AN URBAN BIRD COMMUNITY IN TUCSON, ARIZONA: DERIVATION, STRUCTURE, REGULATION

JOHN T. EMLEN
Department of Zoology
University of Wisconsin
Madison, Wisconsin 53706

Urban and suburban environments, commonly shunned by field ornithologists, provide a special opportunity for studying the formation and regulatory dynamics of avian communities, especially in recently developed areas such as the American West. The establishment of cities may be regarded as ecological experiments in which a relatively simple array of novel features and resources (lawns, ornamentals, buildings, telephone lines, traffic, etc.) are rather suddenly introduced into a restricted area from which many of the natural features have been removed. The new synthetic habitats lie open to invasion and colonization by any birds that can reach them, utilize their peculiar constellation of resources, and survive their special hazards. The structure and balance of the new community will reflect not only the nature of these local resources and features but also the interactions of the species which converge on them from a variety of geographic and ecological sources. Relatively undisturbed tracts of the native landscape can generally be found near a new city to provide directly comparable control sites, while other cities of similar age may be available in the region as experimental replicates.

During the spring of 1972, I censused the adult birds on an 87-acre urban residential area in Tucson, Arizona. To provide a base for comparison, I also censused the birds on a nearby tract of "undisturbed" creosotebush desert selected for the similarity of its vegetation and terrain to the conditions that existed on the residential area before development was started 70 years before. The differences between the modern urban and the modern desert bird life at these two sites are treated in this report as changes attributable to urbanization.

STUDY AREAS

The urban site, a relatively uniform and quiet 24 square block area of small houses and lawns, known as Speedway Heights, lies about 2 miles (3.2 km) east of the center of Tucson at 32°14′ N, 110°57′ W. Bounded by First Street, Tucson Blvd., Fourth Street, and Campbell Ave., the area is a rectangle, six blocks long and four blocks wide covering 87.3 acres (see fig. 1). First surveyed for development between 1906 (west part) and 1920 (east and central parts), the streets were laid out between 1907 and 1924, and most of them paved between 1930 and 1940. Most of the houses were built between 1928 and 1948. The city now extends 10 miles to the east so that the site is located near the center of a sprawling metropolis of about 150 square miles and 370,000 people.

The desert site, a broad area of relatively uniform and undisturbed creosotebush vegetation, lies 10.0 miles (16 km) south of the urban site at 32°04′ to 07′ N, 110°52′ to 57′ W, a few miles south and east of the Tucson International Airport. Selection of this site for its resemblance to predevelopment conditions at the urban site was based on (a) considerations of the local topography, drainage, and soil patterns; (b) studies of old maps including a 1904 USGS map and a 1936 aerial photo map; (c) interviews with early settlers; (d) checks of desert vegetation relics on undeveloped lots in the area; and (e) examination of old photographs.

In this report I will attempt to describe the two habitats, emphasizing avian resources, and compare the bird communities at the two sites in terms of species composition, geographic and ecological provenance, species diversity, population density and biomass, feeding and nesting guild structure, and spacing characteristics. I will also examine the circumstances of urban colonization and the ecological and behavioral attributes of successful urban colonizers and consider the specific habitat changes accompanying urban development in Tucson as factors in population regulation and community balance.

METHODS

First, both areas were mapped using topographic and aerial photo bases. General features and selected special features in each of the habitats were then described, enumerated, and measured. Habitat data included topography, soil characteristics, and measurements of the height, cover, and screening characteristics of the tree, shrub, and ground cover (Emlen 1956). Special features such as cactus plants in the desert and telephone poles in the city were enumerated and recorded in terms of density per unit area.

Particular attention was given to census methods. Only the resident land bird species, those regularly using the resources of the area during the period of the study, were included (see footnote in table 1 for elaboration and explanation). Density estimates are expressed as absolute values in terms of individuals or grams of biomass per 100 acres.

Populations on the desert area were censused along 9.8 miles (15.7 km) of cross-country foot transect (single coverage) on 20, 22, and 26 May, and the tallies for each species converted to absolute density estimates by applying coefficients of detectability (Emlen 1971) obtained during the spring of 1972 from lat-

 The Condor 76:184–197, 1974

TABLE 1. Birds resident on the 87-acre urban census area during the study period with estimates of their numbers. Irregular visitors and transients never constituted more than 2% of the total and are not included.[a]

Species	Estimates in birds per 100 acres urban area			
	CD-412 transects	Map (pts) surveys	Direct count	Best[b] estimate
White-winged Dove	197	44[c]	128	140[c]
Mourning Dove	36	26	25	30
Inca Dove	298	176[c]	199	230[c]
Black-chinned Hummingbird	6	2	4	6
Gila Woodpecker	21	14	13	14
Ash-throated Flycatcher	3	–	1	2
Verdin	14	14	13	14
Cactus Wren	1	2	1	2
Mockingbird	46	47	40	45
Curve-billed Thrasher	1	5	2	5
Starling	49	21	35	35
House Sparrow	717	475	508	520
Cardinal	13	17	14	17
House Finch	214	150	148	170
Totals	1605	995	1130	1230

[a] Species observed in the area and not listed include: Winter residents, Cedar Waxwing (*Bombycilla cedrorum*), Brewer's Sparrow (*Spizella breweri*), White-crowned Sparrow (*Zonotrichia leucophrys*). Migrating transients, Solitary Vireo (*Vireo solitarius*), Yellow-rumped (Audubon's) Warbler (*Dendroica coronata auduboni*), MacGillivray's Warbler (*Oporornis tolmiei*), Yellow Warbler (*Dendroica petechia*), Wilson's Warbler (*Wilsonia pusilla*), Green-tailed Towhee (*Chlorura chlorura*), Dark-eyed (Oregon) Junco (*Junco hyemalis oreganus*), Chipping Sparrow (*Spizella passerina*). Irregular visitors, Gambel's Quail, Common (Gilded) Flicker (*Colaptes auratus chrysoides*), Western Kingbird (*Tyrannus verticalis*), Wied's Crested Flycatcher (*Myiarchus tyrannulus*), Bendire's Thrasher, American Robin (*Turdus migratorius*), Phainopepla (*Phainopepla nitens*), Lucy's Warbler (*Vermivora luciae*), Great-tailed Grackle (*Cassidix mexicanus*), Brown-headed Cowbird, Bronzed Cowbird (*Tangavius aeneus*), Black-headed Grosbeak (*Pheucticus melanocephalus*). Wide-ranging aerial foragers, Cliff Swallow (*Petrochelidon pyrrhonota*).

[b] The best estimate values are adjusted for conditions in early May. Counts made before and after 1 May reveal a marked increase in White-winged Doves and a slight increase in Inca Doves at that time. The low values of the map surveys for these two species (all made in April) reflect the lower April populations.

[c] See text for descriptions of the census methods.

eral distance distribution plottings for 108 miles (173 km) of desert transect at 30 localities in southern Arizona and northwestern México.

Special conditions in the urban area necessitated the application of several semi-independent census methods and a collation of the results to produce a "best estimate" of the total population for each species. The field procedures are described and critically evaluated below.

Converted transect count. Transects were run along the four east-west streets of the census area during the 2 hr after sunrise on 26 March, 23 April, and 15, 28 May and along the four alleys bisecting these blocks on 16 April and 7, 21 May. The length of each transect was 9980 ft or about 1.89 miles (3.03 km). The total distance covered was 13.3 miles (21.4 km). Lateral distance estimates from the alley centers or street curbs were recorded for each bird observation as it was tallied, and lateral distribution curves of all detection points were plotted and used to provide conversion factors for the counts of each species on each census. The values presented in column 1 of table 1 are the means of the alley and street transect means. No adjustments for the inactivity factor were applied.

Densities derived for alley transects were about 1.3 times as high as densities for street transects. An obvious factor in this difference was the concentration of birds on the poles and wires along the alleys. Lateral distribution curves clearly reflected this and other irregularities in the evenness of lateral distributions through the blocks. Houses, averaging about 80 ft from the alleys and 40 ft from the street curbs, introduced a second disruptive factor by producing a backdrop beyond which detections were largely prevented except for high perching vocalizers. Tree rows and lawn strips along the curbs through many blocks formed a third factor by attracting concentrations of feeding, perching, and nesting birds, especially House Sparrows (*Passer domesticus*), House Finches (*Carpodacus mexicanus*), and doves near the base line of the street transects. Since a basic assumption of this method, that there is essentially uniform lateral distribution, does not hold, the values derived by detectability conversion factors are clearly biased.

Home range mapping. Densities derived from spot-mapping procedures are presented in column 2 of table 1. Spot maps were prepared for each species. Again, I followed the streets and alleys, traversing the entire area, this time in irregular patterns, on 3 days in each of three periods (5–9 April, 10–15 April, and 17–21 April). For singing males, dots on the three maps for each species were rounded up in a best possible estimate of the home range or territory of each individual singer for that period. The number of home ranges was then estimated for each period and compared with the other periods for a best estimate of the late April population on the 87-acre tract.

The method appeared to give fairly accurate and complete information for dispersed, highly territorial singers such as the Mockingbird (*Mimus polyglottos*), Cardinal (*Cardinalis cardinalis*), and Cactus Wren (*Campylorhynchus brunneicapillus*); it was clearly inadequate in its usual form for such loosely territorial and irregularly singing species as the House Sparrow, House Finch, and the doves, species that comprised the largest elements of this urban avian community. In view of this situation, I modified the procedure by mapping the point location of all birds encountered, distinguishing between singers and nonsingers by the form of the dots used. The clustering patterns of

FIGURE 1. Aerial photograph of the urban census area in Tucson, Arizona.

points over the 3 days of each survey period were then examined for the irregularly singing species, and the localized groupings, seen in the patchy distribution of points, were circumscribed on the maps. Following the method of Palmgren (1930), the highest count for a single day (distinguished by colors) was adopted as the best indicator of the size of each localized group. The total values derived from the maps for the various species are thus based on several different procedures, each adapted to the conditions encountered in conducting the surveys.

Direct strip count. After noting the biases of both the lateral distribution conversion method and the mapping method for the urban census area, I turned to a direct counting method similar to that used by Graber and Graber (1963) in suburban habitats in Illinois. The results of these direct strip counts are presented in column 3 of table 1. In this method I used the same tallies I had used in the detectability conversion surveys (method 1), but instead of multiplying the total counts by the appropriate conversion factors, I simply totaled the tallies out to 90 ft in the alley transects and out to 70 ft in the street transects and added the two totals. The entire area was thus covered (160 ft between alley center and street curb), each complete coverage requiring two morning surveys. The relatively short distance to the cut-off boundary lines and the usually good visibility to those lines suggested that errors due to reduced detectability toward the back of the strips would be small and could be disregarded.

Theoretically, spot-map data obtained in the home-range mapping in this study could also be used as a basis for direct strip counts, except that all detection points mapped beyond the prescribed limits constitute strip overlap and potential duplication. Also, for strip counts, the procedure of following prescribed transect lines is preferable to the more flexible and irregular coverage used in point mapping.

Best estimates. Best estimates of the population of each species in the urban area, based on comparisons of the values obtained by the three census methods and the biases encountered in deriving these values, are presented in column 4 of table 1. The direct strip counts are considered more representative for the nonterritorial or loosely territorial House Sparrows, House Finches, and doves. Estimates from the map surveys are given greatest weight in the highly territorial Mockingbird, Cardinal, and Cactus Wren. Location of nest sites on the maps was used as the best indicator for the Gila Woodpecker (*Centurus uropygialis*). Converted transect counts (method 1) were useful in weighing the estimates of all the species except those tending to cluster along wires and roadside plantings.

RESULTS AND DISCUSSION

THE HABITAT

Urban area. The urban area is strictly residential with primarily one-story, single family houses on 50 × 150 ft (0.17 acre) lots (fig. 1). The style and distribution of houses is relatively uniform, 13–18 per block (total 350); there are very few vacant lots and only one public building, a small school (one block). The streets are paved, 30–40 ft wide, and bordered by paved or unpaved sidewalks. Most of the houses are flat-roofed, of white stucco or brick, and aligned in open rows along the east-west streets. Typically, each house is fronted by a 30 × 50 ft irrigated lawn (built-in sprinkler systems), bordered by dense ornamental shrubs (*Thuja*, *Cupressus*, *Citrus*, etc.), separated from neighboring houses by unpaved driveways, and backed by a largely

TABLE 2. Features of the urban and desert census areas with estimates of the number of units (trees, etc.) and per cent of area with cover available for use by birds in three strata: high (> 10 ft), middle (3 ft–10 ft) and low (< 3 ft).

Vegetation	Urban area: No. of units in 100 acres	Urban area: Per cent cover[a] High	Urban area: Per cent cover[a] Middle	Urban area: Per cent cover[a] Low	Desert area: No. of units in 100 acres	Desert area: Per cent cover[a] High	Desert area: Per cent cover[a] Middle	Desert area: Per cent cover[a] Low
Trees								
Pine and Tamarisk foliage	120	1.9	1.2	0	0	0	0	0
Broad-leafed foliage	145	1.6	0.6	0	0	0	0	0
Dense ornamental foliage	1700	3.5	3.0	1.0	0	0	0	0
Palm foliage (mostly in rows)	110	0.2	0.1	0	0	0	0	0
Tree cactus	20	trace	trace	trace	0.2	trace	trace	trace
Microphyll desert foliage	120	0.4	0.4	0	150	0.5	0.7	0
Shrubs								
Ornamental shrubs (mostly dense)	2500	0	2.6	2.0	0	0	0	0
Shrub Cactus (Cholla and Prickly Pear)	15	0	trace	trace	500	0	0.2	0.2
Microphyll desert shrubs	—	0	0.3	0.3	32000	0	26.0	26.0
Ground Cover								
Dwarf shrubs	0	0	0	0	15000	0	0	1.3
Sparse low grass and forbs	—	0	0	32.7	0	0	0	72.5
Dense lawns (watered)	—	0	0	16.0	0	0	0	0
Other Features								
Telephone and power poles Telephone and power lines	150ft 11500ft	1.6	0	0	1 100ft	trace	0	0
Telephone and power spurs to houses	28000ft	1.1[b]	1.1[b]	0	0	0	0	0
Fence lines	6000ft	0	0.5[b]	0.5[b]	0	0	0	0
Television aerials on housetops	210	0.1[b]	0	0	0	0	0	0
Buildings (houses and sheds)	360	16.0	4.0	0	0	0	0	0
Paved streets (mostly 40 ft wide)	—	0	0	18.5	0	0	0	0
Unpaved alleys and driveways	—	0	0	9.0	0	0	0	0
Bird feeding stations	19	—	—	—	0	0	0	0
Exposed garbage and trash points	170	—	—	—	0	0	0	0
Total % cover in each stratum		26.4	13.8	80.0[c]		0.5	26.9	100.0

[a] Points in horizontal space in which the feature is represented (some overlap of strata occurs).
[b] Wires, fence lines, and television aerials were regarded as having a functional width of 3 ft, and coverage was determined by multiplying the estimated total length of these linear features by this width.
[c] Surface areas under buildings were regarded as unavailable for use by birds.

untended service or play yard with a garage and other outbuildings. An unpaved alley, carrying power and telephone lines and serving for weekly trash and garbage collections, runs east-west through the center of each block. A few scattered pines (*Pinus halepensis*), gum trees (*Eucalyptus*), and palms (*Washingtonia, Phoenix*) occur in all blocks; rows of low orange trees (*Citrus*), oleander, and palms line sections of some of the streets, alleys, and property lines.

About 10% of the total area is covered (vertical projection) by tree and shrub canopy. The remaining "open areas" are occupied by buildings, 20%; paved streets, 19%; unpaved alleys and driveways, 9%; lawns, 20%; and nontended yards or cultivated gardens, 33% (table 2).

As already noted, special features and artifacts of human origin contribute importantly to the physiognomy and diversity of the urban habitat. House tops and particularly their superstructures such as air-conditioner units and television aerials provide attractive song and resting perches. Edges of tile roofs, ledges under roofs, and dense vines growing on walls provide important nesting cover for several species. Telephone poles and wires provide abundant and well-distributed perches at elevations from 10 to 40 ft, while fence tops provide similar perches at lower levels. Considerable food is generally available around the many poorly covered garbage and trash containers in each city block, but more importantly, bird seed, table scraps, and sugar water were deliberately put out for the birds by residents at 24 homes, regularly at 19 of them.

Desert area. Nearly flat, but classified as lower bajada rather than flood plain, the fine sand plus coarse gravel soil of this area supports a nearly uniform and evenly dispersed stand of creosotebush (*Larrea divaricata*), 4–5 ft high and covering from 20 to 30% of the ground surface with widely spreading, lightly foliaged branches (table 2). A few shrubby acacias (*Acacia constricta* and *A. greggi*), cholla cactuses (*Opuntia*), and mesquite shrubs (*Prosopis juliflora*) are scattered among the creosotebushes but collectively comprise no more than 5–10% of the shrub cover. Trees are limited to an occasional 10–13 ft mesquite or palo verde (*Cercidium microphyllum*), but these average 150–300 ft apart and cover only 0.5% of the surface. The huge sahuaro cactuses (*Cereus giganteus*), a prominent feature of much of the Arizona desert, are represented by an average of less than one decrepit specimen per hundred acres. The ground cover consists of a thin and uneven stand of dry grasses and composites.

Signs of human disturbance are few in this desert tract except for a power line crossing one corner of the area and a few old wheel tracks. A small clump of cottonwoods a mile away marks the site of a cluster of small houses and a well. Such objects and the traces of irrigation and cultivation near them are known to have a marked effect on the local bird life and were assidiously avoided in this study. More subtle effects of man's presence over the years are difficult to assess. There is still much discussion as to the extent to which 200 years of grazing may have altered the grass and shrub cover of the lowland desert. Creosotebush and shrub cactuses have apparently increased in some areas at the expense of the grasses and forbs, but the scope of the change and its effect on bird life is probably slight.

THE BIRD COMMUNITY

Data on the bird community of Speedway Heights are considered below under the following headings: (a) the geographical and ecological derivation of its members; (b) the diversity and balance of its structure; and (c) population density and biomass.

Derivation of the members. Of the 14 species residing in the urban census area, three, comprising two-thirds of the individuals and biomass, are alien invaders from distant lands; five species with 22% of the individuals are native species with wide geographical ranges and ecological tolerances; and six, with 15%, are local species closely identified with southwest desert habitats.

The three alien species invaded the Tucson area independently, each proliferating rapidly and exploiting a wide variety of the area's resources. All are closely identified with urban or suburban environments in their areas of origin, where they have lived for centuries in close association with urban man and his artifacts and where they apparently evolved adaptations to the special disturbances and hazards of these environments. The Inca Dove (*Scardafella inca*) apparently moved northward from México about 1870 and is now found in five southwestern states where it is restricted almost entirely to cities or clusters of ranch buildings in irrigated districts (Phillips et al. 1964). The House Sparrow appeared in Tucson about 1903, moving in from the eastern states where it had been imported from its native home in Europe. Like the Inca Dove this bird is largely restricted to urban situations or farm buildings where it generally nests in crevices or on ledges of buildings. The third member, the Starling (*Sturnus vulgaris*), came from Europe via the eastern states, arriving in the Tucson area about 1946. Less restricted to urban habitats than the others, Starlings range out into irrigated farmlands and even into some desert areas where they nest in cavities in the giant sahuaro cacti.

The five native species characterized as having wide geographic ranges and broad ecological tolerances are, by definition, opportunistic species. In all cases these birds are more successful (are more numerous) in the relatively mesic conditions of the suburb than in the surrounding desert. Three of them, the Mourning Dove (*Zenaida macroura*), Mockingbird, and Cardinal, comprising 7.5% of the community population, occur over much of temperate North America. In the natural habitats around Tucson, they are found primarily in riparian or mesquite thicket situations. The two other species in this group, the House Finch and Black-chinned Hummingbird (*Archilochus alexandri*), are distributed widely over western North America. The House Finch, a dominant species comprising 14% of the community population, is ecologically eurytopic and widely though sparsely dispersed through desert habitats where water is within flying range. The Black-chinned Hummingbird is primarily a bird of the Upper Sonoran Zone and penetrates only minimally into desert habitats. Two other wide-ranging species found in the desert census area, the Loggerhead Shrike (*Lanius ludovicianus*) and the Brown-headed Cowbird (*Molothrus ater*), were absent from the urban census plot but are known to occur sparingly in parts of suburban Tucson.

All of the six geographically limited species deriving from the local fauna are restricted by specialized responses to one or another aspect of the desert habitat. Only one of them, the White-winged Dove (*Zenaida asiatica*), increased significantly under the new conditions, and, like the Mourning Dove of the eurytopic element, this bird naturally nests and roosts in the relatively dense arboreal cover of mesquite thickets and riverine vegetation. The other five species collectively comprise only 3.0% of the community's membership. The three arboreal species, Gila Woodpecker, Ash-throated Flycatcher (*Myiarchus cinerascens*), and Verdin (*Auriparus flaviceps*), increased moderately; the two shrub-cactus species, Cactus Wren and Curve-billed Thrasher (*Toxostoma curvirostre*), declined.

The proximity and extent of natural habitat types in the Tucson vicinity should be considered in evaluating the contribution of each to the urban bird community. Five major types are found within 40 miles of Tucson (fig. 2). Four of these—coniferous forest, juniper-pinyon-oak woodland, chaparral, and desert grassland—occur on the mountain slopes surrounding the Tucson basin. The broad flats and bajadas of the valley floor are covered with desert scrub, a relatively uniform, open, and sparse vegetation, varying only gradually and subtly in density and plant composition according to local patterns of soil texture and subsurface drainage. Lowe (1964) recognizes four divisions of this desert scrub around Tucson: creosotebush scrub, paloverde-sahuaro desert, riparian woodland, and mesquite thicket.

Among the 11 indigenous species of the urban community, the Black-chinned Hummingbird, although now commonly regarded as an urban bird, appears to be associated primarily with the plains grassland habitat under natural conditions. All the others are best represented in the desert scrub. Most of them move quite freely between the various divisions of this vegetation type, but each of them can be assigned with some confidence to a preferred habitat among the four. Six of these birds [Gila Woodpecker, Ash-throated Flycatcher, Verdin, Cactus Wren, Curve-billed Thrasher (*Toxostoma curvirostre*), and House Finch] are best represented in the paloverde-sahuaro desert, characterized by a relatively rich mixture of sclerophyll shrubs, small trees, and cacti. Two species (Mockingbird and Cardinal) are most closely associated with the narrow rows of tall, deciduous willows and cottonwoods and associated undergrowth of the riparian woodlands. Two species (White-winged Dove and Mourning Dove) are most numerous in and around the rather dense but scrubby groves of 20–30 ft mesquites known locally as thickets or bosques. None of the primarily creosotebush species, including the common and widely dispersed Black-tailed Gnatcatcher (*Polioptila melanura*) and Black-throated Sparrow (*Amphispiza bilineata*), occurred in the urban community although the land on which it is located was originally dominated by this type.

Bird species diversity. Three measures of species diversity have been used commonly in recent studies of bird communities: (a) the number of species present; (b) the equitability or evenness of representation of these species; and (c) a general diversity value combining species number and equitability.

The number of species tallied was 21 in the desert habitat and 14 in the urban habitat (table 3, cols. 1 and 2). The indicated 33%

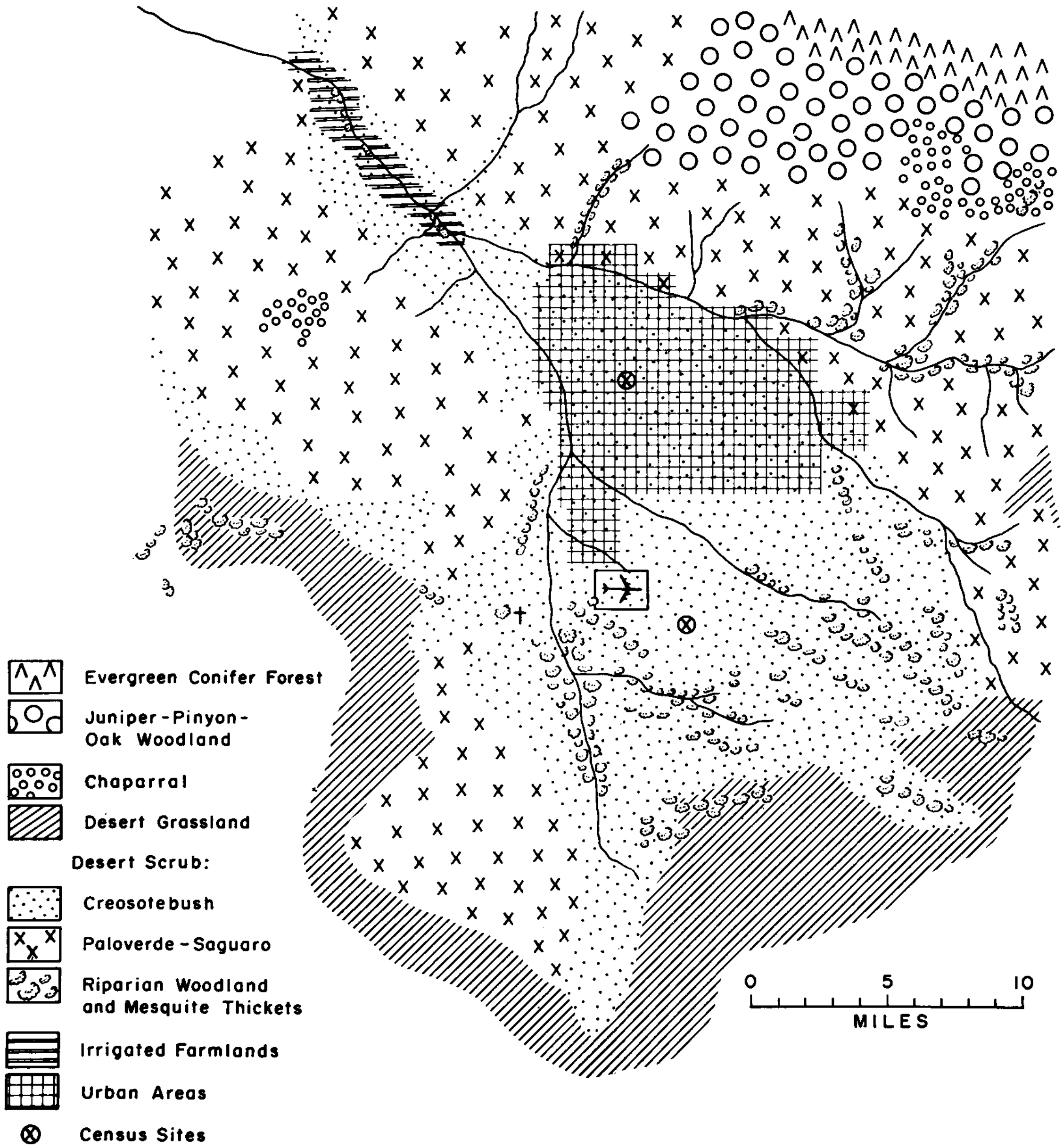

FIGURE 2. Vegetation types of the Tucson area (from a map compiled by R. M. Turner, 1973).

decrease attributable to urbanization resulted from the loss of 12 species and the addition of 5. These lists include all of the resident land bird species tallied during the period of study but exclude transients and irregular visitors (see footnote, table 1).

Since in any census operation based on sampling, rare species are likely to show up with more extended coverage, the adequacy of the 87 acres of urban mapping and the 9.8 miles of desert transect as samples for species numbers may be challenged. These challenges were tested by plotting species-area curves based on counts in fractional segments of the two areas, city blocks and clusters of blocks in the former, single day transects and combinations of transects in the latter (fig. 3A and B). Extrapolation of the first curve (the dashed line) indicates that an extension of the urban tract to an area as large as the desert tract (980 acres) would have added no more than one or two species to the total of 14 recorded. Similarly, an extension of the transect coverage in the desert to 40 or more miles would have raised the total of species by only two or three above the 21 recorded.

The information theory measure of species diversity in a community ($H' = \sum^{s} p_i \log^e p_i$) takes account of both the number of species (s) and their relative abundance (p) (Mac-

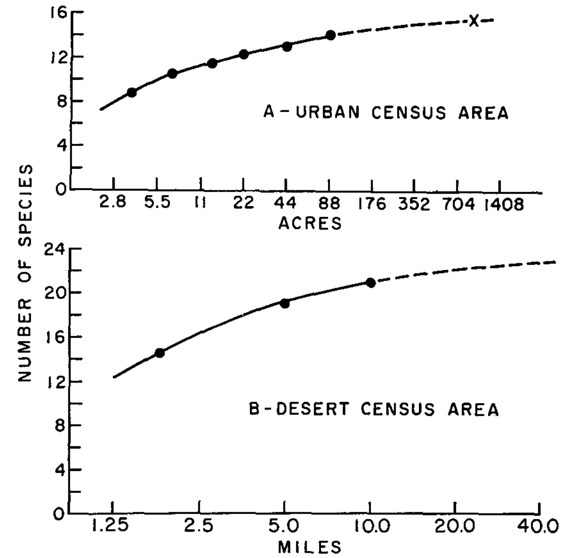

FIGURE 3. Species-area curve for the urban tract (A) and species-distance curve for the desert area (B) showing the number of species recorded in fractional plots or segments of various sizes. The curves are extrapolated by eye (dashed line). The X on the first curve indicates the projected number of species for a tract of 980 acres, the size of the desert census area.

Arthur 1957). The H' values for the urban and the desert communities of this study were 1.734 and 2.189, respectively. The lower diversity value for the urban community reflects the low species number s noted above. To test whether it might also reflect a less even numerical distribution of member species, the diversity for each community was divided by the maximum diversity possible for the given number of species (i.e., when all species are equally numerous). This measure of equitability ($J' = H'/H'$ max) revealed no appreciable difference between the two communities; it was 0.31 for the urban community and 0.29 for the desert community.

Errors in the H' diversity estimates arising from incomplete census coverage would be very small for either the urban or the desert community since rare species have little effect on the calculated values. Equitability estimates would be affected more by incomplete species lists, but the effects would be very similar for the two areas.

Diversity (H') and equitability (J') are based on relative densities and theoretically should not be affected by the large differences in aboslute density that existed between the desert and the urban communities in this study. In practice, however, the sparseness of the desert populations could conceivably influence social behavior or interspecies competition in ways that would lead to changes in the diversity of the community. Species with very low absolute densities, for instance, might be less successful in replacing themselves and tend to drop out of the community, or potentially competing species might be able to coexist only where combined absolute numbers were below a given threshold. No indication of such effects was detected in this study.

Bird species diversity should theoretically increase with habitat diversity (MacArthur and MacArthur 1961). The widely used index of habitat diversity based on total leaf surface in each of these arbitrarily defined foliage levels and termed foliage height diversity (FHD) seems inappropriate for urban situations where tree and shrub foliage is very patchy (concentrated in tight clusters of dense ornamental trees and shrubs), and where nonvegetative structures such as buildings, poles, and wires contribute importantly to the utility of space in the several levels in terms of perches. I accordingly devised a *perch-height diversity* index (PHD) similar to the category diversity index of Karr and Roth (1971), using estimates of perch availability instead of leaf surface in each of the three levels. The per cent of square yard units that contained any solid substrate usable for perching was estimated in vertical projection for each of the three levels and the proportions of the three applied to the information theory equation. The lower stratum included the ground surface and therefore had 100% representation in both the urban and the desert areas; the upper two levels contained many roofs and wires as well as shrub and tree perches in the city, only the latter in the desert. PHD values obtained in this way were 0.853 for the urban area, and 0.546 for the desert, supporting the subjective impression that the urban habitat was considerably more complex in physical structure.

I also calculated a *habitat feature diversity* index similar to that used by Tomoff (1972) in desert habitats and based on the proportional representation of each of the major habitat features, natural and artificial, in the total environment. With 18 features present in the urban situation and only 6 in the desert (see table 2), the H' values not surprisingly showed a much greater habitat diversity in the city (2.132) than in the desert (0.799).

Both the perch-height and the habitat feature diversity indices described above show an inverse relationship with bird species diversity in the urban-desert comparison. This unexpected situation may reflect the historical newness of urban environments in the region and an element of "immaturity" in the bird

TABLE 3. Densities of resident birds and biomass in the urban residential area and on the desert area believed to resemble the urban area as it was 70 years ago. (Hawks, owls, nightjars, and swallows are excluded; the cowbirds in the urban area are regarded as strays.) Territory type and food habits type are shown at right.

	Density (no./100 acres)		Biomass[a] (g/100 acres)				
	Desert area	Urban area	Desert area	Urban area	Territory[b] type	Food[c] type	Nesting[d] substrate
Gambel's Quail	0.3	—	57	—	B	S	G
White-winged Dove	0.5	140	73	20,300	B	S	TB
Mourning Dove	1.9	30	248	3,900	B	S	TB
Inca Dove	—	230	—	6,900	B	S	TB
Roadrunner	0.5	—	120	—	A	Ag	C
Black-chinned Hummingbird	—	6	—	18	B	N	TB
Common (Gilded) Flicker	1.9	—	266	—	A	At	TC
Gila Woodpecker	0.3	14	21	980	A	At	TC
Ash-throated Flycatcher	0.8	2	22	56	A	Aa	TC
Verdin	2.5	14	18	98	A	Af	TT
Cactus Wren	6.8	2	258	76	A	Af	C
Curve-billed Thrasher	6.9	5	552	400	A	Ag	C
Bendire's Thrasher	0.2	—	15	—	A	Ag	C
Mockingbird	0.3	45	14	2,160	A	Ag	TB
Black-tailed Gnatcatcher	1.6	—	10	—	A	Af	Sh
Starling	—	35	—	2,450	B	Ag	TC
Loggerhead Shrike	0.1	—	5	—	A	Ag	TB
Brown-headed Cowbird	0.4	(1)	20	—	B	S	—
Hooded Oriole[e]	0.6	—	16	—	A	Af	TT
House Sparrow	—	520	—	11,960	B	S	Cr
Cardinal	—	17	—	680	A	S	Sh
Pyrrhuloxia	0.6	—	21	—	A	S	Sh
House Finch	0.3	170	6	3,230	B	S	Sh
Brown Towhee	1.2	—	53	—	A	S	Sh
Black-throated Sparrow	16.5	—	215	—	A	S	Sh
Rufous-winged Sparrow[f]	2.5	—	30	—	A	S	Sh
Total	46.7	1230.0	2,020	53,208			

[a] Weights for each species were taken from specimens at the Univ. of Arizona, Dept. of Biological Sciences.
[b] Territory types: A = large with foraging area included; B = small with foraging area excluded.
[c] Food type and foraging habits (dominant selection during spring months): S = seeds, N = nectar, A = animal, a = in air, f = on foliage, g = on ground, t = on tree trunks.
[d] TB = tree branches, TT = tree twigs, TC = tree cavities, Sh = shrubs, C = cactus, Cr = crevices, G = ground.
[e] *Icterus cucullatus.*
[f] *Aimophila carpalis.*

community, currently in the process of evolving a balanced structure in harmony with the new habitat.

Population densities. Contrasting with the substantially lower diversity of species was a 26-fold increase in numbers of individual birds and also of total avian biomass in the urban as compared with the desert community (table 3, cols. 1–4). The level of about 50 birds per 100 acres is characteristic of creosotebush scrub over much of the Sonoran Desert of southern Arizona and northern Sonora (Emlen, unpubl. data). The level of a little over 1200 birds per 100 acres in the urban community approximates densities for cities in the Tampa Bay area of Florida (Woolfenden and Rohwer 1969a, b), and for several cities in Illinois where similar census methods were used (Graber and Graber 1963). It is roughly comparable to values for suburban situations summarized by Pitelka (1942), Campbell (1953), Erz (1966), Cramp and Tomkins (1966), and Siegfried (1968), who concur that community densities tend to be substantially greater in suburban situations than in the surrounding areas. In the Tucson survey plot, the recorded density represents roughly one bird per human inhabitant.

REGULATING FACTORS

Theoretically, the balance of species and the population density attained by each in a community are determined by four basic factors: (a) the nature and quantity of vital resources in the habitat, particularly foraging situations, watering places, and nesting and resting substrates; (b) the nature and magnitude of suppressive factors such as predators, pedestrian and vehicular traffic, etc.; (c) intraspecific social spacing pressures; and (d) interspecific competition. The introduction by man of buildings, exotic plants, and other distinctive features of a modern city onto the desert terrain of southern Arizona during the past hundred years has profoundly altered the first two of these factors and secondarily affected

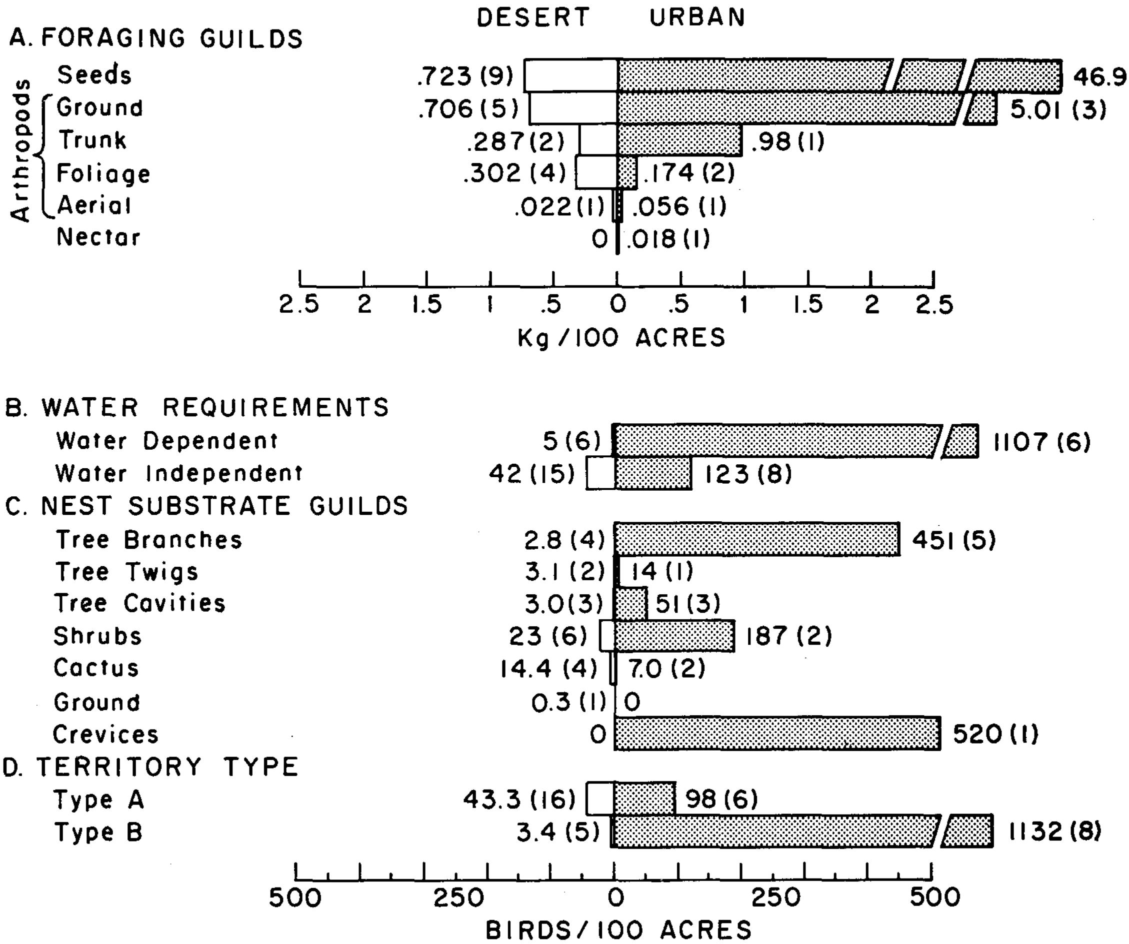

FIGURE 4. Structure of the desert and urban communities compared in terms of foraging guilds, water requirements, nest substrate guilds, and territory types. ( ) = number of species.

the third and the fourth. The nature of these environmental changes and the roles each is thought to have played in shaping the modern urban community and regulating its population densities are discussed in the following paragraphs and summarized in figure 5.

In this discussion I assume: (a) that the boundaries of both the urban and the desert study areas are thoroughly permeable and will allow birds to move freely in either direction and to establish a balance based on resource levels and the ecological and social tolerances of the species; and (b) that any differential in productive capacity across the boundary will be cancelled by these movements and will therefore not feature significantly in the community structure in spring, before the new season's crop of young have been fledged. My analysis is, thus, of the standing crop of adult birds as of the beginning of the breeding season.

Food. Several feeding types or foraging guilds (Winterbottom 1960; Root 1967) may be recognized among the species in the desert and urban communities under examination, each related to a particular class or category of food (table 3, footnote c). Published summaries of food habits (Martin et al. 1951) supplemented with personal observations of local foraging behavior during the study period provided a basis for assigning each of the species in the two communities to a guild reflecting its primary food preferences (table 3, col. 6). Comparisons of the relative representation of these guilds in the two communities (fig. 4) shed light on the nature and causes of the differences.

Most of the 26-fold increase in biomass from the desert to the urban habitat is attributable to the seed-eaters. The biomass of these birds jumped from 723 to 46,970 g/100 acres, a 65-fold increase. Ninety per cent of the biomass of the urban influx were seed-eaters; less than half of the biomass of desert species that failed to adapt to the urban habitat were seed-eaters.

Insect-eaters also increased in the city, but the changes were less dramatic. The biomass

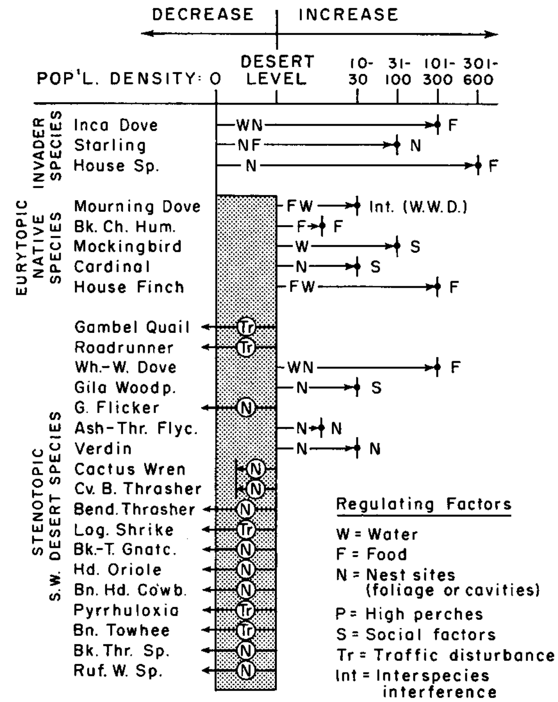

FIGURE 5. Population responses of available bird species to urban conditions at Speedway Heights with indications of the presumed key regulating factors operating during early steps of urbanization (first symbols) and at present (terminal symbols at far right).

of all insect-eaters increased 4.7-fold. Among these, the trunk-gleaners increased 3.4-fold; the aerial-gleaners, 2.5-fold; and the ground-gleaners, 7.0-fold. The foliage-gleaner biomass decreased by one-half.

Food supplies are generally difficult to evaluate quantitatively in nature, and I have no measurements and only a few useful indicators of the abundance of natural food resources in this study. Seeds and sugar-water provided in the urban area by the human residents were estimated, however, and were clearly of major significance to the seed- and nectar-feeders there. These are the two foraging guilds that increased most spectacularly with urbanization. The presence of Black-chinned Hummingbirds in the city is probably attributable to artificial feeding, as regularly serviced hummingbird feeders were maintained and patronized at at least five homes in the area (spring, 1973 survey) and probably at several others.

Grasses and forbs were sparse in the desert following the dry winter of 1972 and, with the seeds of creosotebush largely rejected by birds, the available seed supply there was clearly low. In town, on the other hand, lawn grasses and weeds were abundant, and apparently producing large quantities of small seeds in late spring, especially on poorly tended and trampled lots. Inca Doves, House Sparrows, and especially House Finches fed extensively on these lawns or moved out to the playing fields in a nearby public park. More significant, however, was the large quantity of bird seed (mainly millet, canary grass, sunflower), scratch feed (mainly sorghum, cracked maize, wheat), and table scraps distributed by householders. A survey in the spring of 1973 revealed that seed was put out for birds at 22 homes in the area. Between 0.2 and 2.5 pounds were provided regularly at 16 of these homes, with a total daily output of about 15.0 pounds (5700 g). Inca Doves, White-winged Doves, House Sparrows, and House Finches swarmed to these feeding stations together with smaller numbers of Mourning Doves, Cardinals, and others. Calculating for a total biomass of 47,000 g of seed-eaters, and assuming a 25% of body weight consumption per day, the seeds supplied at feeding stations probably provided about half of the community's total needs.

In the absence of quantitative data on insect populations, a rough appraisal of insect-supporting substrates provides an indirect approach to the supply-demand relationship for desert-urban habitat comparisons. The sevenfold increase of ground-gleaning insectivores is probably related to the establishment of lawns in the urban habitat. Mockingbirds and Starlings are the principal members of this guild responsible for the urban increase. Similarly, the 3.4-fold increase in bark-gleaners is probably related to the appreciable increase in tree-trunk surfaces in the city. I have no data on flying insects to correlate with the 2.5-fold increase in flycatchers. It is possible, however, that this is related to the introduction of many well dispersed high lookout perches in the city in the form of telephone lines and tall trees.

Water. Several mobile desert species including the White-winged Dove, Mourning Dove, and House Finch are water-dependent and are encountered in the desert only where water is within flying range (Bartholomew and Cade 1963; Smyth and Coulombe 1971). The introduction of many well-distributed watering places in the Tucson urban area probably contributed to the invasion of doves and House Finches, although in natural settings, these birds often fly many miles to watering places. Other species such as the Mockingbird, Gila Woodpecker, and Cardinal, although possibly not completely dependent on free water, have taken advantage of the ready availability and benefited thereby. House Sparrows and Starlings presumably could not survive in waterless desert areas.

Nesting substrate. Six nest substrate guilds were recognized in the two communities: tree-crown nesters, tree-cavity nesters, palm-crown and crevice nesters, shrub nesters, cactus nesters, and ground nesters (table 3, col. 7). Matching the introduction of shade trees into the city, tree-nesting species increased from 6 birds per 100 acres in the desert to 465 in the urban setting (fig. 4). Cavity nesters similarly increased from 3 to 51, and shrub nesters from 23 to 187 birds per 100 acres. Among desert shrub nesters, only one of the species that characteristically build in relatively sparse foliage colonized the urban habitat. This species, the Verdin, apparently found an acceptable alternate to its preferred Paloverde twig substrate in the introduced *Parkinsonia* of the urban environment. The two shrub-nesting species that tend to favor dense foliage in the desert, the Cardinal and the House Finch, readily accepted the urban ornamentals and attained high nesting densities in them. Cactus nesters declined from 14 to 7 birds per 100 acres in line with the near demise of their preferred substrate in the city, and ground nesters failed to establish themselves, perhaps because of disturbances (see below, suppression factors). The palm-crown and crevice nesters, a guild absent from the desert and containing a single species in the city, the House Sparrow, had the largest membership of any guild, 520 birds per 100 acres, concentrated in the street-bordering palm trees and the crevices under roofing tiles.

Suppressive factors. Population-suppressing factors were drastically altered in the transition from desert to urban conditions. Predation pressures were changed and selectively intensified with the replacement of a diverse assemblage of lesser carnivores and predatory omnivores by one highly efficient mammalian predator, the house cat. Disturbances produced by human activity, notably pedestrian traffic, playing children, exploring dogs, and vehicular traffic, essentially absent in the desert, constitute a persistent menace to breeding success and even foraging activities for certain species in the city. Arboreal species are relatively immune but ground nesters such as Gambel's Quail (*Lophortyx gambelii*) and Roadrunners (*Geococcyx californianus*) were probably eliminated and prevented from reinvading the urban tract by one or more of these factors since these species do persist and breed in many less congested but structurally similar suburban situations nearby. The absence of three low-flying brush species, the Bendire's Thrasher (*Toxostoma bendirei*), Pyrrhuloxia (*Pyrrhuloxia sinuata*), and Brown Towhee (*Pipilo fuscus*), and of one ground-pouncing arboreal species, the Loggerhead Shrike, from the urban area is probably also attributable to the relentless disturbances of traffic and other human activities.

Intraspecific social spacing. Aggressive interactions among the members of a species population during the breeding season may act as a dispersive force, spacing the individuals and thereby influencing population density and community composition (Brown 1969). Males of some species regularly exclude conspecific challengers from a rather clearly delineated territory large enough to provide all the essential resources needed for raising a brood (type A territory). In other species, aggression is less consistent and tends to be restricted to a small, vaguely defined area near the nest. Such territories, here labeled type B, provide only a fraction of the required resources, and their owners must fly out for varying distances to forage.

Birds with type A territories (all essential resources included) dominated in the desert community, with 71% of the species and 93% of the individuals; in the city, on the other hand, they constituted only 43% of the species and a mere 8% of the individuals. The big influx into the urban area, 95% of the population increment, was by birds with type B territories (obtain most food, etc., beyond the territory boundaries).

Species with type B territories in these communities are primarily seed-eaters, perhaps because of the relatively coarse patchy distribution of seed supplies *vis-à-vis* insects and the need for such birds to feed at common feeding grounds some distance from their widely scattered nests. The dramatic increase in the proportion of type B species in the city (fig. 4D) may thus be incidental to the equally dramatic increase in seed-eaters noted earlier.

While type B species dominated in the invading element of the city, type A species did not decline, in fact most of them made substantial gains (table 3). We have noted that improved nest-site facilities and in some cases food may have contributed to these increases, but extensive use of the abundant and well-distributed telephone lines and television antennas as song and calling perches by Mockingbirds, Cardinals, Gila Woodpeckers, and others suggests that these structures contributed an important element, perhaps a critical feature, for type A territory defenders.

The potential role of territorial aggression or interference competition in regulating bird populations has been controversial (Brown 1969). Theoretically, it provides a ceiling to population growth when and where all vital resources are in excess of requirements and all suppressive factors ineffective. Presumably, the density level at which it becomes effective in limiting a population has been genetically determined in the species through selection for maximum fitness under these optimum environmental conditions. In this study I implicate it only where (a) all essential resources appear to be in excess of requirements; (b) the type A territories of the species are contiguous over the whole area; and (c) census data from other parts of the species' range do not show populations appreciably larger. Two species, the Mockingbird and the Gila Woodpecker, seem to meet these criteria on the Tucson urban tract. A third, the Cardinal, may fit although it does not completely meet the second and third criteria.

Interspecific competition. Interspecific competition, often implicated in discussions of population regulation, can act through the induced depression of supplies of shared resources below critical levels (exploitation competition), or through direct interference in gaining access to such resources (interference competition) (Miller 1967). Critical food shortages are difficult to demonstrate directly in nature, but the daily concentration (in time and space) and frantic feeding activity of doves, finches, and sparrows at certain stations where grain was dispensed at regular hours suggested an unfavorable balance between supply and demand during the period before weed seeds were abundant.

Competition for nesting sites in the few remaining cholla cactuses may have been operating between the few Curve-billed Thrashers and Cactus Wrens in the urban area; both species strongly favor these cactuses in their natural desert environment. Evidence of spatial separation of nesting White-winged Doves and Mourning Doves in the urban area and two observed instances of interspecies aggression near nest sites suggest the possibility of interference competition between these two species in the city.

SUMMARY

The size and structure of the land-bird community on an 87-acre tract of urban residential habitat in Tucson, Arizona, were studied and compared with those on a tract of undeveloped desert closely similar to that on which the urban site was constructed 70 years before.

Sixty-five per cent of the birds in the urban community belonged to three invader species (exotics) already adapted to urban habitats when they arrived. Thirty per cent belonged to five widely distributed North American species all relatively eurytopic but favoring mesic situations such as the urban habitat under study. The remaining 5% belonged to six southwestern desert species with specialized habitat responses; four of these species increased, and two decreased in the urban area. Twelve local desert species failed to colonize the new habitat.

The urban community had lower diversity than the desert community both in numbers of species (14:21) and H' values (1.73:2.19) despite a higher diversity of the habitat according to a perch-height diversity index (0.85:0.55) and a habitat feature index (2.13: 0.80). Bird species equitability (J') was similar in the two communities.

The total population density (all species) was 26 times as high in the city as in the desert (1230:47 birds per 100 acres). The total avian biomass was also 26 times as great in the city.

Community members categorized according to their feeding, nesting, and social characteristics showed strikingly different responses to the urban environment. Among six recognized foraging guilds, seed-eaters increased most sharply (65-fold increase in biomass) while the various categories of insect-eaters increased between 2.5- and 7.0-fold or decreased by one-half (foliage gleaners). Water-dependent species increased much more strongly than water-independent species. Tree and shrub nesters increased markedly while cactus and ground nesters declined. Strongly territorial (type A) species dropped from 93% of the community population in the desert to 8% in the city; 95% of the urban increase was by weakly territorial (type B) species.

Factors underlying the population changes that have occurred in the urban community since its establishment and factors regulating the current population levels in both communities were assessed by appraising the resources and hazards of the two habitats. Seed supplies were enhanced in the urban habitat by the introduction of weedy lawns and home feeders; the latter source apparently supplied about one-half of the urban community's seed requirements in 1973. Foliage, bark, and ground insects were not sampled but presumably responded positively to the introduction of shade trees, ornamentals, and watered leaves. Water, nearly absent in the desert area for much of the year, was well distributed in the city. Nesting sites were greatly in-

creased for arboreal, cavity, and crevice nesters by plantings and concurrently reduced for cactus nesters and certain shrub nesters by plant removals. Overhead wire and other high song perches presumably enhanced the value of the urban environment for territorial species. Traffic hazards and disturbances were selectively detrimental to ground nesting and low shrub foraging birds. Intraspecific territorial competition may be currently restricting further increase in two highly aggressive species, and interspecific competition for limited supplies of food and nest sites may be operating in two or three cases.

ACKNOWLEDGMENTS

The work was supported in part by the National Science Foundation (Grant GB-15304). I am grateful to Raymond Turner for help in determining the "original" vegetation conditions at the urban site and in selecting an appropriate desert site for the control community, and to Stephen Russell, Glen Woolfenden, Edward Beals, and J. Merritt Emlen for critical comments and suggestions on the manuscript.

LITERATURE CITED

BARTHOLOMEW, G. A., AND T. J. CADE. 1963. The water economy of land birds. Auk 80:504–539.

BROWN, J. L. 1969. Territorial behavior and population regulation in birds. Wilson Bull. 81:293–329.

CAMPBELL, B. 1953. A comparison of bird populations upon industrial and rural farmland in south Wales. Cardiff Nat. Socs. Rep. Trans. 131:4–65.

CRAMP, S., AND H. D. TOMKINS. 1966. The birds of inner London. Brit. Birds 59:209–233.

EMLEN, J. T. 1956. A method for describing and comparing avian habitats. Ibis 98:565–576.

EMLEN, J. T. 1971. Population densities of birds derived from transect counts. Auk 88:323–342.

ERZ, W. 1966. Ecological principles in the urbanization of birds. Ostrich Suppl. 6:357–364.

GRABER, R. R., AND J. W. GRABER. 1963. A comparative study of bird populations in Illinois, 1906–1909 and 1956–1958. Bull. Ill. Nat. Hist. Surv. 28:383–528.

KARR, J. R., AND R. R. ROTH. 1971. Vegetation structure and avian diversity in several new world areas. Amer. Nat. 105:423–435.

LOWE, C. H. 1964. Arizona's natural environment. *In* The vertebrates of Arizona. Univ. Ariz. Press, Tucson.

MACARTHUR, R. H. 1957. On the relative abundance of bird species. Proc. Nat. Acad. Sci. 43:293–295.

MACARTHUR, R. H., AND J. W. MACARTHUR. 1961. of bird species. Proc. Natl. Acad. Sci. 43:293–295.

MARTIN, A. C., H. S. ZIM, AND A. L. NELSON. 1951. American wildlife and plants. McGraw Hill, New York.

MILLER, R. S. 1967. Pattern and process in competition. Advan. Ecol. Res. 4:1–74.

PALMGREN, P. 1930. Quantitativ Untersuchungen uber die vogelfauna in der Waldern Sudfinnlands. Acta Zool. Fennica 7:1–218.

PHILLIPS, A., J. MARSHALL, AND G. MONSON. 1964. The birds of Arizona. Univ. of Ariz. Press, Tucson.

PITELKA, F. A. 1942. High population of breeding birds within an artificial habitat. Condor 44: 172–174.

ROOT, R. B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. Ecol. Monogr. 37: 317–350.

SIEGFRIED, W. R. 1968. Ecological composition of the avifaunal community in a Stellenbosch suburb. Ostrich 39:105–129.

SMYTH, M., AND H. N. COULOMBE. 1971. Notes on the use of desert springs by birds in California. Condor 73:240–243.

TOMOFF, C. S. 1972. Breeding bird diversities in the Sonoran desert creosotebush association. Ph.D. thesis (unpubl.), Univ. Ariz., Tucson.

WINTERBOTTOM, J. M. 1960. The ecological relationships of birds of African townships. Rev. Zool. Bot. Afr. 62:246–260.

WOOLFENDEN, G. E., AND S. A. ROHWER. 1969a. Breeding birds in a Florida suburb. Bull. Florida St. Mus. 13:1–83.

WOOLFENDEN, G. E., AND S. A. ROHWER. 1969b. Bird populations in the suburbs and two woodland habitats in Pinellas County, Florida. Florida St. Board of Health Monogr. 12:101–117.

Accepted for publication 1 June 1973.