal	AQ
Anthus spinoletta	Water Pipit	OI
A. spragueii	Sprague's Pipit	OI
Aphelocoma coerulescens	Scrub Jay	MS
Aquila chrysaetos	Golden Eagle	RA
Auriparus flaviceps	Verdin	BS
Bartramia longicauda	Upland Sandpiper	MS
Buteo jamaicensis	Red-tailed Hawk	RA
B. regalis	Ferruginous Hawk	RA
B. swainsoni	Swainson's Hawk	RA
Calamospiza melanocorys	Lark Bunting	WS
Calcarius mccownii	McCown's Longspur	WS
C. ornatus	Chestnut-collared Longspur	WS
Calidris mauri	Western Sandpiper	AQ
Callipepla squamata	Scaled Quail	DQ
Campylorhynchus brunneicapillus	Cactus Wren	BS
Carpodacus mexicanus	House Finch	WS
Cathartes aura	Turkey Vulture	RA
Catharus ustulatus	Swainson's Thrush	MS
Charadrius vociferus	Killdeer	AQ
Chlorura chlorura	Green-tailed Towhee	WS
Chondestes grammacus	Lark Sparrow	WS
Chordeiles acutipennis	Lesser Nighthawk	OI
C. minor	Common Nighthawk	OI
Circus cyaneus	Marsh Hawk	RA
Colaptes auratus	Common Flicker	MS
Contopus sordidulus	Western Wood Peewee	OI
Corvus cryptoleucus	White-necked Raven	RA
Dendrocopos scalaris	Ladder-backed Woodpecker	MS
Dendroica coronata	Yellow-rumped Warbler	OI
D. petechia	Yellow Warbler	OI
D. townsendi	Townsend's Warbler	OI
Empidonax difficilis	Western Flycatcher	OI
Eremophila alpestris	Horned Lark	WS
Eugenes fulgens	Rivoli's Hummingbird	MS
Falco mexicanus	Prairie Falcon	RA
F. sparverius	American Kestrel	RA
Geococcyx californianus	Roadrunner	RA
Guiraca caerulea	Blue Grosbeak	WS
Gymnorhinus cyanocephalus	Pinyon Jay	MS
Hirundo rustica	Barn Swallow	OI
Icterus parisorum	Scott's Oriole	BS
Junco sp.	Junco sp.	WS
Lanius ludovicianus	Loggerhead Shrike	BS
Limnodromus scolopaceus	Long-billed Dowitcher	AQ
Megaceryle alcyon	Belted Kingfisher	AQ

APPENDIX. *Continued.*

Scientific Name	Common Name	Category
Melospiza lincolnii	Lincoln's Sparrow	WS
Mimus polyglottos	Mockingbird	BS
Molothrus ater	Brown-headed Cowbird	MS
Myiarchus cinerascens	Ash-throated Flycatcher	BS
Numenius americanus	Long-billed Curlew	MS
Oporornis tolmiei	Macgillivray's Warbler	OI
Oreoscoptes montanus	Sage Thrasher	OI
Passerculus sandwichensis	Savannah Sparrow	WS
Petrochelidon pyrrhonota	Cliff Swallow	OI
Pheucticus melanocephalus	Black-headed Grosbeak	WS
Pipilo erythrophthalmus	Rufous-sided Towhee	WS
P. fuscus	Brown Towhee	WS
Piranga ludoviciana	Western Tanager	OI
Polioptila melanura	Black-tailed Gnatcatcher	BS
Pooecetes gramineus	Vesper Sparrow	WS
Regulus calendula	Ruby-crowned Kinglet	OI
Salpinctes obsoletus	Rock Wren	OI
Sayornis saya	Say's Phoebe	BS
Selasphorus platycercus	Broad-tailed Hummingbird	MS
Sialia currucoides	Mountain Bluebird	OI
Speotyto cunicularia	Burrowing Owl	RA
Spiza americana	Dickcissel	WS
Spizella breweri	Brewer's Sparrow	WS
S. pallida	Clay-colored Sparrow	WS
S. passerina	Chipping Sparrow	WS
Steganopus tricolor	Wilson's Phalarope	AQ
Sturnella magna or *neglecta*	Meadowlark sp.	BS, summer WS, winter[c]
Sturnus vulgaris	Starling	MS
Tachycineta thalassina	Violet-green Swallow	OI
Thryomanes bewickii	Bewick's Wren	OI
Toxostoma curvirostre	Curve-billed Thrasher	OI
T. dorsale	Crissal Thrasher	BS
Tringa solitaria	Solitary Sandpiper	AQ
Troglodytes aedon	House Wren	OI
Tyrannus verticalis	Western Kingbird	BS
Vermivora luciae	Lucy's Warbler	OI
V. virginiae	Virginia's Warbler	OI
Wilsonia pusilla	Wilson's Warbler	OI
Xanthocephalus xanthocephalus	Yellow-headed Blackbird	MS
Zenaida asiatica	White-winged Dove	DQ
Z. macroura	Mourning Dove	DQ
Zonotrichia leucophrys	White-crowned Sparrow	WS

[a] AQ = aquatic or semi-aquatic species, RA = raptors, BS = breeding species, OI = nonbreeding insectivores, WS = nonbreeding seed-eaters, DQ = doves and quail, MS = miscellaneous species.

[b] *A. bilineata* is a permanent resident which was considered insectivorous in the summer and seed-eating in the winter in the totals for these categories.

[c] *S. magna* is a minor breeding species and is largely insectivorous in the breeding season. Both species are abundant and seed-eating in winter. Separate seasonal designations reflect these differences in diet and relative importance.