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BIRD ABUNDANCE AND DIVERSITY ALONG AN URBAN-RURAL GRADIENT: A COMPARATIVE STUDY BETWEEN TWO CITIES ON DIFFERENT CONTINENTS[1]

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Abstract. We compared the avifauna in two cities, Québec (Canada) and Rennes (France), in order to define general responses of wildlife in an urban ecosystem. These cities have a similar urban structure that permits investigation along an urbanization gradient from downtown to rural residential areas. However, they are in opposite temperate climate and imbedded in a forested and an agricultural landscape, respectively. Plots ranging from 10 to 20 ha were surveyed in winter and spring by recording all birds seen or heard. Most plots could be located along a gradient according to proportions of vegetated open space. Both the Shannon-Wiener and Simpson indices of diversity indicated a pattern of increasing diversity from most to least urbanized areas in spring. Winter species diversity and richness was low in Québec compared to Rennes, reflecting the much harsher winter conditions in Québec. Breeding densities of House Sparrows (*Passer domesticus*) and European Starlings (*Sturnus vulgaris*) were quite similar in Québec and Rennes, as were densities of European Blackbirds (*Turdus merula*) and its ecological equivalent in Québec, the American Robin (*Turdus migratorius*). The type of surrounding landscape can not explain the variation of species numbers within the city. If we examine the urban environment as a new ecological system rather than a degraded environment, we can regroup birds in two major species groups: the omnivorous species adapted to the urban environment and its particular food resources such as garbage and the species that find, in the urban environment, resources which they normally exploit in their usual habitat.

Key words: avifauna structure, biodiversity, Canada, France, landscape ecology, urban ecosystem.

INTRODUCTION

Urban ecosystems have only recently attracted the attention of ecologists. Initially, they were analyzed in terms of energy transfer with neighboring ecosystems (Duvigneaud 1974). It is only since the 1970s that urban ecosystems have been examined more broadly, revealing that in spite of extreme urbanization they retained a variety of vegetative structures and supported several wildlife species (Gilbert 1989, Pontier and Yoccoz 1991, Adams 1994).

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However, despite several descriptive studies of urban flora and fauna (Gilbert 1989), little research currently is conducted in these ecosystems. Because of their high heterogeneity and dynamic nature, they offer a quasi-experimental set up to study several ecological processes (McDonnell and Picket 1990, Natuhara and Imai 1996). Urban ecosystems are in perpetual change. The progressive urban expansion, the aging of neighborhoods, and the modifications of the structure and functions of urban spaces can affect species abundance and composition (Lancaster and Rees 1979, Dowd 1992). Urban studies could yield interesting answers on the response of wildlife to their environment, permit integrating urban landscape in wildlife conservation plans, and could provide pertinent information for regional land-planning exercises (Gilbert 1989, Adams 1994).

Habitat and environmental modifications induced by urbanization appear generally similar across large geographical areas. However, general conceptualizations are risky as most urban bird studies deal with several sites in a single city (Lucid 1974, DeGraaf 1976, Savard 1978).

Thompson et al. (1993) compared garden birds between several European countries and revealed important regional differences. For example, they showed that the number of species in urban, suburban, and rural gardens was similar in countries of northern Europe but not in western and southern Europe. Few studies have even discussed the importance of the landscape surrounding cities when it could have a strong influence on the composition and structure of urban vegetation and wildlife (Forman and Godron 1986, Mills et al. 1989).

We compared the bird communities of two cities that are quite close structurally (two old cities of European style in a temperate climate), so that they should have a similar avifauna, yet differed in one city being in a warm Atlantic temperate climate vs. cold inland temperate climate and in an agricultural landscape vs. a forested one. We employed a method based on urbanization gradients (McDonnel et al. 1993) used recently on birds (Blair 1996) to compare the city of Québec (Canada) and Rennes (France).

We examined how the structure and composition of bird communities were affected by levels of urbanization and we compared their response in the two cities. More specifically, our objectives were to (1) quantify seasonal changes in bird abundance and diversity along a gradient from downtown to rural areas and (2) identify common attributes of these communities.

METHODS

STUDY AREAS

Rennes is a city of about 200,000 residents located inland in Bretagne, France. It is well vegetated and mainly surrounded by agricultural areas with only a small forest. Québec has about 650,000 residents which are spread over a much wider area than those of Rennes. It is located on the north shore of the St. Lawrence River and is surrounded mostly by forested landscapes with a few agricultural sectors.

Sites were located by the same persons in the two cities with a concern for selecting comparable features along the urbanization gradient. We used spatial names as defined by geographers: the historic center of the town, i.e., the downtown, the peripheral residential areas with a pericentral and a peripheric sector, and the periurban sector which surrounds the town. We selected seven residential plots in Québec along an urbanization gradient (Table 1); three in or around the downtown area: downtown, Limoilou, and Montcalm, two in peripheral residential areas: Sillery, and Les Saules, and two in the periurban sector: Saint-Augustin, and Ancienne-Lorette. Six plots were selected in Rennes along a similar urbanization gradient (Table 1); three in or around the downtown area: downtown, Sévigné, and Ste-Thérèse, one in a peripheral residential sector: Ste-Elizabeth, and two in the periurban fringe: St-Erblon and La Frinière.

We also selected two large apartment building complexes in the peripheral sector of each city. These two complexes differed in terms of age and level of urbanization. In Québec, the most urbanized complex was Charlesbourg, located on the outskirts of the old part of the city. The other plot selected was Pointe Ste-Foy, a newly built apartment complex. In Rennes, the most urbanized complex was Le Blosne and the least urbanized Beaulieu. We listed these complexes at the end of the gradient to maintain a more simple gradient in terms of % of vegetated open areas. In fact, they are located at different places in the gradient whether we use the building or vegetation components. We excluded all natural areas such as parks, woodlots, or ponds from the

TABLE 1. Habitat features of selected plots along an urbanization gradient in Québec and Rennes.

Plot	Area (ha)	% cover: Buildings	% cover: Vegetated open areas	% cover: Paved areas	Type of buildings (number of stories)	Number of buildings	Landscape type
Québec							
Downtown	13.0	49.8	16.5	33.7	3–5	207[a]	Downtown
Limoilou	10.2	30.7	28.7	40.7	3–5	259[a]	Residential center
Montcalm	14.5	24.3	47.8	27.9	2–3	259[a]	Residential center
Sillery	13.5	13.5	66.1	20.3	1–2	127[b]	Residential peripheral
Les Saules	10.3	15.9	67.0	17.1	1	145[b]	Residential peripheral
Saint-Augustin	11.2	11.3	71.7	16.9	1	128[b]	Residential periurban
Ancienne-Lorette	20.0	5.1	86.4	8.5	1	44[c]	Agricultural periurban
Charlesbourg	11.5	21.6	42.2	36.1	4–5	84[d]	Residential center
Pointe Sainte-Foy	12.9	13.6	46.9	39.5	4–5	35[d]	Residential peripheral
Rennes							
Downtown	10.5	51.0	1.1	47.9	3–5	236[a]	Downtown
Sevigné	12.9	24.0	35.2	40.8	1–2	331[a]	Residential center
Ste-Thérèse	12.6	24.5	36.6	38.9	1–2	343[a]	Residential center
St-Élizabeth	12.0	25.0	39.0	36.0	1	278[b]	Residential peripheral
St-Erblon	14.2	15.0	47.0	38.0	1	151[b]	Residential periurban
La Frinière	15.3	4.5	76.6	18.9	1	36[c]	Agricultural periurban
Le Blosne	12.1	15.9	39.4	44.7	4–12	56[d]	Residential peripheral
Beaulieu	12.1	13.5	53.2	33.3	4–5	21[d]	Residential peripheral

[a] Semi-detached housing, large houses.
[b] Bungalows.
[c] Farms.
[d] Large apartment building complexes.

gradient selected, and based the urbanization gradient on plot location, percentage of built up area, and proportion of public and private gardens interspersed with buildings.

SURVEYS

Each plot was surveyed by walking in the morning and recording all birds seen or heard, according to the mapping method of Svensson (1974). A minimum of 1-1/2 hr was spent in each plot to insure a minimal coverage, and up to 2 hr were spent in plots with high numbers of birds to ensure complete coverage of the plot. Care was taken to avoid counting the same birds twice. Results are presented as mean number of birds detected per 10 ha. Plots ranged in size from 10 to 20 ha (Table 1). Four surveys were conducted in spring 1995 and two in winter 1995 in all Québec and Rennes plots. Québec plots also were surveyed three times in the winter of 1996. All winter surveys were conducted in January and February. Spring surveys were conducted from March to June in Rennes and late May to end of June in Québec. Proportions of vegetated open space and of human structures were derived from maps and aerial photographs (digitalization and analysis by GIS).

In Québec, we classified species as native or introduced. Introduced species included the House Sparrow, European Starling, and Rock Dove (scientific names in Appendix). Although not introduced in Rennes, these species also have been grouped together in this town to facilitate comparisons between sites. Diet of birds were adapted from Voous (1960) for Europe and from Gauthier and Aubry (1996) for Canada. Feeding types included insect feeder, seed and vegetation feeder, omnivore, and carnivore.

Cluster analysis was performed by the cluster procedure of SAS using the average linkage method (SAS 1989). We used the Shannon-Wiener and the Simpson indices of diversity. Evenness was measured using the Shannon index (Magurran 1988). Similarity indices were calculated using Horn index (Krebs 1989). Means ± SE are presented.

RESULTS

HABITAT FEATURES

Selected plots can be ordered along an urbanization gradient reflected by the proportions of vegetated open space and human made structures (buildings and roads). In Québec, vegetated open areas ranged from 17% in the downtown area to 86% in the rural area (Table 1).

TABLE 2. Bird species diversity and density per 10 ha in spring along an urbanization gradient.

	Shannon-Wiener	Simpson's	Evenness	Richness[a]	Bird density/ 10 ha	% of introduced species[b]
Québec						
Downtown	1.72	2.4	0.67	13	64.1	68
Limoilou	1.65	3.5	0.63	19	104.9	73
Montcalm	2.14	6.0	0.73	25	63.6	52
Sillery	2.60	11.5	0.81	31	70.3	34
Les Saules	2.33	7.9	0.74	25	116.2	35
Saint-Augustin	2.47	10.3	0.82	23	141.8	27
Ancienne-Lorette	2.53	9.7	0.77	27	74.5	48
Charlesbourg[c]	1.58	3.2	0.62	14	79.8	75
Pointe Sainte-Foy[c]	2.11	6.0	0.68	27	48.4	51
Rennes						
Downtown	1.75	4.1	0.62	17	281.4	52
Sévigné	2.42	7.0	0.77	23	155.0	26
Ste-Thérèse	2.20	5.3	0.72	21	213.5	27
St-Élizabeth	2.42	7.8	0.77	23	182.7	43
St-Erblon	2.62	11.3	0.80	26	124.6	25
La Frinière	2.69	10.4	0.79	30	117.3	34
Le Blosne[c]	2.30	6.3	0.72	24	137.6	47
Beaulieu[c]	2.63	10.4	0.82	25	169.4	36

[a] All species.
[b] Species included are House Sparrow, European Starling, and Rock Dove.
[c] Large apartment building complexes.

Charlesbourg and Pointe Ste-Foy are distinct from other areas by the presence of large apartment buildings and large amounts of paved sections.

In Rennes, the gradient was less gradual with only 1% open areas in the downtown area and more than 35% in the residential center and peripheral areas (Sévigné, Ste-Thérèse, St-Élizabeth) (Table 1). The amount of open space increased to 47% in St-Erblon and to 77% in La Frinière, the agricultural periurban plot. The two multistory large apartment building complexes differed in their proportions of open vegetated and paved areas with Le Blosne being the less vegetated one (Table 1).

BIRD DIVERSITY DECREASES WITH URBANIZATION

Bird diversity can be expressed in various ways depending upon emphasis put on richness or evenness (Magurran 1988). All indices used suggested an increase in diversity from most to least urbanized plots in spring (Table 2) and winter (Table 3) in both cities. However, a significant correlation between vegetated cover percentage and each bird diversity index was obtained in spring in both regions (Spearman r always > 0.77 and P always < 0.04), whereas no correlation was found in winter. In this last season, some urban plots (e.g., Sillery or Beaulieu) had better diversity than periurban plots and seem to act as refuge for some species.

In Québec, during spring, the downtown and Limoilou plots had less diverse bird communities than more peripheral residential areas. The old and more urbanized apartment building plot (Charlesbourg) supported a less diverse and even bird community than the newly built plot (Pointe Ste-Foy). As in Québec, the downtown area in Rennes had a lower diversity than peripheral and periurban areas, and the more urbanized apartment complex (Le Blosne) had a lower diversity than the more vegetated one (Beaulieu).

In Québec, all diversity indices were much lower in winter than in spring ($Z = 2.67$, $P = 0.01$, Wilcoxon test), but there was no difference in Rennes ($Z = 0.85$, $P = 0.40$). Some residential areas were more diverse in winter, especially areas adjacent to the downtown center (Sévigné and Ste-Thérèse). Winter species diversity and richness was quite low in Québec compared to Rennes. Winter diversity indices were nearly twice as high in Rennes compared to Québec. Evenness was lowest in the downtown area in both cities and in the most urbanized apartment building complex, more so in Québec (0.59 vs 0.72, respectively) than in Rennes (0.81 vs 0.86, respectively). As a whole, evenness of bird com-

TABLE 3. Bird species diversity and density per 10 ha in winter along an urbanization gradient.

	Shannon-Wiener		Simpson's		Evenness		Richness[a]		Bird density		% of introduced species[b]	
	1995	1996	1995	1996	1995	1996	1995	1996	1995	1996	1995	1996
Québec												
Downtown	0.67	0.47	1.5	1.3	0.48	0.34	4	4	48.1	36.2	99	99
Limoilou	0.89	0.93	2.1	2.0	0.64	0.52	4	6	102.0	111.5	98	98
Montcalm	1.10	1.26	2.1	2.5	0.57	0.57	7	9	54.8	67.5	86	74
Sillery	1.93	1.94	5.3	5.7	0.80	0.74	11	14	49.7	48.1	49	44
Les Saules	1.55	1.10	4.0	2.1	0.75	0.53	8	8	36.0	52.0	69	89
Saint-Augustin	1.71	1.44	4.0	3.3	0.71	0.65	11	9	64.6	90.9	77	88
Ancienne-Lorette	1.03	0.86	2.3	2.1	0.57	0.54	6	5	36.3	41.6	96	96
Charlesbourg[c]	0.95	0.86	2.3	1.9	0.59	0.53	5	5	95.7	95.9	98	91
Pointe Sainte-Foy[c]	1.00	1.05	2.4	2.6	0.72	0.65	4	5	37.7	37.9	89	91
Rennes												
Downtown	1.30		2.5		0.49		14		249.0		75	
Sévigné	2.50		9.2		0.83		19		100.7		47	
Ste-Thérèse	2.45		8.1		0.80		20		113.2		45	
St-Élizabeth	2.30		6.6		0.74		21		163.3		47	
St-Erblon	2.46		9.5		0.83		18		105.3		26	
La Frinière	2.52		8.5		0.79		24		109.6		36	
Le Blosne[c]	2.38		8.2		0.81		19		115.5		38	
Beaulieu[c]	2.63		11.3		0.86		21		96.6		30	

[a] All species seen or heard.
[b] Species included are House Sparrow, European Starling, and Rock Dove.
[c] Large apartment building complexes.

munities did not differ significantly in Rennes between spring and winter ($Z = 0.93$, $P = 0.35$, $n = 8$, Wilcoxon test) nor in Québec ($Z = -1.61$, $P = 0.11$, $n = 9$). In Québec, for at least four plots (downtown, Limoilou, St-Augustin, Ancienne-Lorette), evenness was lower in winter (Tables 2, 3). In Rennes, evenness was lower in winter than in spring in the downtown area but not in other areas (Tables 2, 3).

BIRD ABUNDANCE INCREASES WITH URBANIZATION

In Québec, during the breeding season, bird abundance varied greatly between plots, showing a bimodal distribution with a peak in the most urbanized residential plot, Limoilou, and another peak in residential areas with the most vegetation and open space, Les Saules and St-Augustin (Table 2). Bird abundance was especially low in the downtown area and in the newly built Pointe Ste-Foy. Introduced species were most numerous in the more urbanized plots where they also accounted for a greater proportion of the birds. Indigenous species were most abundant in the well-vegetated residential areas.

In winter (Table 3), more urbanized areas had higher densities of birds, whereas less urbanized areas supported fewer birds. The increase in the urbanized areas was due to introduced species (House Sparrow, European Starling, Rock Dove), which represented over 90% of the winter bird community. Their dominance was lower in less urbanized plots, although they still represented a greater proportion of the avifauna in winter than spring.

Breeding bird densities were higher in Rennes than Québec, especially in the most urbanized areas. Density in the downtown area was nearly four times greater in Rennes than in Québec. Overall, bird density averaged only 84.8 ± 10.0 birds per 10 ha in Québec compared to 172.7 ± 19.1 for Rennes. The variation in density between plots was similar in Rennes (CV = 31.4%) and in Québec (CV = 35.9%). Rock Doves, European Starlings, and House Sparrows did not dominate the avifauna in Rennes, although they were abundant. The gradient of decreasing dominance of these species from downtown to peripheral areas also was apparent in Rennes during the breeding season.

As expected, winter bird densities were higher in Rennes (131.7 ± 18.3) than in Québec (58.4 ± 8.3 in 1995; 64.9 ± 9.5 in 1996), but differences were smaller than during the breeding season. Winter bird densities in Rennes were lower in winter than spring in all plots, contrasting with Québec where bird densities were higher in winter in some of the most urbanized plots (Table 3). In Rennes, Rock Dove, European Starling, and House Sparrow dominance as a group was higher in winter in the three most urbanized plots but not in the other plots. As in spring, these three species dominated less the winter avifauna of Rennes than that of Québec.

The contribution of introduced and native species to the total breeding density varied along the urbanization gradient and contrasted between Québec and Rennes. In Québec, breeding densities of introduced and native species tended to be negatively correlated ($r = -0.22$, $n = 9$), whereas in Rennes they were positively correlated ($r = 0.40$, $n = 8$). Winter densities of introduced and native species tended to be negatively correlated along the urbanization gradient, especially in Québec ($r = -0.49$, $n = 9$) compared to Rennes ($r = -0.20$, $n = 8$). Although not statistically significant, these correlations suggest differences in the organization of bird communities in relation to the urbanization gradient and to the importance of introduced species in bird communities. Bird abundance increased with urbanization as introduced species increased. Densities of other species seemed more dependent on climatic conditions and features of urban plots.

COMMUNITY STRUCTURE

Bird communities are structured according to their species richness, composition, and abundance. Similarity indices combine these parameters and provide a global comparison of bird communities. In Québec, patterns of species richness and abundance indicated differences in bird communities between plots and seasons. Similarity measures (Horn index, Krebs 1989) regrouped the most urbanized plots (downtown, Limoilou, and Charlesbourg) together in spring and winter (Fig. 1). In spring, the rural area differed from all other plots, whereas in winter it was Sillery, an urban plot, that had quite a distinct bird community. The two most vegetated residential areas with small trees (St-Augustin and Les Saules) had fairly similar bird communities in spring.

In Rennes, plot grouping also reflected the urbanization gradient (Fig. 1). The downtown area contrasted greatly with other plots having a distinct bird community in both spring and winter.

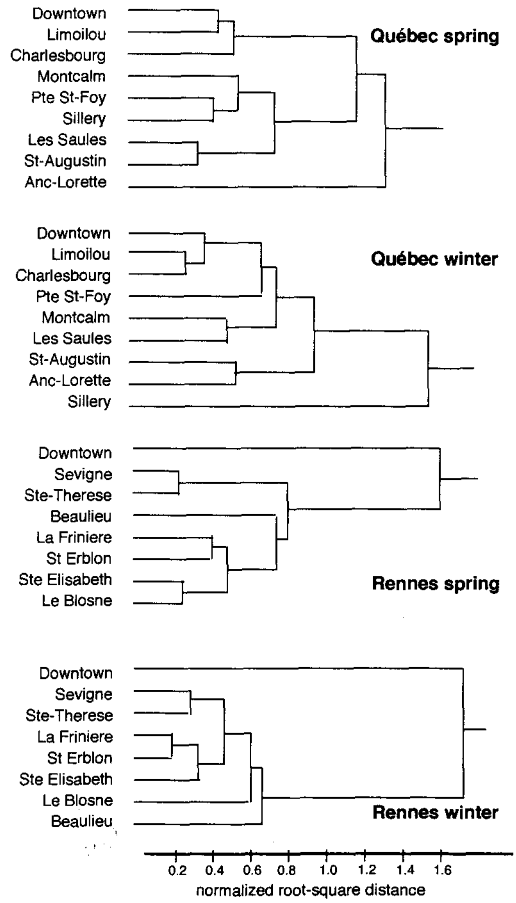

FIGURE 1. Groups of bird communities based on Horn similarity index in Québec and Rennes. The smaller the root-squared distance of a given branching is, the more similar are the bird communities of the plots or group of plots.

The two residential plots close to downtown were regrouped together in both seasons, as were the periurban plots. Classification of other plots differed in spring and winter reflecting changes in bird communities triggered by different factors in the two seasons. In winter, the large lawns of Beaulieu and Le Blosne were used by similar bird communities. In spring, differences observed reflected the different quality of open spaces (more trees and shrubs at Beaulieu) and a difference in human disturbance (Beaulieu less disturbed). Thus the urban gradient has a greater influence on the structure of bird communities in spring and winter.

Among the four feeding guilds, the insect feeders were the most sensitive to the quality of

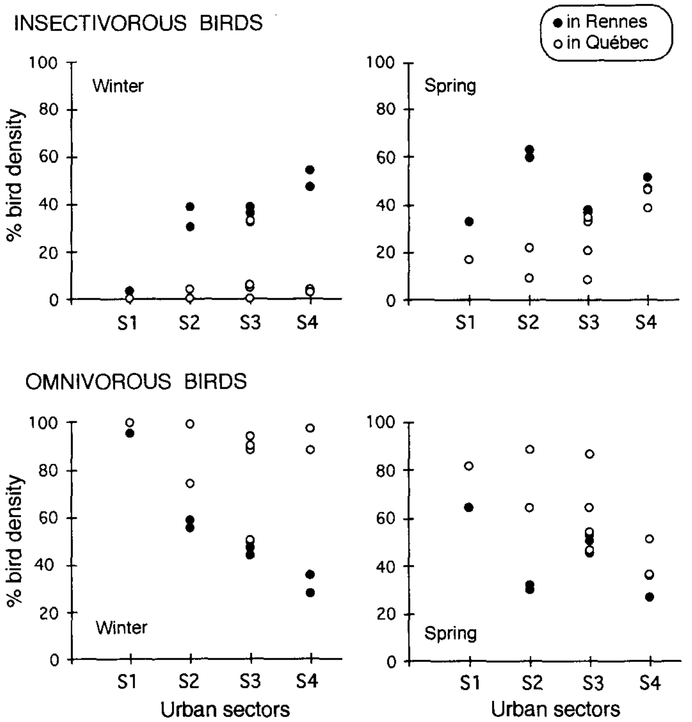

FIGURE 2. Relative abundance (%) of insectivorous and omnivorous birds at each plot. Data are presented among sectors of the urbanization gradient: S1 = downtown, S2 = pericentral sector, S3 = peripheric sector, S4 = periurban sector.

the environment and responded differently in the two cities (Fig. 2). In Rennes, these birds were nearly absent from downtown (S1) in winter. They represented 30–40% of the bird community in other urban plots (S2–S3) and 50% in periurban plots (S4). In spring, they represented similar proportions of the bird community in S3 and S4 as they did in winter, but nearly 20% more in the most urbanized sectors (S1 and S2). This highlights the small seasonal differences observed in Rennes and the spring influx of aerial insect feeders (swifts) in the most urbanized plots.

In Québec, insect feeders were nearly absent from the city in winter. Only one plot (Sillery, S3) supported a proportion of insect feeders similar to that of Rennes, probably because of its well developed vegetation (old trees). In spring, the proportion of insect feeders in the community followed the urbanization gradient coming close to, but not over, proportions in Rennes.

The omnivorous guild was clearly the typical guild of urbanized sectors. In Rennes, they represented a large proportion of the community in terms of numbers, their dominance decreasing along the downtown-rural gradient in both spring and winter. In Québec, they accounted for more than 95% of the birds seen in winter and still dominated the spring avifauna, representing up to 40% of the birds.

MAIN SPECIES IN TOWN

Like most bird communities, urban communities were dominated by a few abundant species. In Québec, during spring, the three most numerous species accounted on average for 59.1 ± 5.2% of the birds of a given area. In Rennes, they averaged 53.7 ± 4.7% of the birds. In both cities dominance was highest in the most urbanized portion of the gradient and lowest in the least urbanized. Three species, the House Sparrow, European Starling, and Rock Dove occurred in both cities and, as a group, dominated the avifauna of most plots in both spring and winter.

Spring densities of House Sparrows were similar in both cities, averaging 25.1 ± 4.2 birds per 10 ha in Québec and 29.5 ± 4.0 birds in Rennes. The highest density was found in Limoilou, Québec (50.7 birds per 10 ha), and the lowest density in Beaulieu, Rennes (12.2 birds per 10 ha). Winter densities averaged higher in Québec (32.6 ± 5.2 per 10 ha in 1995; 38.2 ± 5.2 per 10 ha in 1996) than in Rennes (25.7 ± 4.4 birds per 10 ha), but the difference was not statistically significant in either year (1995: $T = 1.45$, $P = 0.17$; 1996: $T = 1.00$, $P = 0.33$; t-test). House Sparrow densities in Québec were higher in winter than spring in most residential areas.

Spring densities of European Starlings also were similar in both cities, averaging 13.0 ± 1.5 birds per 10 ha in Québec and 14.2 ± 3.3 birds per 10 ha in Rennes. The highest density was found in Beaulieu, Rennes (32.9), and the lowest in Sévigné, Rennes (4.1). Average winter densities were similar in Québec (13.0 ± 4.6 in 1995; 10.4 ± 2.5 in 1996) and Rennes (10.8 ± 2.2) and were just slightly lower in winter than in spring in both cities. However, their distribution along the urban gradient differed between spring and winter in Québec, increasing in winter in some areas and decreasing in others. In Rennes, densities of starlings were higher in winter than in spring in the downtown area (17.8 vs 10.8) and in Sévigné (14.6 vs 4.1), a residential area adjacent to downtown. In Québec, old residential areas near downtown also had higher densities of starlings in winter (i.e., Limoilou 30.9 and 23.9 vs 12.0 in spring), but not the downtown area (4.2 and 2.8 vs 21.9).

Densities of Rock Doves were much lower in Québec than Rennes in both spring (3.8 ± 1.4 vs 20.7 ± 12.5) and winter (4.9 ± 1.0 and 7.3 ± 3.5 vs 26.1 ± 17.4). The major contrast between the two cities was the use of the downtown area by pigeons. In Rennes, densities reached 107.6 birds per 10 ha in winter and 147.0 birds in spring compared to less than 5 birds per 10 ha in Québec downtown area in either season.

In Rennes, Common Swifts were mostly observed in the downtown area, being nearly absent from other plots. A similar pattern was observed for Chimney Swifts in Québec. Two other species can be considered ecological equivalents: the American Robin and the European Blackbird. In Québec, the American Robin was mostly associated with well-vegetated residential areas where it reached densities of 20.3 birds per 10 ha. The European Blackbird reached its highest density in St-Élizabeth (29.6 birds per 10 ha), a residential sector comparable to those favored by American Robins in Québec. The European Blackbird also was present in winter in Rennes but in lower densities than in spring (10.7 ± 1.4 vs 16.7 ± 2.9) and with a similar pattern of distribution along the urbanization gradient as in spring.

The "introduced species" (non-native in America, synanthropical in Europe) are major species in the two cities with similar densities (except pigeon in downtown). Two equivalent thrushes also are well represented according to vegetated plots. However, these forest birds are not more common in Québec, a city surrounded mostly by forested landscapes, than in Rennes.

DISCUSSION

GRADIENT CONCEPT AND BIRD DIVERSITY

The urban environment is characterized by an urbanization gradient with increasing vegetation and decreasing human made structures from downtown to periurban areas. The gradient concept implies that environmental variability is spatially structured and that this pattern influences ecological processes and annual population dynamics (McDonnell and Pickett 1990, Blair 1996). The gradient concept in urban areas applies as well to social, demographic, and physical characteristics (Michelson 1970, Detwyler and Marcus 1972, Stearns and Montag 1974). In urban ecosystems, bird richness is affected by both the abundance and diversity of vegetation and by habitat heterogeneity (Lancaster and Rees 1979, Dowd 1992, Natuhara and Imai 1996). However, the highest richness is not always in the most natural habitats but often occurs in moderately perturbed ones (Nuorteva 1971, Petraitis et al. 1989, Jokimaki and Suhonen 1993). We observed a similar pattern in Québec and to a lesser degree in Rennes, that is, a decrease in species richness with increasing urbanization as shown in other urban studies in America (Batten 1972, Walcott 1974, Blair 1996) or in Europe (Marchetti 1976, Tatibouet 1981, Taylor et al. 1987). The lower response to the urbanization gradient in Rennes could be attributed to the well vegetated nature of the city. The age of a residential area influences directly species richness through the development of its vegetation, mainly the tree strata. In Québec, Sillery was an older residential area than Les Saules or Saint-Augustin and supported a richer avian community, although Sillery was more distant from the forest which can act as a species source. A similar increase in species richness with suburb age has been reported in several studies (Vale and Vale 1976, Hohtola 1978, Munyenyembe et al. 1989) and seems typical of most urban ecosystems. However, this increase in richness stabilizes when vegetation reaches its full development and even decreases in very old suburbs where trees form a continuous canopy (Savard 1978, Munyenyembe et al. 1989).

The relative spatial and temporal stabilities of the avifauna of Rennes (downtown excepted) likely reflect the quality of residential areas surrounding the center of the city which, because of their high and heterogeneous vegetative component, attract several insectivorous species. This is confirmed by comparisons with other large cities where residential areas adjacent to downtown areas are less vegetated and thus have more depauvrished bird communities. This is the case of Marseille in the south of France (Marchetti 1976), where the avifauna responded similarly to the downtown rural gradient as it did in Québec.

The higher bird diversity in spring than winter in Québec is typical of Canadian cities (Savard 1978) and is due mostly to the harsh winter climates. It contrasts with the pattern of higher winter diversity observed in Rennes. The lower evenness observed in the downtown area compared to other sectors in Québec and Rennes was not observed in Toronto, Canada (Savard 1978) or Syracuse, New York (Johnsen and Vandruff 1987). However, as in our study, the most natural area in Toronto had the highest evenness, and evenness tended to be higher in spring than winter (Savard 1978).

Our results permit us to generalize the response of the avifauna to the structure of temperate cities: the number of species decreases with level of urbanization. We also can qualify it in relation to intrinsic plot features, especially the importance of vegetation and climate, particularly snow on the ground. As most urban avifauna is composed of species not common in the surrounding landscape, the landscape context does not seem to play a crucial role in structuring the urban bird community. This is amplified by the functional differences of urban ecosystems compared to natural ones (Davis and Glick 1978). In large cities, local habitat features seem more important than the landscape setting of the city. This may be in part a question of scale as ecotone effect becomes more and more slight in large cities (Tomialojc 1970, Davis and Glick 1978). However, Luniak (1990) in his comparative study underscores the absence of correlation between urban avifauna and city size. In Tucson, Arizona, several species present in the city were absent from the surrounding landscape (Emlen 1974, Mills et al. 1989). Jokimaki et al. (1996) found no relationships between the structure of urban bird communities and latitude in northern Europe. Thus, the landscape setting of the city does not greatly influence the structure of the urban bird community.

BIRD ABUNDANCE AND AVIFAUNA STRUCTURE IN CITIES

The pattern of breeding bird abundance, unlike that of species richness, was not directly associated with the urbanization gradient in Québec or Rennes. In Québec, the clear bimodal pattern reflected the relative contribution of introduced and native species. Similar patterns were observed in Toronto (Savard 1978), with a higher bird abundance in residential areas adjacent to downtown than in the downtown area itself, a decrease in old residential neighborhoods with tall trees, and an increase in more open and young residential neighborhoods, followed by a decrease in the least urbanized sectors. Although less obvious, there also was a decrease in bird abundance in Rennes from downtown to agricultural areas, indicating that this pattern may be common to most urbanized areas (Weber 1972, Savard 1978).

The increase in bird densities in winter in the most urbanized plots of Québec suggests a shift from peripheral areas to plots with more favorable microclimates, shelters, and dependable food sources. Greater winter densities for resident birds are to be expected as populations include young birds and are more social, i.e., less territorial. Lack of such increase in density in Rennes may be attributed to the milder climate which may not concentrate birds as much as the harsh Québec climate. Movements of House Sparrows and European Starlings into more urbanized sectors of the city have been noted in winter in other North American studies (Johnsen and Vandruff 1987, Sears and Anderson 1991).

In Québec, Rock Doves were especially abundant in the harbor adjacent to the downtown area. Presence of grain elevators there may have contributed to the low abundance of Rock Doves downtown. Several species of swifts have adapted to the urban environments where they find suitable breeding substrates (Huhtalo and Jarvinen 1977, Savard 1978, Blair 1996). Rennes architecture is likely more suitable to breeding swifts than that of Québec. Savard and Falls (1982) showed that Rock Doves, House Sparrows, and European Starlings responded positively to building features that provided nesting and resting places. In Syracuse, New York, Rock Dove density was positively correlated to the age of structures, supporting the importance of architectural properties of buildings in the urban distribution of that species (Johnsen and Vandruff 1987).

Part of the answer may also be "historic-climatic:" the harsh winter of Québec forces birds south in the winter and it may be more difficult for migratory species to adapt to the urban environment. Differences in climate also seem to affect mostly native species, as introduced species had comparable densities in Québec and Rennes. Urban ecosystems are in constant change as exemplified by bird responses: for example, the recent colonization of several Canadian cities by Merlin *Falco columbarius* (Oliphant and Haug 1985, Sodhi et al. 1992), the expansion of the Mourning Dove and the House Finch in Québec city (Paquin 1995, Hill 1993), and the spectacular increase of starlings, gulls, and doves in European cities (Isenmann 1990, Clergeau et al. 1996).

These changes emphasize the highly dynamic and evolving nature of urban ecosystems. It is interesting to find similar breeding densities of both House Sparrows and European Starlings in the two cities. This suggests that ecological conditions found in the urban environment are similar for these species in the two cities. Urban bird communities are composed mostly of omnivorous species which have adapted or are adapting to human behavior and to various human by-products. Other species (seed eaters, insectivores, and frugivores) join that group according to the availability of other resources. Even under extreme conditions as in Québec during winter, a residential area can support a high bird diversity and abundance (comparable to residential areas with much milder climates) if it has good vegetative cover and sufficient food resources. Jokimaki et al. (1996) reached a similar conclusion for northern Europe. The quality of the landscape surrounding the city does not seem to play a preponderant role in bird abundance and community structure.

Our results confirm several patterns previously documented in other cities and provide a greater understanding and generalization of the features structuring urban bird communities. Indeed, we show that local features (site level) are more important than regional features (landscape level) in structuring urban bird communities. For us, the urban habitat is an original ecosystem with its own biological processes and its particular species. However, more ecological studies are needed, as for example, comparisons between cities especially including some tropical cities or quantification of biological rural-urban exchanges (e.g., role of corridor). A better understanding of these newly created and evolving ecosystems should help us understand natural ecosystems, contribute to a better management of increasing bird-people conflicts, and assist us in improving the quality of urban life.

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APPENDIX. Bird species and mean density (bird/10 ha) in Rennes (8 plots) and Québec (9 plots).

French species		Guild[a]	Rennes spring	Rennes winter	Canadian species		Guild[a]	Québec spring	Québec winter 95	Québec winter 96
Common Swift	*Apus apus*	i	29.7		House Sparrow	*Passer domesticus*	o	25.1	32.6	38.2
House Sparrow	*Passer domesticus*	o	29.5	25.7	European Starling	*Sturnus vulgaris*	o	13.0	13.0	10.4
Pigeon sp[b]	*Columba sp.*	o	20.8	26.2	American Robin	*Turdus migratorius*	i	7.1	0.3	
European Blackbird	*Turdus merula*	i	16.7	10.7	Common Grackle	*Quiscula quiscula*	o	5.1		
European Starling	*Sturnus vulgaris*	o	14.2	10.8	American Goldfinch	*Carduelis tristis*	g	5.0	0.1	0.4
Common Wren	*Troglodytes troglodytes*	i	7.2	5.7	Rock Dove	*Columba livia*	o	3.8	4.8	7.3
Great Tit	*Parus major*	i	6.7	7.2	Pine Siskin	*Carduelis pinus*	g	2.8	0.5	
Chaffinch	*Fringilla coelebs*	g	5.9	5.7	Tree Swallow	*Tachycineta bicolor*	i	2.8		
Greenfinch	*Carduelis chloris*	g	5.4	6.6	Ring-billed Gull	*Larus delawarensis*	o	2.7		
European Robin	*Erithacus rubecula*	i	5.1	5.5	Cedar Waxwing	*Bombycilla cedrorum*	i	2.5		
Herring Gull	*Larus argentatus*	o	4.7	7.9	Mourning Dove	*Zenaida macroura*	g	1.8	0.9	1.3
Dunnock	*Prunella modularis*	i	4.1	3.3	American Crow	*Corvus brachyrhynchos*	o	1.8	0.7	0.6
European Magpie	*Pica pica*	o	4.0	3.8	House Finch	*Carpodacus mexicanus*	g	1.3	1.0	1.0
Goldfinch	*Carduelis carduelis*	g	3.8	0.9	Chimney Swift	*Chaetura pelagica*	i	1.3		
Collared Dove	*Streptopelia decaocto*	g	2.7	0.6	Chipping Sparrow	*Spizella passerina*	g	1.0		
Carrion Crow	*Corvus corone*	o	2.6	2.0	Black-capped Chickadee	*Parus atricappilus*	i	1.0	2.1	1.7
Chiffchaff	*Phylloscopus collybita*	i	1.8	1.0	Cliff Swallow	*Hirundo pyrrhonota*	i	0.8		
Serin	*Serinus serinus*	g	1.8	0.5	Red-winged Blackbird	*Agelaius phoeniceus*	i	0.8		
Blue Tit	*Parus caerulus*	i	1.1		Yellow-rumped Warbler	*Dendroica coronata*	i	0.7		
Blackcap	*Sylvia atricapilla*	i	0.9	4.9	Barn Swallow	*Hirundo rustica*	i	0.5		
European Swallow	*Hirundo rustica*	i	0.7		Song Sparrow	*Melospiza melodia*	g	0.5		
Black Redstart	*Phoenicurus ochruros*	i	0.7		Brown-headed Cowbird	*Molothrus ater*	i	0.4		
Song Thrush	*Turdus phillomelos*	i	0.6	0.4	Yellow Warbler	*Dendroica patechia*	i	0.4		
House Martin	*Delichon urbica*	i	0.3		Kildeer	*Charadrius vociferus*	i	0.2		
Grey Heron	*Ardea cinerea*	c	0.3	0.1	Red-eyed Vireo	*Vireo olivaceus*	i	0.2		
Pied Wagtail	*Motacilla alba*	i	0.3	0.6	Bobolink	*Dolichonyx oryzivorus*	i	0.2		
Mallard	*Anas platyrhyncos*	g	0.2	0.2	Purple Finch	*Carpodacus purpureus*	g	0.1	0.9	
Great Spotted Woodpeck	*Dendrocopos major*	i	0.2		American Kestrel	*Falco sparverius*	c	0.1		
Short-toed Tree Creeper	*Certhia brachydactyla*	i	0.1	0.3	Savanah Sparrow	*Passerculus sandw.*	g	0.1		
Nuthatch	*Sitta europaea*	i	0.1	0.1	Creat-crested Flycatcher	*Myiarchus crinitus*	i	0.1		
Linnet	*Acanthis cannabina*	i		0.6	Tennessee Warbler	*Vermivora peregrina*	i	0.1		
Common Jay	*Garrulus glandarius*	o		0.2	Red-breasted Nuthatch	*Sitta canadensis*	i	0.1		0.1
European Kestrel	*Falco tinnunculus*	c		0.1	White-breasted Nuthatch	*Sitta carolinensis*	i	0.1	0.0	0.0
Green Woodpecker	*Picus viridis*	i		0.1	Downy Woodpecker	*Picoides pubescens*	i	0.1	0.1	0.0
Other species[c]			0.4	0.0	Evening Grosbeak	*Coccothraustes vespertin.*	g		0.5	0.1
					Blue Jay	*Cyanocitta cristata*	o	0.0	0.3	0.1
					Bohemian Waxwing	*Bombycilla garrulus*	g			1.0
					Northern Cardinal	*Cardinalis cardinalis*	g			0.1
					Northern Shrike	*Lanius exubitor*	c			0.1
					Other species[c]			0.7	0.2	0.2
Total bird density			172.7	131.7				84.8	58.5	64.6
Total number of species			30 (39)[c]	28 (29)[c]				34 (58)[c]	15 (19)[c]	15 (20)[c]

[a] i = insect feeder, g = seed and vegetation feeder, o = omnivorous bird, and c = carnivorous bird.
[b] Pigeon sp. includes Rock Dove (*Columba livia*) and Wood Pigeon (*C. palumbus*).
[c] Including other species whose mean density was under 0.1 bird/10 ha.