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John Faaborg

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QUALITATIVE PATTERNS OF AVIAN EXTINCTION ON NEOTROPICAL LAND-BRIDGE ISLANDS: LESSONS FOR CONSERVATION

By JOHN FAABORG

Division of Biological Sciences, University of Missouri, Columbia, Missouri 65201, U.S.A.

SUMMARY

(1) Previous application of island biogeographic theory to the design of nature preserves has focused primarily on the number of species that can survive in a given area with time.

(2) Here I examine qualitative patterns in Neotropical land-bridge island avifaunas to show the extent to which we can predict the types of species that will survive in bird communities of varying size.

(3) Each avian family shows consistent differences in its representation in mainland regions or on islands, in accordance with the total size of the avifauna present. Regressions of these data allow us to predict the smallest community in which a family member can exist.

(4) Distribution patterns within families show that species with wide ranges tend to survive on land-bridge islands in disproportionate numbers. This bias in survival ability would lead to increased convergence in preserved avifaunas.

(5) With these qualitative patterns and previously described quantitative formulas for extinction rates we should be able to predict both the rate of species extinction on a preserve and the species most extinction prone. Application of this knowledge on a regional basis might allow us to design an optimal system of refuges.

INTRODUCTION

In the past few years, ecological principles first delineated by island biogeographic studies have been used to explain numerous mainland situations (Vuilleumier 1970; Culver 1970; Brown 1971; etc.). The crowning achievement of this trend has been the application of island principles to conservation practices and the design of nature preserves (Diamond 1975a; Terborgh 1974, 1975; Wilson & Willis 1975; Diamond & May 1976). Islands have long been known to have a distinctive relationship between area and species number, a relationship which MacArthur and Wilson (1963, 1967) explained as a dynamic balance between colonization rate and extinction rate. Diamond (1972) noted that large land-bridge islands (islands connected to the mainland during the low ocean levels associated with Pleistocene glaciations) contained more species than area alone would predict, while smaller land-bridge islands contained the appropriate number of species. He suggested that islands that are supersaturated with species after severance of land connections should exhibit an excess of extinctions over colonizations (a process termed 'relaxation') until equilibrium is reached. While equilibrium has apparently been

achieved for smaller islands, the approximately 10 000 years since severance of land-bridges has apparently not been long enough for the largest islands to equilibrate.

With these observations in mind, it was easy for the authors mentioned above to see parallels between supersaturated land-bridge islands and extinctions that may occur when nature preserves are surrounded by inhospitable habitat. They predict that 'habitat islands' would lose species at a rate related to the area of the preserve and its separation from similar habitats. Support for this application has come from patterns of extinction on Barro Colorado Island, a reserve that is only 60 years old but has lost numerous forest species (Willis 1974), and from some isolated forest tracts in Brazil (Willis 1978).

So far this application of island biogeographic theory has primarily made predictions about the number of species that would survive in given areas through time. The suggested conservation practices have necessarily been crude. Generally, increasing the area preserved and decreasing the distance between areas have been suggested. Knowledge of differences among species in the ability to survive on land-bridge islands or reserves is essential to meaningful application of these principles; with random survival probabilities, a series of small preserves may be adaptive (Simberloff & Abele 1976), but with any consistent patterns of extinction the construction of many small parks could be a disaster due to convergence in the species that survive.

Previous analyses of qualitative patterns of land-bridge islands have been either too vague or too species-specific. In the former category are observations that certain families rarely or never appear on land-bridge islands. In the latter category we have the 'incidence functions' of Diamond (1975b), which point out extreme differences in extinction rates but which have limited predictive value. Observations that species with large territories and species with specialized foods or feeding techniques tend to be extinction prone are of value, but the fate of a majority of the avifauna is still unknown.

In this paper, I examine several Neotropical land-bridge islands for qualitative patterns that might be important to the proper design of tropical nature reserves. These islands are compared to several mainland areas for general patterns at the family level and their exact specific composition is compared with that of their presumed source areas in an attempt to delineate the amount of convergence between faunas of distant land-bridge islands. Though still of a general nature, the qualitative patterns shown here, when combined with the quantitative extinction rates computed by Terborgh (1975), put us a step closer to accumulating the detailed information needed to optimize preserve design in the Neotropics.

STUDY AREAS AND METHODS

Locations for which data were gathered are listed in Table 1 with the area, number of land bird species, and the source of ornithological data for each. Unlike the situation in the south-west Pacific, the Neotropics have a limited number of land-bridge islands. The four listed were selected because they covered a gradient in size and species number, they all contained relatively tall forest if not, in fact, rain forest, and they presumably received species from source faunas separated by about 1500 km (Fig. 1). All of Panama is considered the potential source area for Coiba, Rey, and San Jose, while for Trinidad the source fauna was compiled by listing the birds found in the Venezuelan states of Anzoategui, Sucre, Monagas, and Delta Amacuro. The four areas considered mainland controls were selected because they are not adjacent to the land-bridge islands, they have well-studied avifaunas, and they are not geographically very large. In the

TABLE 1. Characteristics of areas examined and sources of data

	Area (km ²)	Number of Bird Species	Source
Land-bridge islands			
Trinidad	4828	190	French 1973
Coiba	453	68	Wetmore 1957
Rey	249	42	MacArthur, Diamond & Kerr 1972
San Jose	47	36	Wetmore 1946
Mainland source faunas			
Panama	75 649	544	Ridgely 1976
North-eastern Venezuela	124 198	400	Meyer de Schauensee & Phelps 1978
Mainland control areas			
Costa Rica	50 699	486	Slud 1964
Honduras	112 087	365	Monroe 1968
Guatemala	108 000	365	Land 1970
Surinam	144 000	421	Haverschmidt 1968

compilation of lists only resident species were included and extremely rare species were deleted. Only non-raptorial land birds are included in this analysis (from Columbidae through the Fringillidae excluding the owls).

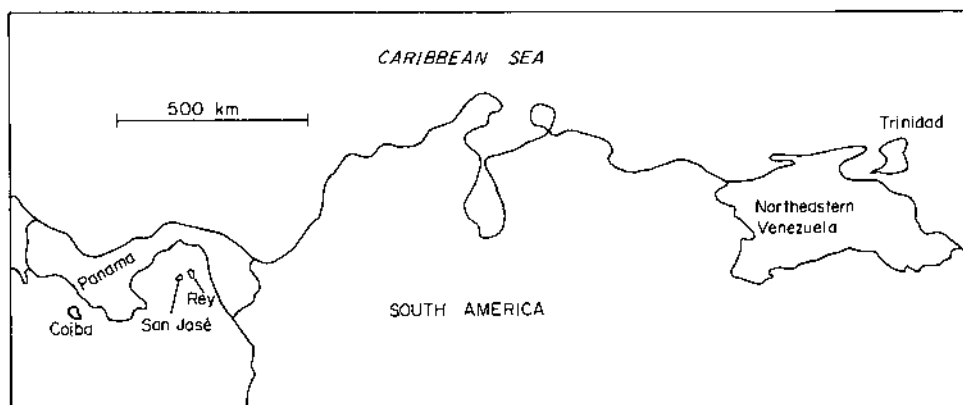


FIG. 1. Map showing the sizes and locations of the land-bridge islands and mainland source areas discussed in the text.

FAMILIAL PATTERNS IN LAND-BRIDGE AVIFAUNAS

Terborgh (1973) showed that the composition of West Indian bird communities could be analysed by family with resulting tight regressions of species number versus area for each family. Following his lead, I examined patterns in the number of species in a family versus the total number of species in the island or mainland community. The results from these regressions for twenty-four families or multiple family groups are shown in Table 2. The multiple family groups are either families of debatable taxonomic separation (*Vireonidae* & *Vireolanidae*) or families of similar ecology (*Nyctibiidae* with *Caprimulgidae* and combining large-billed insectivores in the *Momotidae*, *Buconidae*, and *Galbulidae*). Figure 2(a) plots these regressions for four families with rather similar slopes but different mainland densities, while Figure 2(b) plots two families with much flatter slopes.

TABLE 2. Characteristics of the regression of the number of species in a family with the logarithm of the total number of species in an area or island for families or multiple family groups on land-bridge islands and the mainland control areas

Family	slope	y-intercept	correlation coefficient	y = 1
Columbidae	14.493	-20.239	0.934	29
Psittacidae	13.543	-20.010	0.888	36
Cuculidae	6.868	-10.219	0.949	43
Nyctibiidae-Caprimulgidae	4.979	-5.533	0.791	21
Trochilidae	35.013	-55.331	0.925	41
Trogonidae	13.746	-28.354	0.795	137
Alcedinidae	2.827	-2.764	0.945	15
Momotidae-Galbulidae-Bucconidae	29.981	-66.438	0.943	178
Ramphastidae	13.541	-30.032	0.879	196
Picidae	14.507	-24.225	0.935	55
Dendrocolaptidae	29.350	-62.833	0.997	150
Furnariidae	15.438	-28.761	0.844	85
Formicariidae	25.883	-42.602	0.769	49
Pipridae	11.291	-21.208	0.786	93
Cotingidae	20.399	-37.623	0.838	79
Tyrannidae	41.961	-59.352	0.926	28
Troglodytidae	12.616	-20.329	0.770	50
Turdidae	11.326	-19.794	0.787	69
Vireonidae-Vireolaniidae	5.340	-7.706	0.937	43
Coerebidae	4.574	-5.515	0.903	27
Parulidae	9.175	-13.955	0.729	43
Icteridae	14.365	-22.705	0.936	45
Thraupidae	20.050	-47.244	0.902	46
Fringillidae	28.994	-44.744	0.914	38

We can see that each family loses species in a systematic fashion, but that the slopes of the regressions vary among families. Given different initial species densities, we see a wide range of x-intercepts. Perhaps more meaningful is the $y = 1$ value on the table, for it tells us the smallest species total in a community in which a family would still be represented. These values vary from 196 species for Ramphastidae and 178 species for the combined Momotidae-Bucconidae-Galbulidae to just fifteen species for the Alcedinidae. Because these regressions cover only land-bridge islands, the predictions for the avifaunas of small islands would not be accurate. On such small islands, most purely land-bridge species have probably gone extinct and the effects of colonization should largely determine the composition of the community. Thus, while the regressions predict no columbids or coerebids in avifaunas below twenty-seven species, colonizing members of these families appear in much smaller communities. For larger communities, though, these regressions do give us some feeling for the sensitivity of various families to insularity and the relative order in which they might disappear during the relaxation process.

Although the regressions for nearly all the families have high correlation coefficients, two major sources of scatter are readily apparent. The first of these is the scatter within the mainland control areas. In some families, the number of species in Surinam is grossly different from that found in the Central American areas. In some cases this may be a zoogeographic phenomenon, with ecological equivalents from the Neotropics and Nearctic replacing one another. For example, Surinam has forty-six Formicariidae but only three Parulidae; Costa Rica has twelve parulids but only twenty-nine formicariids.

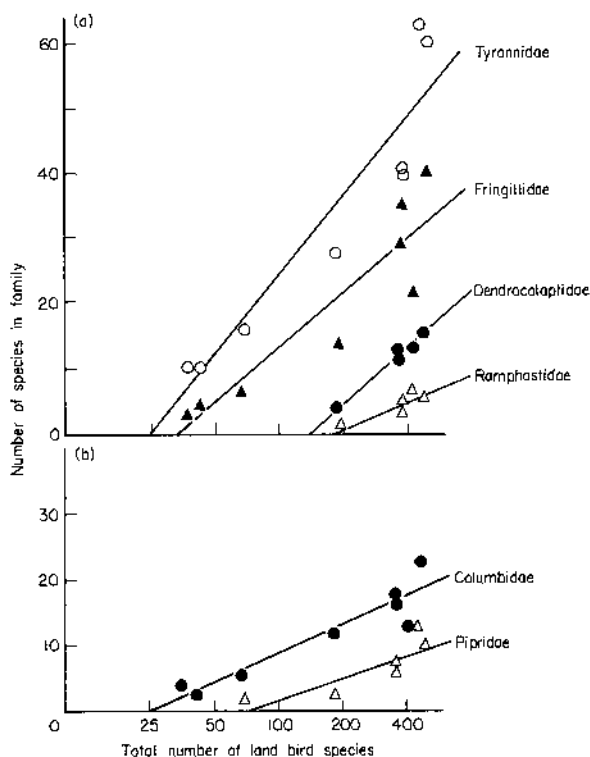


FIG. 2. Data points and regressions for (a) four and (b) two further families of Neotropical birds found in the mainland control areas and on at least one of the land-bridge islands.

The second source of variability in the regressions involves the fit of the island patterns with the mainland controls. For the small or specialized families very tight patterns appear. For large families which survive on smaller islands (such as the Tyrannidae and Fringillidae of Fig. 2), the points could often best be explained by a curve rather than a line. Although the insular points often form a straight line, this line tends to predict fewer species in the mainland faunas than actually occur. This discrepancy supports Terborgh's (1975) observation that extinction rates should be initially high on land-bridge islands. It also suggests that significant changes may be occurring within these families shortly after separation from the mainland when communities are at 200 to 300 species.

While of a general nature, the above material gives a good idea of the patterns of extinction expected to take place in a Neotropical nature preserve. The extinction process is quite orderly by family, but few broad patterns appear. Small families tend to have a higher probability of extinction than large families, but even this is variable. The dendrocolaptids and columbids do not differ greatly in their species densities on the mainland, yet the former will disappear in anything less than a 150 species community. The kingfishers (Alcedinidae) present an interesting case. In the Neotropics these birds are primarily aquatic and it is not surprising that they seem the least affected by insularity. The alcedinids of New Guinea are forest interior insectivores (much like the momotids and buconids) and there they are quite susceptible to insularity (Faaborg 1978). It

seems that specialized families or families with large-sized members (such as the Trogonidae, Momotidae, Bucconidae, Galbulidae, Pipridae, Cotingidae, and Turididae) are among the more extinction prone.

PATTERNS OF SURVIVAL AT THE SPECIES LEVEL

The previous material delineates patterns of general application. We can see that whole families will disappear if large enough bird communities are not preserved. With such orderly patterns by family, we must next examine specific patterns within families. How random is the survival of species within families, or how much might the presence of good survivors in a family lead to convergence in the species preserved in different areas?

When land-bridge islands were part of the mainland, it is assumed they contained a mainland species composition. Since they became islands they have lost species, but in 10 000 years it is assumed that the adjacent mainland pool should not have changed greatly. Thus the list of birds found in Venezuela adjacent to Trinidad should approximate that island's source fauna while the birds of Panama should approximate the source fauna for Coiba, Rey and San Jose. Table 3 compares the numbers of species of each family present in the two mainland areas with those appearing in the combined land-bridge island list.

The faunas of Panama and north-eastern Venezuela share certain species (which we shall call widespread species). If these species survive at the same rate as all other species, a uniform percentage of them should be expected in land-bridge avifaunas. Table 4 shows that this is not the case. Of 758 total species found in north-eastern Venezuela and Panama, 186 are shared (47% of the Venezuelan species and 34% of the Panamanian species). Of 229 total species preserved on the land-bridge islands, 125 come from this pool of widespread species. In other words, 60% of the birds of Trinidad are also found in Panama while 65% of the birds preserved on Coiba are found in north-eastern Venezuela, over 1700 km away.

Some of the widespread species are undoubtedly good colonists. A mobile species could be expected to be widespread, it could get to islands better than non-colonists, and many of them have been shown to invade forest in the absence of competition (MacArthur, Diamond & Karr 1972). Yet increased survival of these widespread species is shown among families known to be relatively poor colonists. Of twenty-eight Picidae in the source pool, six have survived on land-bridge islands and five of these are widespread species. Many families with one or two land-bridge representatives possess remnant widespread species. Even among the Tyrannidae, with a potential pool of 104 species, 60% of the species found on land-bridge islands are widespread on the mainland. Thus, whatever it is that allows these species to inhabit such large ranges must also give them exceptional powers of survival in insular conditions.

This predominance of widespread species may give us some insight into the problem noted earlier with the family regressions. If some families contain both highly specialized species (which are found only in large avifaunas, have restricted ranges, and are extinction prone (similar to the high S species of Diamond (1975b)) and more generalized, widespread species, rapid extinction of the specialized forms may occur even in communities above 200 species. Widespread species—be they mobile colonists of second-growth or just good surviving generalists—will benefit from the absence of specialists by increasing

TABLE 3. Summary by family of the number of species found in and shared by the mainland source faunas and the occurrence of these shared species on land-bridge islands

Family	No. in north-east Venezuela	No. in Panama	No. shared	Total species pool	No. on islands	No. shared species on islands
Columbidae	15	20	8	27	13	7
Psittacidae	23	21	6	38	12	3
Cuculidae	9	8	7	10	7	5
Steatornithidae	1	1	1	1	1	1
Nyctibiidae	2	2	2	2	1	1
Caprimulgidae	8	7	4	11	6	4
Apodidae	10	7	6	11	9	6
Trochilidae	34	51	11	74	24	8
Trogonidae	3	11	2	12	3	2
Alcedinidae	5	5	5	5	5	5
Momotidae	1	4	1	4	1	1
Galbulidae	2	4	1	5	1	1
Bucconidae	5	8	1	12	0	0
Capitonidae	0	3	0	3	0	0
Ramphastidae	5	6	0	11	1	0
Picidae	15	19	6	28	6	5
Dendrocolaptidae	12	17	11	18	4	4
Furnariidae	11	22	4	29	6	3
Formicariidae	22	37	10	49	10	5
Rhinocryptidae	1	3	0	4	0	0
Cotingidae	14	20	5	29	5	2
Pipridae	5	11	4	12	3	2
Oxyruncidae	0	1	0	1	0	0
Tyrannidae	67	71	34	104	35	21
Hirundinidae	7	5	2	10	6	2
Corvidae	2	4	0	6	0	0
Cinclidae	0	1	0	1	0	0
Troglodytidae	8	20	4	24	3	3
Mimidae	2	1	1	2	1	0
Turdidae	7	12	1	18	5	1
Sylviidae	2	4	2	4	2	2
Motacillidae	1	1	1	1	0	0
Ptilonotidae	0	2	0	2	0	0
Vireonidae	5	9	4	10	4	4
Coerebidae	9	10	5	14	6	5
Parulidae	8	13	5	16	5	3
Zeledoniidae	0	1	0	1	0	0
Icteridae	15	17	6	26	10	4
Tersinidae	1	1	1	1	1	1
Thraupidae	29	49	11	67	15	8
Fringillidae	34	35	14	55	18	6

their densities and perhaps moving into new habitats. After this has occurred, the relaxation rate should slow down. As noted earlier, Terborgh (1975) has suggested similar patterns in a more general way. This could only be properly tested with field studies comparing the structure of mainland and land-bridge island communities, but the research of MacArthur, Diamond & Karr (1972) and observations of the sources used in this study note the increased densities of many of the land-bridge island populations. Through these ecological interactions, one might expect high extinction rates in reserves during their early years of existence before more stable bird communities develop.

TABLE 4. Summary of the occurrence of widespread species in mainland source faunas and on land-bridge islands

Area	No. of species	No. of widespread species	Percentage of widespread species
Trinidad	190	112	59
Coiba	68	44	65
Rey	42	32	76
San Jose	36	27	75
Total species preserved	229	125	55
North-eastern Venezuela	400	186	47
Panama	544	186	34
Total species pool	758	186	25

CONCLUSIONS FOR CONSERVATION

The preceding analysis shows us that land-bridge islands possess highly non-random assemblages of surviving bird species. Each family exhibits a characteristic extinction rate that is correlated with the diversity of the community. Several families will survive only in complex avifaunas; to preserve them we must have large areas. We have also seen that certain members of each family are better able to survive in island reserves. Unfortunately, these are often widespread species and the result of their survival will be increased similarity of separated park avifaunas with time. Once again, the degree of expected convergence is related to refuge area; large refuges can be expected to preserve more species with restricted ranges.

With the above patterns and the quantitative relaxation formula of Terborgh (1975), a park designer who knows the area of a proposed refuge and the bird species list should be able to predict not only how many species will exist over the years but what most of these species will be. With refinement of the technique and a regional approach, one could optimize the placement of reserves to ensure maximum preservation of diversity in the future. The biggest problem with the Terborgh formula is that it only estimates the initial rate of extinction. The rapid qualitative shifts that we have seen support this hypothesis, but further analysis of patterns in the early stages of relaxation is vital. The loss of a large percentage of the Neotropical avifauna over a few thousand years is a frightening thought; the possibility exists that without proper planning such a catastrophe could occur in even a few hundred years.

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REFERENCES

- Brown, J. (1971). Mammals on mountaintops: nonequilibrium insular biogeography. *American Naturalist*, 105, 467-478.
- Culver, D. C. (1970). Analysis of simple cave communities: niche separation and species packing. *Ecology*, 51, 949-958.

- Diamond, J. M. (1972). Biogeographic kinetics: estimation of relaxation times for avifaunas of Southwest Pacific Islands. *Proceedings National Academy of Science, U.S.*, **69**, 3199-3203.
- Diamond, J. M. (1975a). The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation*, **7**, 129-146.
- Diamond, J. M. (1975b). Assembly of species communities. *Ecology and Evolution of Communities*. (Ed. by M. L. Cody and J. M. Diamond), pp. 342-444. Belknap, Cambridge, Massachusetts.
- Diamond, J. M. & May, R. M. (1976). Island biogeography and the design of natural reserves. *Theoretical Ecology*. (Ed. by R. M. May), pp. 163-186. W. B. Saunders, Philadelphia.
- Faaborg, J. (1978). Patterns in the nonpasserine component of tropical avifaunas. *Proceedings XVII International Ornithological Congress* (in press).
- French, R. (1973). *A guide to the birds of Trinidad and Tobago*. Livingston, Wynnewood, Pa.
- Haverschmidt, F. (1968). *Birds of Surinam*. Oliver and Boyd, London.
- Land, H. (1970). *Birds of Guatemala*. Livingston, Wynnewood, Pa.
- MacArthur, R. H., Diamond, J. M. & Karr, J. R. (1972). Density compensation in island faunas. *Ecology*, **53**, 330-342.
- MacArthur, R. H. & Wilson, E. O. (1963). An equilibrium theory of island zoogeography. *Evolution*, **17**, 373-387.
- MacArthur, R. H. & Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- Meyer de Schauensee, R. & Phelps, W. H. Jr. (1978). *A Guide to the Birds of Venezuela*. Princeton University Press, Princeton, New Jersey.
- Monroe, B. L. Jr. (1968). A distributional survey of the birds of Honduras. Ornithological Monograph no. 7, American Ornithologists' Union.
- Ridgely, R. S. (1976). *A Guide to the Birds of Panama*. Princeton University Press, Princeton, New Jersey.
- Simberloff, D. S. & Abele, L. G. (1976). Island biogeography theory and conservation practices. *Science*, **191**, 285-286.
- Slud, P. A. (1964). The birds of Costa Rica. *Bulletin American Museum of Natural History*, **128**, 1-430.
- Terborgh, J. (1973). Chance, habitat and dispersal in the distribution of birds in the West Indies. *Evolution*, **27**, 338-349.
- Terborgh, J. (1974). Preservation of natural diversity: the problem of extinction prone species. *Bioscience*, **24**, 715-722.
- Terborgh, J. (1975). Faunal equilibria and the design of wildlife preserves. *Tropical Ecological Systems: Trends in Terrestrial and Aquatic Research*. (Ed. by F. B. Golley and E. Medina), pp. 903-916. Springer-Verlag, New York.
- Vuilleumier, F. (1970). Insular biogeography in continental regions. The northern Andes of South America. *American Naturalist*, **104**, 373-388.
- Wetmore, A. (1946). The birds of San Jose and Pedro Gonzalez Islands, Republic of Panama. *Smithsonian Miscellaneous Collections*, **106**, no. 1.
- Wetmore, A. (1957). The birds of Isla Coiba, Panama. *Smithsonian Miscellaneous Collections*, **134**, no. 9.
- Willis, E. O. (1974). Populations and local extinctions of birds on Barro Colorado Island, Panama. *Ecological Monographs*, **44**, 153-169.
- Willis, E. O. (1978). The composition of avian communities in remanescent woodlots in southern Brazil. *Proceedings XVII International Ornithological Congress* (in press).
- Wilson, E. O. & Willis, E. O. (1975). Applied biogeography. *Ecology and Evolution of Communities*. (Ed. by M. L. Cody and J. M. Diamond), pp. 522-534. Belknap, Cambridge, Massachusetts.

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