RANGE EXPANSION OF THE CARDINAL AND OTHER BIRDS IN THE NORTHEASTERN STATES

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THE populations of the Cardinal (*Richmondena cardinalis*) and the Tufted Titmouse (*Parus bicolor*) have recently "exploded" in southern New England and the adjacent Hudson River Valley. The Carolina Wren (*Thryothorus ludovicianus*) and the Mockingbird (*Mimus polyglottos*) are also undergoing a range expansion in the same area, although to a much slighter degree. Both the Cardinal and the Tufted Titmouse are newcomers as breeding birds in the region east of the Hudson River and north of Long Island Sound. The Mockingbird, on the other hand, seems to be reinvading a territory it occupied several hundred years ago (Merriam, 1877). The Carolina Wren became established as a breeding bird in Stamford, Conn. about 1895 (Sage, 1913).

It is the purpose of this paper to investigate the characteristics of these range and population changes and to examine possible reasons for them.

SOURCES OF DATA AND METHODS OF STUDY

Audubon Christmas Counts have been used as a basis for determining population and range changes. Stewart (1954) has considered carefully many valid objections to these figures. He concludes that their "application . . . should be restricted to the indication of trends in population. . . ." With this restriction in mind, one notes that the figures do present a plausible and consistent picture, one not analyzable by refined mathematical techniques, but one which is nevertheless useful as a point of departure. Moreover, the general population trends so shown are substantiated by independent observations noted in *Audubon Field Notes, Records of New England Birds*, and other local ornithological publications.

Local or regional Christmas Count figures have been converted to numbers of birds seen per 100 party hours. (Stewart would prefer a conversion based on mileage rather than time, unfortunately an impossibility under present reporting methods.) No other adjustments have been attempted because of the difficulties in applying them equably.

Table 1 shows numbers of birds seen per 100 party hours for the four species for several contrasting regions. "Southern New England" includes the states of Connecticut, Massachusetts, and Rhode Island, and Long Island and the Hudson River Valley in New York State as well.

Figure 1 illustrates the changes in distribution and abundance of the four species from 1945 to 1960 in the area defined as "Southern New England." Figures 2 and 3 show details of individual counts for the Cardinal and the

TABLE 1

NUMBER OF BIRDS PER 100 PARTY HOURS ON AUDUBON CHRISTMAS COUNTS

Species and place	Number of birds by year																						
	1938	'39	'40	'41	'42	'43	'44	'45	'46	'47	'48	'49	'50	'51	'52	'53	'54	'55	'56	'57	'58	'59	'60
Tufted Titmouse																							
Southern New England							0	0.5	0	2	11	7	9	8	12	13	11	11	17	18	21	29	52
New Jersey		72	65	70	145	120	168	94	88	99	90	102	115	84	80	106	96	85	105	130	119	142	185
Pennsylvania		120	159	116	149	124	149	100	110	129	134	166	113	96	87	132	120	128	108	174	111	139	158
Michigan	72	65	38	92	101	28	97	96	84	46	52	48	78	57	45	49	57	49	40	57	112	70	73
Carolina Wren																							
Southern New England							0.2	0.2	0.2	0.2	0	0.4	0.8	0.9	2	2	3	2	6	9	4	7	11
New Jersey		5	1	2	3	5	8	2	13	10	5	5	15	17	13	10	14	13	17	19	16	22	10
Pennsylvania		6	4	6	7	5	13	3	7	8	7	12	9	11	9	15	20	15	15	34	15	23	15
Mockingbird																							
Southern New England							0	0.5	0	0	0.1	0.5	0.2	0.3	0.9	0.6	0.2	0.4	1	0.8	0.7	1	1
New Jersey		1	0.5	0	3	2	0.7	2	1	0.8	0.9	1	0.8	2	3	6	9	12	8	31	20	38	45
Pennsylvania		0.3	0.5	0.5	0.5	0	0.3	0.5	0.6	0.5	0.5	1	2	1	2	5	6	12	6	26	23	37	41
Cardinal																							
Southern New England							7	3	5	6	7	6	9	11	7	14	14	21	26	31	31	51	90
New Jersey		47	34	48	55	67	80	66	56	70	78	63	90	87	89	127	108	142	136	154	144	174	221
Pennsylvania		173	149	148	179	158	149	103	150	124	164	163	161	156	131	160	163	179	153	260	170	186	231
Michigan	122	155	109	114	257	120	266	114	156	152	108	151	154	170	171	137	108	148	144	181	206	156	210
Ontario	3	13	39	49	27	54	62	69	68	82	127	104	78	86	110	59	85	110	94	82	127	155	108
Eastern South Dakota											37	96	40	56	39	45	54	42	6	21	28	23	23
Pasadena, California									43	17	19	30	19	26	32	85	19	32	15	6	8	3	2

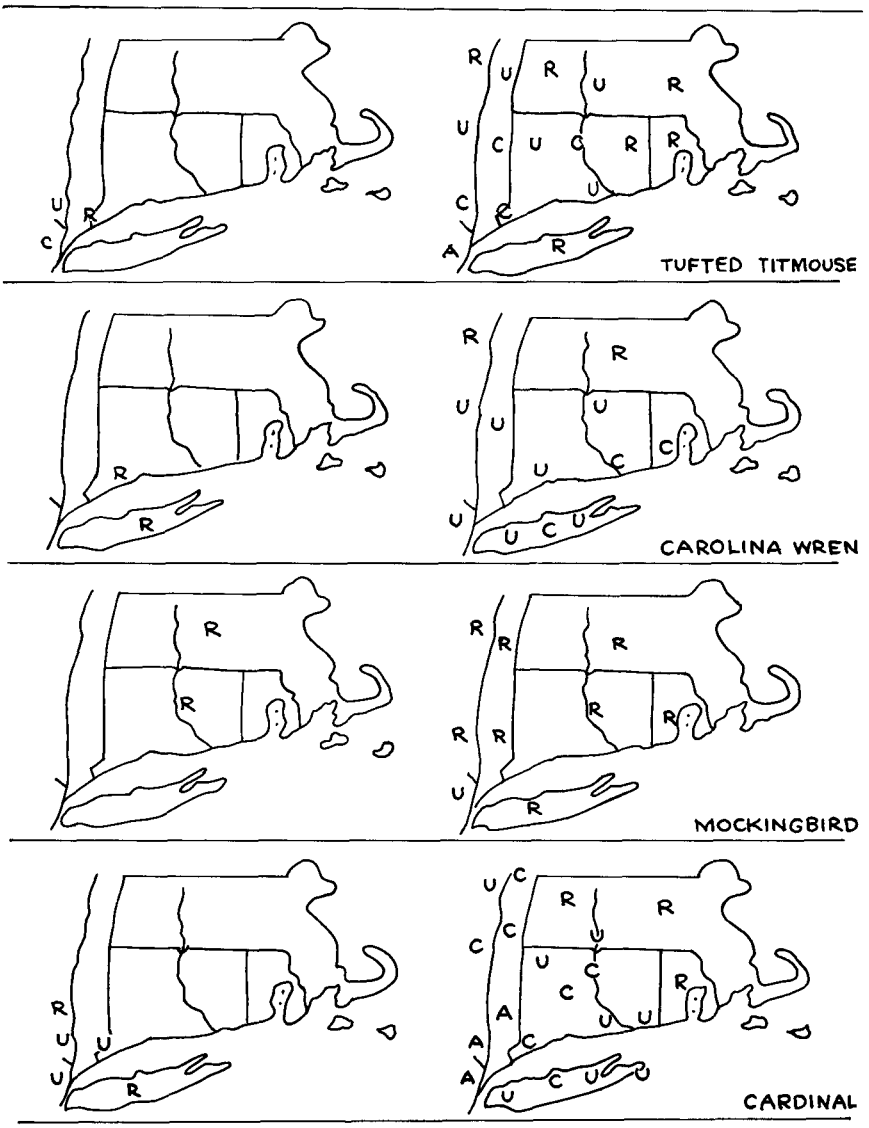

FIG. 1. Changes in distribution and abundance of four species of birds, 1945–1960, in Connecticut, Massachusetts, Rhode Island, and in Long Island and the Hudson River Valley, New York, based on Audubon Christmas Counts. Rare: 1–10 birds per 100 PH (party hours); Uncommon: 10–50/100 PH; Common: 50–250/100 PH; Abundant: over 250/100 PH.

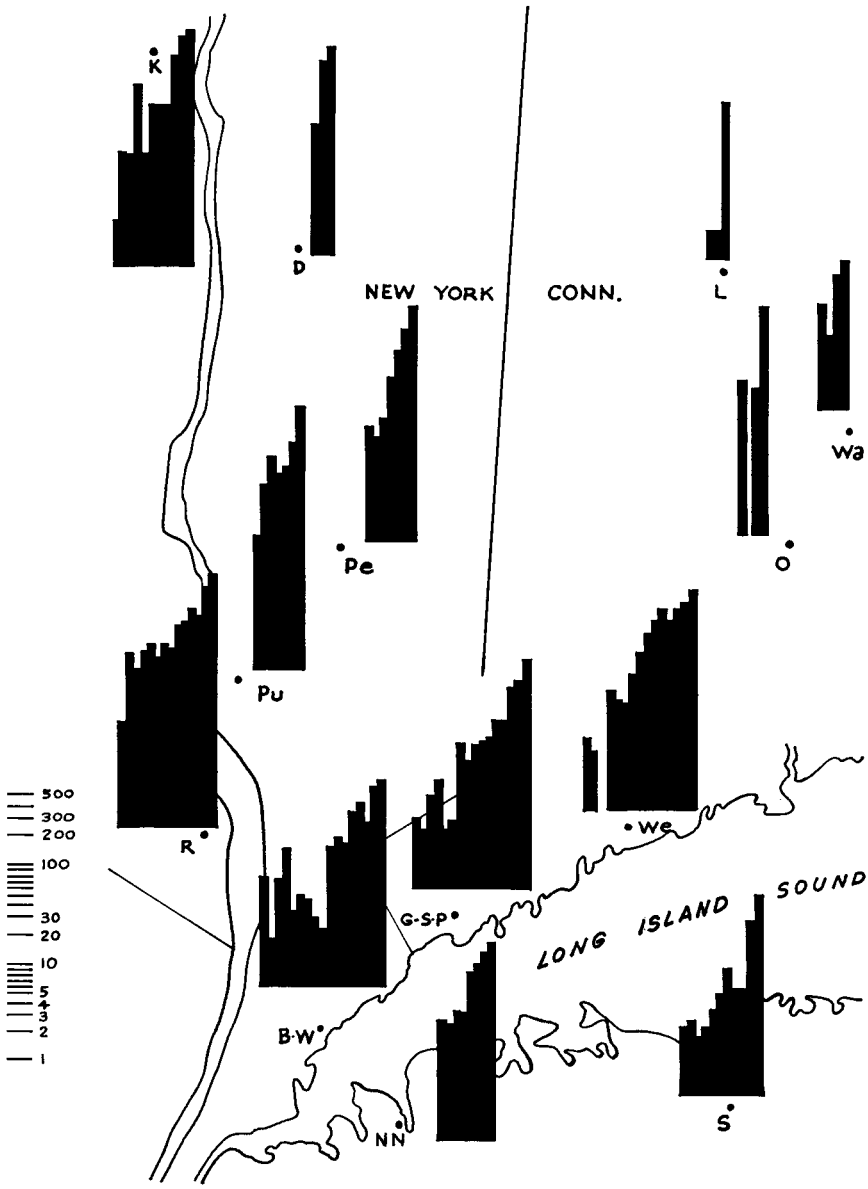

FIG. 2. Rate of population growth of the Cardinal, 1945–1960, in southeastern New York and southwestern Connecticut, based on Audubon Christmas Counts (see text). Last bars on right refer to 1960.

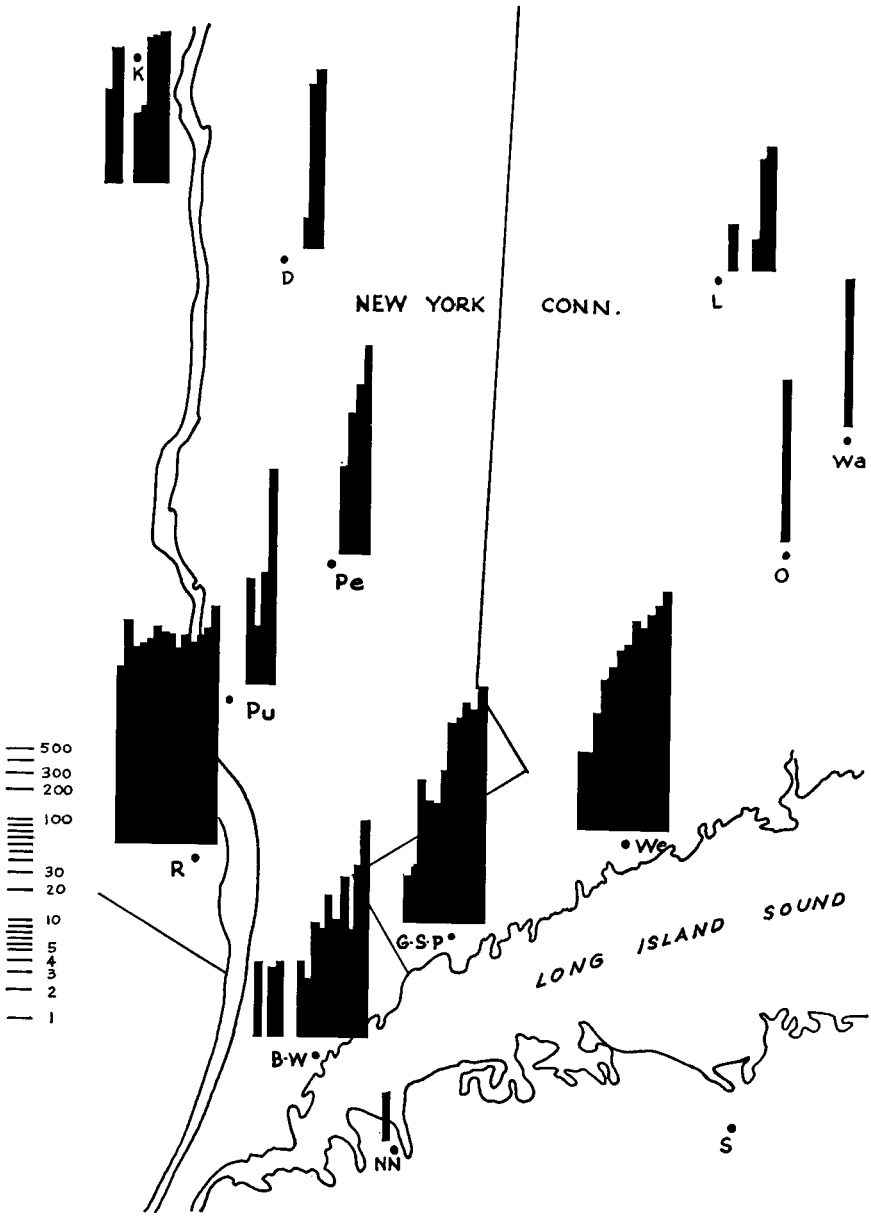

FIG. 3. Rate of population growth of the Tufted Titmouse, 1945–1960, in southeastern New York and southwestern Connecticut, based on Audubon Christmas Counts (see text). Last bars on right, or single bars, refer to 1960.

Tufted Titmouse in the area that includes the lower Hudson River Valley (Bronx-Westchester Region, Dutchess Co., Kingston—Lake Mohonk, Peekskill, Putnam Co., Rockland Co.), northern Long Island (Northern Nassau Co., Smithtown), and southwestern Connecticut (Greenwich—Stamford—Portchester, Litchfield Hills, Oxford, Waterbury, Westport). A logarithmic scale has been used to indicate rate of growth.

RANGE AND POPULATION CHANGES

The Cardinal population in Southern New England has increased spectacularly in the past 15 years. This species first nested in Connecticut around 1943, and in eastern Massachusetts in 1958 (*Audubon Field Notes*). Westward across the Hudson River it is now a common year-round resident in Rockland Co., N.Y., although 30 years ago it was confined to the southeastern corner of this county (Rockland Audubon Society, 1959). The New Jersey population has been increasing steadily for the past 20 years. In Pennsylvania there has been an increase in the northeastern part of the state, although in general the population has been relatively stable for the past 20 years (based on state and local Christmas Counts). An earlier increase in this state is noted by Sutton (1928). Relative stability has also been reached in Michigan, following an increase that began about 1900 (Burns, 1958). The apparently related increase in Ontario, dating from about 1938 (Snyder, 1951), is now slowing down. The population in South Dakota, on the other hand, shows a marked decline in the last decade. The Cardinal population is also decreasing in Pasadena, California, where the species was successfully introduced in 1923 (Grinnell and Miller, 1944). At its present rate of decline it appears headed for extinction there.

The Tufted Titmouse is much less widely distributed in Southern New England than the Cardinal, but the pattern of its population growth is similar. This species first nested in Connecticut in 1946 and in eastern Massachusetts in 1958 (*Audubon Field Notes*). It has become established in Rockland Co., N.Y., within the past 30 years (Rockland Audubon Society, 1959). The recent increases in New Jersey are actually confined to a few places in the northern part of the state, while there has been little recent change in Pennsylvania.

The Carolina Wren population has also increased in Southern New England. It is quite limited in both distribution and numbers, however, being largely confined to areas along Long Island Sound. Earlier upward trends in New Jersey and Pennsylvania have leveled off.

The Mockingbird population has increased slightly in Southern New England but, at the rate of one bird seen per 100 party hours, it is certainly far from common. On the other hand, the New Jersey and Pennsylvania popu-

lations have increased as sharply as have those of the Cardinal and Tufted Titmouse in New England, although the numbers are smaller. An earlier increase in Maryland dates from about 1900 (Stewart and Robbins, 1958).

A population buildup within the original range preceding an extension of the range was suggested by Odum and Johnston (1951) as a factor in the southward movement of the House Wren. Population pressure does appear to play a part in the northward movement of the four species considered here (see Table 1; Figs. 1 and 2). Such a buildup and the resulting population pressure may also lead to the successful crossing of geographical barriers and the invasion of previously isolated territory (see below). The conditions encountered in such new and isolated territory must be unusually favorable to permit more than temporary occupation of it. This seems to have been true for the Cardinal and the Tufted Titmouse in Southern New England. The rapid increase in their numbers is still continuing, resulting in fairly large, native populations which are no longer dependent on irregular immigration.

Furthermore, such a rapid increase implies a high survival rate, greater success in rearing young, an increase in clutch size or number of broods, or some combination of these factors. It is possible that the Cardinal may be more successful in rearing a large brood in this area where the population density is still comparatively low and intraspecific competition presumably less intense. Four live young have been reported several times in New England (*Audubon Field Notes*). At a similar latitude in southeastern Michigan where the Cardinal is common, Sutton (1959) found that only three eggs hatched in the two nests where four were laid. Three successful broods have been reported for a pair of Cardinals and two for a pair of titmice in Massachusetts (*Audubon Field Notes*), both high for the species involved.

Another point is the rapidity of the response to changing environmental conditions. Since time would be required for the population buildup, Odum and Johnston (1951) concluded that a time lag would exist between changing biotic conditions and range extension. This lag may also exist in connection with climatic changes (see below).

FACTORS INFLUENCING RANGE AND POPULATION CHANGES

Relevant characteristics of the birds are their general adaptation and adaptability and their general mobility; significant environmental factors are climate and weather, available habitat, geographical barriers, and man. There is constant interaction among all these factors whose relative importance also varies according to species, location, etc.

Adaptation and adaptability.—Here is meant the general type of habitat for which the species is adapted and its ability to make use of changed conditions. The Cardinal, Carolina Wren, and Mockingbird show a preference for thick-

ets, tangles, underbrush, and shrubbery (Bent, 1948; Burleigh, 1958; Hundley, 1953; Laskey, 1944; Pough, 1946). Thus, activities of man which increase this sort of habitat should be beneficial to these species. This seems to be true for the Cardinal and Mockingbird, which also show great adaptability to the presence of man himself. Wilson (1831) noted that all except the Carolina Wren were common around farm houses, particularly in winter. The behavior of the Carolina Wren, the least common of the four species, shows considerable ambivalence (Bent, 1948; Pough, 1946). Some individuals are willing to accommodate themselves to man as a close neighbor and others are not. Certainly this species' chances of long-term survival would be improved if its acceptance of man were increasing.

The Tufted Titmouse is largely a forest bird (Pitelka, 1941), although it may wander in more open areas outside the nesting season. It shows great adaptability to man himself, being a frequent visitor at feeding stations. But its general adaptation to a forest habitat means that its success is limited by the availability of this habitat.

Mobility.—Powers of dispersal are naturally important in a discussion of range extension. All four species are considered to be nonmigratory, but a certain amount of movement does exist and can be demonstrated in various ways. Banding records for individual birds indicate a minimum amount of movement for the Cardinal (Geis, pers. com.; Hundley, 1953; Laskey, 1944; Lincoln, 1939; Stewart and Robbins, 1958). In general, those recovered have been found within a distance of five miles of the banding station, although long distance records do exist. The Titmouse is found within an even smaller area (Van Tyne, 1948). The Mockingbird has been recovered at greater distances (Lincoln, 1939). This indeed seems a necessary corollary to the small, widely scattered population in New England.

Of equal interest are the birds which are never seen again, generally a rather high percentage of those banded. Either they have died, become trap-shy, or moved on. That there must be a good deal of movement, particularly during the winter, is shown by the marked seasonality of the appearance and disappearance of Cardinals where banding has taken place at one location over a period of time (Geis, pers. com.; Hundley, 1953; Laskey, 1944). The largest numbers of new birds are banded in the months from November to February. This point is also corroborated by *Records of New England Birds*, which reports twice as many Cardinals seen in these same months as in the remainder of the year.

Another method of demonstrating movement is to compare occurrence and population density in the winter-bird and breeding-bird censuses published in *Audubon Field Notes* (see Table 2). No attempt has been made to compare habitats because of the many difficulties involved in classifying them. How-

TABLE 2

COMPARISON OF WINTER-BIRD AND BREEDING-BIRD CENSUSES, 1956–1960*

Species	Winter-bird censuses				Breeding-bird censuses**			
	Present on		Over 13/100 acres		Present on		Over 13/100 acres	
	No.	%†	No.	%‡	No.	%†	No.	%‡
Tufted Titmouse	75	51.3	20	26.7	75	40.0	38	52.0
Carolina Wren	51	35.0	5	9.8	60	32.8	17	28.4
Mockingbird	25	17.3	2	8.0	16	8.75	3	18.8
Cardinal	98	67.0	11	11.2	88	47.0	51	59.2

* From *Audubon Field Notes.*
** Pairs converted to individuals, young not included.
† Per cent of total censuses.
‡ Per cent of censuses where present.

ever, it is clear that for each species the winter populations are both more widely dispersed (with the possible exception of the Carolina Wren) and less dense than the summer populations. The change in density is plainly shown by the winter and summer censuses taken at two locations in El Dorado, Arkansas (see Table 3). The winter decrease in density must be attributed more to dispersal than to mortality since the species are then found at more places, and the succeeding increase in breeding-bird density does not include young of the

TABLE 3

COMPARISON OF WINTER-BIRD AND BREEDING-BIRD POPULATIONS, EL DORADO, ARKANSAS*

	Number/100 acres					
	Tufted Titmouse		Carolina Wren		Cardinal	
	Winter	Breeding**	Winter	Breeding**	Winter	Breeding**
Year	Upland pine and pine–oak woodland					
1953	9	26	9	38	+	34
1954	9	30	9	30	+	34
1955	9	44	4	30	4	30
1956	13	48	13	26	4	60
1957	13	52	13	60	9	74
	Mature oak–pine stream bottomland					
1951		40		18		54
1952	9	54	9	40	4	50
1953	25	36	10	50	5	50
1954	15	112	20	50	15	70
1955	25	90	10	56	15	60
1956	25	60	25	122	10	56
1957	30	80	20	150	40	70

* From *Audubon Field Notes.*
** Pairs converted to individuals, young not included.

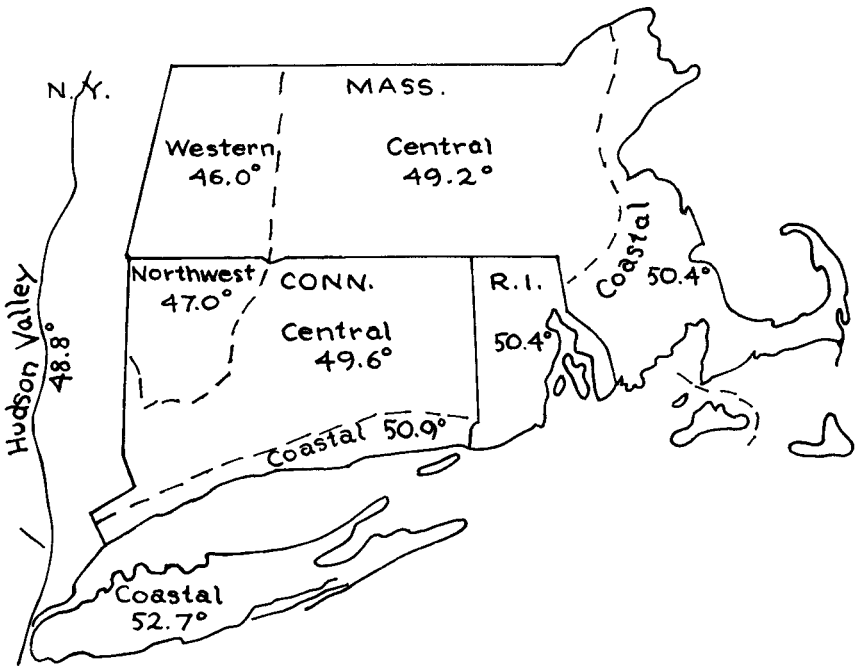

FIG. 4. Climatic divisions, with mean annual temperatures, 1931–1955. From U.S. Weather Bureau data.

year. This implies a winter dispersal followed by a withdrawal (to more favorable breeding areas?) before the breeding season begins.

Thus, a certain amount of exploratory activity occurs in all four species, making range extension possible under advantageous conditions.

Climate and weather.—Little is known about the temperature tolerances of birds. Nevertheless, it seems possible to draw certain general conclusions from present distribution and abundance (based on local Christmas Counts). These have been compared with the mean annual temperature of the climatic divisions of the states as drawn by the U.S. Weather Bureau (1959, 1960). Figure 4 summarizes this information for Southern New England.

The Cardinal is the most temperature tolerant of the four species. It is common in all the climatic divisions of Pennsylvania with a mean annual temperature above 48 F, although it is also present in the two colder divisions, the Pocono Mountains and the Upper Susquehanna. In Southern New England, only northwest Connecticut (47 F) and western Massachusetts (46 F) fall below 48 F, an indication that climatic conditions in most of this area are generally suitable for the Cardinal. Here one might note that northwest

Connecticut appears to be a barrier and that the Cardinal seems to be spreading up the Hudson River Valley and the Connecticut River Valley more or less independently (see Figs. 1 and 2).

The Tufted Titmouse is fairly numerous in all the climatic divisions of Pennsylvania with a mean annual temperature of 50 F and above. On this basis, one would expect the main population growth of the titmouse in New England to be confined to coastal areas and the lower Hudson River Valley. Northward movements into New Hampshire and even Maine were noted in the fall of 1961 (*Audubon Field Notes*); it will be interesting to see if breeding records follow.

The Carolina Wren is found in Pennsylvania and New Jersey where mean annual temperatures range from 50 to 53 F, although it is more numerous in the warmer sections. Again, one would expect the principal development in New England to be in the coastal areas. It is commonly noted in the literature, however, that this species is subject to winter kill. Its numbers are very erratic within a wide span along its northern boundary.

The Mockingbird is relatively common in those climatic divisions of Pennsylvania and New Jersey having mean annual temperatures of 53 F and above. It seems unlikely, on this basis, that the Mockingbird will become common in New England under present conditions.

All of these species appear to have definite climatic limitations. From this it may be deduced that climatic warming would favor northward expansion and, conversely, that climatic cooling would lead to a contraction of range at the northern edge. Figure 5 shows the mean annual temperature above and below the long-term average for the states of Connecticut, Massachusetts, and Rhode Island combined, since 1900. The long-term trend has been upward, although the most recent years suggest a reversal of this trend. The trend for New Jersey follows a similar pattern. In Pennsylvania, however, the peak was reached in 1931 and the trend has been downward ever since.

Drury (1957, 1958) notes the vegetational changes in old-field successions in southern New England as a result of climatic warming. There has been a northward expansion of red cedar (*Juniperus virginiana*) and gray birch (*Betula populifolia*), and an accompanying northward retreat of new white pine (*Pinus Strobus*).

In looking for relationships in the trends, one finds that the Cardinal became established in Southern New England in the late 1940's and the early 1950's, during the long period of above average temperatures which began in 1931. The previous increases in New Jersey and Pennsylvania may well have been sparked by the rising temperature trends there. It is noteworthy, however, that the Cardinal has continued to increase in New England while weather conditions in recent years have become much more severe. From

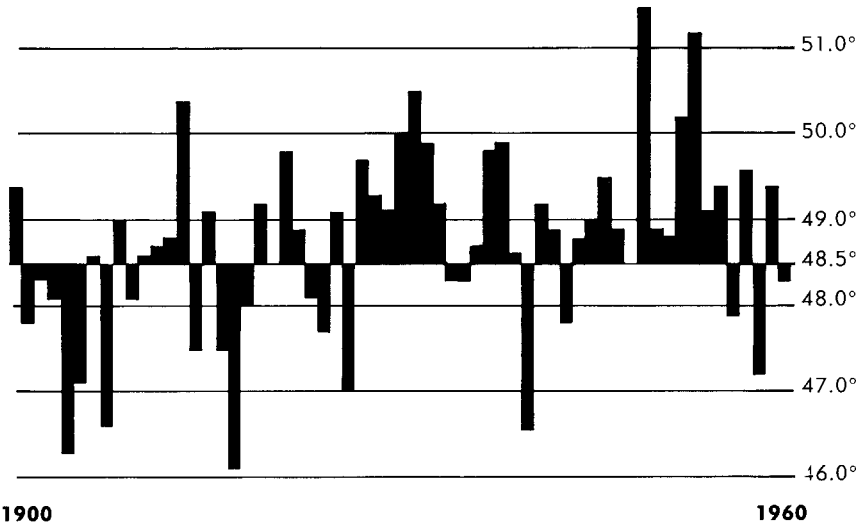

FIG. 5. Mean annual temperatures, 1900–1960, for Connecticut, Massachusetts, and Rhode Island, with deviations from long-term average (1888–1960). Based on U.S. Weather Bureau data.

this one may conclude that the mild period permitted the population to build up to a size sufficient to withstand the recent harsher period. The less hardy birds might not now survive, but this would not cause the destruction of a sufficiently large and generally hardy population. The same reasoning may be applied to the Tufted Titmouse and perhaps also to the Carolina Wren in New England (though see above), and to the Mockingbird in New Jersey and Pennsylvania.

In Michigan the temperature trend has been relatively steady for the past 30 years, following an earlier increase. The relative stability of the Cardinal and Tufted Titmouse populations in this state may be a reflection of this condition.

A long-continued temperature decrease might, however, cause a reversal of these population trends. In South Dakota there was a strong upward temperature trend, culminating in the year 1931, followed by a sharp decrease. Mean annual temperatures averaged by decades show an increase from 44.6 F for 1911–1920 to 47.1 F for 1931–1940, and a subsequent decrease to 45.6 F for 1951–1960. In spite of this, both the breeding and wintering ranges of the Cardinal continued to extend northward there into the early 1950's (Krause and Froiland, 1954). The population, however, has now begun to decrease (see Table 1), possibly as a delayed reaction to decreasing temperatures.

The decreasing temperature trend in Pennsylvania apparently has not reached a point where it is causing any decrease in the well-established Cardinal and Tufted Titmouse populations, although it may be affecting the much more sparse population of the Carolina Wren and slowing down the increase in the Mockingbird population.

If the Mockingbird really was an early inhabitant of New England, perhaps one of the reasons for its extirpation was the long cold period extending from 1811 to 1904. This was interrupted by only three very short warmer periods (based on the record at New Haven, Connecticut; Kirk, 1939). Connecticut Mockingbird records going back to the 1860's (Sage, 1913) fall generally in the warmer periods. This long cold period may have affected the other species adversely as well.

Habitat.—Habitat changes have been extensive in the area under consideration. Deforestation became important after 1800 as agriculture made increasing demands on the land. This trend was reversed with the opening of the West. The resulting farm abandonment has continued in New England to the present day. One hundred years ago only 27 per cent of Connecticut land was in forest. At the present time, 63 per cent of this land is covered by forest, though much of it is young and scrubby. At the same time, there has been a large increase in human population. This has caused other changes in land use, ranging from rural to suburban to completely urban conditions. With the exception of parks, the latter obviously are unsuitable for the four species of birds, and in fact may act as a barrier to quite sedentary birds. Where human population is less dense, the four species of birds have reacted in different ways.

The Cardinal first became established in southwestern Connecticut in the 1940's. Per cent of land used for agriculture in Fairfield County, Connecticut, declined from 53 per cent in 1935 to about 8 per cent in 1959. The abandoned farm land resulted in an increase in brush and young forest, i.e., habitat suitable for the Cardinal. At the same time, residential land use increased rapidly, also providing habitat suitable for this species. Perhaps the "tip point" has been reached here, however, for the most spectacular growth of Cardinal populations has taken place not in Fairfield County, Connecticut (human population density 1,033/sq. mi.), but in Putnam County, New York (135/sq. mi.) and northwestern Westchester County, New York. At the same time, it has been noted that range expansion of the Cardinal has occurred in settled rather than in unsettled areas in northern New Jersey (Fables, 1955) and in Michigan (Burns, 1958). In other words, some human settlement is a favorable factor, but a point may be reached where human density is too great.

The Carolina Wren and the Mockingbird are more limited climatically, but there are further differences. The Carolina Wren has done comparatively

well in the less heavily settled areas on Long Island Sound, confirming previous remarks on its rather poor adaptability to the presence of man. The scarcity of the Mockingbird must be due more to climate, since it is the most "domesticated" of the four.

The Tufted Titmouse is quite limited by its habitat requirements. Although much of the forest in the oak-hickory region of Southern New England is young (Thomson, 1958), enough older forest apparently exists to allow the titmouse a foothold. The increase in the Tufted Titmouse population in New Jersey is largely confined to areas of less dense human population in the northern part of the state. Increasing warmth has not led to an increase in titmice where the habitat is not suitable.

Food supply does not appear to be an important limiting factor at present for any of the species, with the probable exception of the Carolina Wren. This species is almost completely insectivorous throughout the year. The Cardinal, Tufted Titmouse, and Mockingbird are typical of the songbirds wintering in New England in eating a large proportion of seeds, nuts, and fruits at this time of year (Martin, Zim, and Nelson, 1951). However, the reportedly poor acorn crop in 1961 may have been a factor in the northward expansion of the Tufted Titmouse in the fall of that year. At times of short supply, the prevalence of feeding stations may be valuable to the Cardinal and Tufted Titmouse, both of which are constant winter visitors.

Geographical barriers.—Geographical features such as mountains, rivers or other bodies of water, and metropolitan areas (man-made, but a fact of geography all the same) may have opposite effects on range extension, depending particularly on population pressure.

The importance of these features as barriers can be deduced from various sources. None of these species is common in the high northwestern section of New Jersey (local Christmas Counts; Fables, 1955). In addition, many Christmas Counts have been made at various altitudes in the Appalachian Mountains. Arranged according to decreasing importance of altitude as a barrier, the four species may be listed as follows: Mockingbird, Carolina Wren, Cardinal, Tufted Titmouse. None of them reaches the highest points.

The importance of water as a barrier can also be deduced from the Christmas Counts (see Figs. 1–3). Again arranged according to decreasing importance of the barrier, the species may be listed as follows: Tufted Titmouse, Cardinal, Carolina Wren, and Mockingbird. As recently as 1942, Cruickshank considered the Tufted Titmouse to be only a rare possibility east of the Hudson River or on Long Island. The population buildup in Rockland County, New York began about this time and led to the successful crossing of the Hudson River. The subsequent increase in southeastern New York and southwestern Connecticut has apparently resulted in its re-invasion of Long Island, where

it is once again listed as a breeding bird (Buckley, 1961). It seems probable that the Cardinal followed the same route, although it is impossible to prove this without banding data. Rivers may be barriers, while their valleys may be pathways for expansion. The climate of the Hudson River Valley is milder than that of the higher lands on either side and thus could be expected to be more suitable for climatically limited species.

The land passageway north from New Jersey is further narrowed for the Cardinal and the Tufted Titmouse by the New York metropolitan region.

A small population in New Jersey that has limited access to new territory may find northward expansion impossible. But population pressure may turn these barriers into a funnel leading to the successful invasion of new territory. This seems to apply to the Cardinal and the Tufted Titmouse, for both of which New England was a relatively isolated area. On the other hand, New England has long been within the reach of both the Carolina Wren and the Mockingbird. Their more modest success seems related rather to less suitable climatic and/or habitat conditions.

Man.—All four species were present on Long Island 100 years ago (Giraud, 1844). By about 1900, the Cardinal had become uncommon around New York City, the Mockingbird was rare, and the Tufted Titmouse only accidental on Long Island (Chapman, 1906; Cruickshank, 1942; Eaton, 1910; Griscom, 1923). The Mockingbird had disappeared from the Philadelphia area as early as 1830 (Wilson, 1831), and near the turn of the century was listed as very rare in eastern Pennsylvania and New Jersey (Stone, 1894). Both the Cardinal and the Mockingbird were called shy and difficult to approach by Gentry (1876).

Much of this reduction in numbers seems due to direct intervention by man. Both the Cardinal and the Mockingbird were popular as cage birds, at prices ranging from ten dollars and up per bird. Songbirds were used as food and for decorative purposes. Hunting and trapping would thus have been important in limiting numbers, especially at the edges of ranges. Early deforestation posed an equally serious threat to the Tufted Titmouse. These much-reduced populations would have made settlement of new areas unlikely, even if they were suitable. The relaxation of hunting pressure has undoubtedly contributed to the present increase in Cardinal and Mockingbird populations, while the renewed growth of the forest has aided the Tufted Titmouse.

SUMMARY AND CONCLUSION

Granting the imperfections in the data, as previously noted, it still seems possible to venture some conclusions.

The Cardinal has become a common-to-abundant resident in southern New England and the lower Hudson River Valley within the past 15 years. Al-

though resident in the area around New York City 100 years ago, it had become very rare there by 1900, probably as a result of hunting pressure and of the long cold period in the 1800's. Increasing temperatures and a relaxation of hunting pressure, plus sufficient suitable habitat, led to a population increase in New Jersey. The resulting population pressure brought about the successful crossing of the Hudson River. The firm establishment of the population in southern New England occurred during a period of maximum warmth. With suitable habitat available, it seems that the Cardinal will continue to prosper in southern New England and the lower Hudson River Valley, threatened only by a long-continued temperature decrease or a drastic change in habitat.

The Tufted Titmouse has followed a similar pattern, although it is more limited by climatic and habitat requirements than is the Cardinal and is, therefore, not likely to achieve as great a success in southern New England. Change in amount of suitable habitat (deforestation and reforestation) was a more important influence than hunting pressure. The titmouse seems firmly established in southern New England and, with the increasing age of forests, may even have added habitat available. Its future here seems fairly secure, barring the leveling of the forests or a long-continued temperature decrease.

The Carolina Wren is apparently responding to changes in temperature and is succeeding moderately well along Long Island Sound. At the same time, it seems to be the most sensitive of the four species to the presence of man. Its stricter temperature and habitat requirements do not pressage a bright future for it in New England. Furthermore, increasing human population density, which seems a fairly certain prospect, would militate against it; decreasing temperatures would have an additional depressing effect.

The Mockingbird's record is similar to the Cardinal's, although on a more elongated scale geographically. Its northeastern population was reduced both by hunting and by decreasing temperatures, and the reversal of these conditions has led to an increase in numbers. It is the most limited climatically of the four species but, at the some time, apparently the most wide-ranging. Therefore, a small, though not necessarily self-sustaining, population in New England is a likelihood, while any great increase is an improbability. A long-continued temperature decrease would be detrimental.

Range extension of these sedentary species seems to be preceded by a population increase within the original range. This increase may be stimulated by climatic warming (all four species), habitat changes (favorable for all but the Carolina Wren), or relaxation of hunting pressure (Mockingbird, Cardinal). A time lag in responding to these changes, particularly the climatic changes, is evident. Possibilities for range expansion, given proper conditions,

are always present in the winter exploratory activity exhibited by all four species.

The pressure resulting from these population increases may lead to gradual range extension where geographical barriers are unimportant and the new area is more or less suitable (Carolina Wren, Mockingbird). The results may be more dramatic, however, when this pressure leads to the invasion of a suitable area from which the species had been excluded by geographical barriers (Tufted Titmouse, Cardinal).

It does not seem necessary to postulate evolutionary changes in these species of birds to account for the range and population changes discussed above. The species are occupying areas in southern New England and the Hudson River Valley that might be expected on the basis of their distribution elsewhere and that seem in accord with biotic and climatic changes. However, the new, rapidly expanding and relatively isolated populations of both the Cardinal and the Tufted Titmouse might well result in evolutionary changes. This possibility requires further study.

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