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DIFFERENCES IN REPERTOIRE SIZE, SINGING BEHAVIOR, AND ASSOCIATED NEUROANATOMY AMONG MARSH WREN POPULATIONS HAVE A GENETIC BASIS

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ABSTRACT.—Among songbirds, adult song forms usually are determined culturally during an individual's early experience. In the Marsh Wren (*Cistothorus palustris*), we have demonstrated that the quantity of this learned behavior (i.e. song repertoire size), its style of delivery, and the size of controlling nuclei in the forebrain have a genetic basis. Nestling males taken from New York and California and reared under standardized conditions in the laboratory still develop population-typical behavior and neuroanatomy. We do not know the developmental mechanisms responsible for these differences, but we believe that year-round residency, high densities, and polygynous mating systems are likely factors contributing to an escalation of vocal abilities in the western populations. Received 20 July 1984, accepted 6 February 1985.

VARIATION in vocal behaviors both within and among populations is abundantly evident in many songbird species. Within populations, for example, individual variation in song morphology among neighbors allows individuals to recognize one another based on song alone (Falls 1982). Song repertoire sizes also may vary considerably among males in the same population. Repertoires of Common Chaffinches (*Fringilla coelebs*) may range from 1 to 6 (Slater 1981), of Great Tits (*Parus major*) from 1 to 8 (McGregor et al. 1981), and of Bewick's Wrens (*Thryomanes bewickii*) from 13 to 20 (Kroodsma 1974).

Variation among populations is equally well documented. Many studies have demonstrated that songs vary microgeographically (Payne 1981, Munding 1982, Slater 1983) and that many, if not most, songbird species sing unique, learned song variants at different locations. Song repertoire sizes also may vary considerably; in the Song Sparrow (*Melospiza melodia*), sedentary males of San Francisco Bay marshes appear to sing about 50% more song types than

males of other populations (Mulligan 1966, Harris and Lemon 1972, Eberhardt and Baptista 1977). In the Winter Wren (*Troglodytes troglodytes*), both song repertoire and song complexity change markedly from Oregon to New York (Kroodsma 1981a).

Many of these differences among individuals and populations appear to be a consequence of vocal learning and therefore are based on cultural and not genetic differences. Thus, male White-crowned Sparrows (*Zonotrichia leucophrys*) are adept at imitating songs of both the natal and alien dialects of the same species (Marler and Tamura 1964, Baptista and Petrinovich 1984), indicating that these observed interpopulational song variations are cultural differences. When deprived of conspecific songs in the laboratory, juvenile males of many songbird species will even imitate songs of other species, verifying that many oscines are capable of imitating a wide variety of songs (Kroodsma and Baylis 1982). Another factor, intrapopulation variability in repertoire size, may be largely a result of environmental factors in-

fluencing the learning process; male Bewick's Wrens that hatch early in the season learn more songs than those hatching later in the season. This is probably a consequence of fewer adult models singing late in the season and the shorter time available for developing songs before the first winter (Kroodsma 1974).

There are clearly nonlearned, genetic differences among *species* that direct the process of vocal learning and generate species-typical vocal behaviors (Marler and Peters 1977), but the existence of such differences among individuals either within or between *populations* of the same species has been more difficult to document. While male Brown-headed Cowbirds (*Molothrus ater*) are able to learn and sing a variety of songs typical of either the *M. a. ater* or *M. a. obscurus* subspecies, the females appear resilient to experience, and innately prefer males that sing songs of their own subspecies (King and West 1983). This appears to be the only published study demonstrating nonlearned, or innate, population differences in songbird vocal behaviors (or a response to those behaviors). In other songbird species it is not known to what extent genetic factors and environmental factors (which in turn influence the learning process) contribute to the differences in repertoire sizes, song complexity, or singing styles among populations.

In addressing this question, we chose the Marsh Wren (*Cistothorus palustris*) for a study species. In our studies of free-living adult males, we found that San Francisco males, when compared to New York males, learn 2.6–2.7 times as many song types, present a much greater variety of song forms during a brief time span, and devote more brain tissue to controlling these vocal behaviors (Canady et al. 1984). There are significant differences in the behavioral ecology of these two populations: western birds are sedentary, while eastern birds are migratory; western males are more polygynous; western birds typically defend much smaller territories than the eastern birds; and the breeding and singing season is much longer in the west than in the east (Welter 1935; Kale 1965; Verner 1965, 1975).

By taking young males from each population into the laboratory and studying their vocal development under controlled environmental conditions, we wanted to determine whether these population differences would persist. If

they did persist, and laboratory subjects sang like adult males from their natal population, then we would conclude that the population differences are in large part genetically based (Hailman 1982). On the other hand, a convergence in the behavior of the laboratory subjects from the two populations would suggest that the population differences are in large part a consequence of vocal learning occurring in different environments, and that the differences therefore lack a substantial genetic basis.

METHODS

Twelve male Marsh Wrens were the subjects for this experiment. Each was collected as a 7–10-day-old nestling from marshes on the Hudson River at Tivoli, New York ($n = 6$) or from Grizzly Island wildlife area north of San Francisco, California ($n = 6$). There is no evidence that Marsh Wren nestlings learn song types in nature or in the laboratory before day 10 (Kroodsma 1981b, unpubl. data), and we therefore believe that experience in the natal marsh had a negligible effect on subsequent vocal development in our laboratory experiments. Each bird was hand-reared in the laboratory, placed in an individual cage, and maintained on a 42°N latitude photoperiodic cycle in small isolation chambers (IAC-1) or larger acoustically isolated rooms.

Males were tutored over loudspeakers with 200 different Marsh Wren song types, 150 from the California and 50 from the New York population. The sequence of 200 songs, with 3 western songs alternating with 1 New York song, was presented 10 times each morning from approximately day 20 to day 80, the period of maximal song learning for Marsh Wrens (Kroodsma 1978).

The rationale for this tutor-tape design was as follows. In nature individual males from the California population sing approximately 150 song types, and those from the New York population sing approximately 58 (Canady et al. 1984); laboratory subjects generally learn fewer songs than wild males, and the tutor tapes were designed to saturate the males with an overabundance of vocal models. Eastern males readily learn songs of other species [e.g. Sedge Wren (*Cistothorus platensis*), Yellow Warbler (*Dendroica petechia*); Kroodsma and Pickert 1984], so we did not expect our subjects to be predisposed to learn songs of their own subspecies. This proved to be the case, for both western and eastern males imitated 2–4 times as many western than eastern song models, roughly in proportion to the number on the training tape.

The songs of the wrens stabilized at approximately 10–11 months of age, indicating that song development was complete. We then recorded from 273 to 778 songs (median = 400) from each individual. Songs

TABLE 1. Comparison of song repertoire data for western (CA) and eastern (NY) Marsh Wrens reared in the laboratory.

Bird	No. of songs sampled (<i>n</i>) ^a	Song types in sample (<i>N</i>)	Sample coverage (θ) ^b	Estimates of repertoire size	
				<i>N</i> / θ ^c	Exponential curve ^c
CA-1	380 (431)	113	0.966	117.0	117.7
CA-2	302 (403)	112	0.914	122.6	122.4
CA-3	348 (400)	101	0.943	107.2	104.8
CA-4	319 (400)	90	0.959	93.8	93.0
CA-5	316 (400)	107	0.921	116.2	114.2
CA-6	618 (778)	109	0.990	110.1	109.4
Median	334 (401.5)	108	0.951	113.1	111.8
NY-1	242 (407)	41	0.996	41.2	41.1
NY-2	213 (302)	56	0.972	57.6	57.4
NY-3	112 (273)	26	0.982	26.5	26.4
NY-4	171 (302)	34	0.982	34.6	34.2
NY-5	197 (457)	64	0.924	69.3	67.7
NY-6	147 (335)	46	0.925	49.7	48.3
Median	177 (318.5)	43.5	0.975	45.4	44.7

^a Males often sing 1 or 2 renditions of a song type, either in succession or with 1 or 2 other song types occurring in between. If 10 other songs occurred between successive renditions of a given song type, we considered these 2 renditions independent occurrences of that type. The total number of independent occurrences of a song type are given here, with the total number of songs sampled in parentheses. (See Canady et al. 1984 for additional explanation of this approach.)

^b The sample coverage is an estimate of the probability that the next song sampled will be of a type already sampled. See text for further details.

^c See text for explanation of these two estimates of the actual repertoire size based on the sample.

were graphed on a PAR model 4512 FFT real-time spectrum analyzer and filmed with a Grass oscilloscope camera on 35-mm photographic paper.

As with wild birds, each song consisted of a few brief notes preceding and following the most distinctive portion of each song, a series of repetitions (5–20) of a harmonically complex sound syllable [see Fig. 1 in Kroodsmas (1978) and Figs. 2–5, 7–9 in Verner (1975) for samples of sound spectrograms from eastern and western populations, respectively]. Despite the large song repertoires, Marsh Wrens sing discrete and distinctly different song types that are readily and objectively classified; this unambiguity of categories also undoubtedly facilitates recognition of song types during complex interactions among wild birds (Verner 1975). We measured the repetition rate of these repeated syllables, and then arranged the entire song sample for one bird from slow to fast rates of repetition. If sound syllables looked identical yet differed by more than 10% in the rate, we called them different song types. Renditions of a given song type usually were sufficiently stereotyped and distinctive that we rarely had to invoke the 10% rule.

Recorded samples for each male were sufficiently large that additional song types were encountered only rarely near the end of a sample. Nevertheless, we used two methods to estimate the actual repertoire size based on our samples. The first method

involved exponential curve-fitting, using $n = R(1 - e^{-N/R})$, where n = the number of distinct song types in the sample, R = the number of distinct song types in the repertoire, and N = the number of independently occurring songs in the sample (see Wildenthal 1965, Canady et al. 1984, and Table 1 for further details). The second method involved a correction for sample coverage, using $R = n/\theta$, where $\theta = 1 - (S/N)$ and S = the number of song types that occurred only once in the sample. The sample coverage is an estimate of the probability that the next sampled song will be of a type already encountered (Good 1953, Fagen and Goldman 1977). Sample coverage for our data ranged from 0.914 to 0.996 (median = 0.963).

After the songs were sampled, each wren was weighed, given an overdose of anesthesia, and perfused intracardially with 0.9% saline followed by 10% formalin in 0.9% saline. Brains were then excised, weighed, and processed for histology (see Nottebohm et al. 1976 for techniques). Brain sections 50 μ m thick were stained with cresyl violet, and volumes were reconstructed by measuring the area of each brain section.

RESULTS

Song repertoires.—There is no simple or “correct” way to determine the actual repertoire size

TABLE 2. Comparison of the singing behavior of western (CA) and eastern (NY) Marsh Wrens.^a

	Laboratory males		Wild males			
	CA	NY	CA	NY		
Recurrence numbers ^b	56 (38-92)	**	9 (1-19)	67.5 (56-96)	**	25.5 (2.5-3.6)
Percent recurrence numbers $\leq 2^c$	18 (14-32)	*	34 (22-56)	6 (10-18)	**	43 (20-60)

^a Asterisks between values indicate significant differences; * $P < 0.05$ and ** $P < 0.01$ (2-tailed Mann-Whitney U -test).

^b Values are the median recurrence numbers, with range of individual males in parentheses. Six laboratory males and 5 wild males were used from both the CA and NY populations. Sample sizes for individual birds ranged from 71 to 120 in NY laboratory males, 78 to 82 in CA laboratory males, and 10 or 11 randomly chosen recurrence numbers for the wild males.

^c Sample sizes and format are the same as in footnote b.

that a male Marsh Wren is capable of singing. Large samples are a prerequisite, and only when the rate of appearance of new song types occurring in the sample declines considerably can one begin to feel confident that the male has performed most of his repertoire. Use of statistical estimating procedures prior to this point is inaccurate because of the nonrandom fashion in which the males use their songs (Kroodsma 1982). After the curve of song types sampled vs. total songs begins to reach an asymptote at the actual repertoire size, the two statistical approaches used here are valuable tools that help take into account the differences in sample coverage for each male (Table 1). The sample coverage estimator raised the estimate over the sample by a median of 2.4% (range, 0.5-8.3%) for eastern and 5.1% (range, 1.0-8.9%) for western birds, while the exponential raised the value by 2.0% (0.2-5.8%) and 4.0% (0.4-9.3%).

In nature, the San Francisco Marsh Wren males sing 2.6-2.7 times as many songs as the New York males; using the exponential estimator (149.8/58.2, median estimates of wild western and eastern males, respectively = 2.6), the sample coverage estimator (151.9/57.0 = 2.7), or merely the number of song types in the samples (143.0/52.5 = 2.7) made little difference (Canady et al. 1984). The resulting ratios for the laboratory males were strikingly comparable. Using the median number of song types in the samples or either of the two estimates of actual repertoire size, the results were the same: western males developed 2.5 times as many song types as did the eastern birds. The population ranges are nonoverlapping and reveal a clear difference in the ability of males from these two populations to develop large

song-type repertoires (2-tailed Mann-Whitney U -test, $P = 0.002$).

Singing behavior.—Differences in singing behavior between the eastern and western males in nature were also evident among hand-reared males in the laboratory (Table 2). In the field, western males tend to speed through their song repertoire, often singing as many as 50 different songs in succession (Verner 1975, Canady et al. 1984). The median recurrence number, the number of other songs occurring between successive renditions of a given song type, for 5 California males was 67.5, with only 6% of all recurrence numbers being 0, 1, or 2. On the other hand, recurrence numbers for 5 New York males were much lower (median 25.5). This is not simply a consequence of their possessing smaller repertoires; eastern males tend to alternate song types more, such as ABAB-CABCDBCD, and in our sample from wild birds 43% of all recurrence numbers were 2 or less.

In the laboratory, these population differences persisted. Median recurrence intervals were 56 for California males but only 9 for New York males. More importantly, the percentage of recurrence intervals that were 2 or less was significantly lower in the New York than the California laboratory males (18 vs. 34; see Table 2 for details of data and statistical tests).

Neuroanatomy.—Among wild males, the population differences in behavior match neuroanatomical differences in the size of song control nuclei in the forebrain (Table 3; Canady et al. 1984). Even though western males have a slightly smaller body and brain weight, the volumes of two telencephalic nuclei, the hyperstriatum ventralis, pars caudalis (HVc), and the robust nucleus of the archistriatum (RA),

TABLE 3. Comparison of morphological data for the western (CA) and eastern (NY) Marsh Wrens.

	Median (range) ^a		Ratio of medians, CA/NY ^b	CA-NY differences? ^c P =
	CA males	NY males		
Body weight (g)	11.0 (10.1-11.3)	12.4 (12.0-13.8)	0.89 (10.7/11.4 = 0.94)	0.002
Brain weight (g)	0.488 (0.470-0.506)	0.494 (0.479-0.515)	0.99 (0.503/0.522 = 0.96)	0.310
Total HVC (mm ³) ^d	0.634 (0.481-0.867)	0.504 (0.351-0.629)	1.26 (0.677/0.481 = 1.41)	0.123
Total RA (mm ³)	0.264 (0.230-0.308)	0.205 (0.152-0.226)	1.29 (0.128/0.106 = 1.21)	0.002
Total Rot (mm ³)	1.097 (0.972-1.187)	1.539 (1.053-1.651)	0.71 (1.256/1.451 = 0.87)	0.030
Total SpM (mm ³)	0.135 (0.115-0.174)	0.181 (0.127-0.202)	0.75 (0.074/0.079 = 0.94)	0.080

^a Sample sizes are 6 CA and 6 NY males for body weight, and 6 CA and 5 NY males for brain data.

^b For comparison with the data from laboratory-reared males, data for wild-caught adults from the two populations are given in parentheses (CA median/NY median). Sample sizes are 15 CA and 15 NY males. Eastern and western wild males were significantly different ($P < 0.01$, 2-tailed Mann-Whitney U -test) in all cases except brain weight and SpM. Data for RA and SpM are for the left nucleus only, not the left and right nuclei combined (i.e., "total"; see footnote d). To be consistent with the nonparametric approach used on the smaller sample sizes in this study of laboratory-reared males, medians also are reported for the wild birds; parametric statistics (with means) were used in the original study by Canady et al. (1984).

^c Statistical comparisons of CA and NY subjects were by 2-tailed Mann-Whitney U -tests.

^d We found no left/right asymmetries in brain nuclei; "total" therefore indicates the sum of the left and right brain nuclei.

both intimately involved in the song control pathway, are 41 and 21% larger in the western birds. Two other brain nuclei, Rotundus (Rot) and Spiroformis medialis (SpM), were chosen for comparison because they have discrete boundaries in the brain and are not part of the vocal control pathway. Among the wild wrens these nuclei displayed a reversed trend, being larger in the eastern males than in the western wrens, presumably reflecting the slightly larger body or brain size of these eastern birds.

These neuroanatomical differences between eastern and western birds were also evident in the laboratory (Table 3). California males weighed about 11% less than the New York males, although the brain weight was essentially identical in males from the two populations. In spite of the comparable brain weight, the total volume of the two nuclei involved in the song control pathway, HVC and RA, were 26 and 29% larger, respectively, in western birds with the larger song repertoires. While this difference was statistically significant for RA ($P = 0.004$, 2-tailed Mann-Whitney U -test), it was not for HVC, presumably because of the small sample sizes (6 California and 5 New York males) and increased variability in the volume of the HVC nucleus. As with the wild males, the two nuclei used for comparison, Rot and SpM, were smaller (29 and 25%, respectively) in the western than in the eastern birds, just the opposite

of the trend in the forebrain nuclei involved in song control (the Rot difference was statistically significant, while the SpM was not; see Table 3).

DISCUSSION

We have demonstrated that population differences in song repertoire size, singing behavior, and neuroanatomy between wild Marsh Wren adults from New York and San Francisco persist when males are raised from the nestling stage under controlled conditions in the laboratory. The singing behavior and its associated neural control pathway that are characteristic of these two populations therefore are based on genetic differences (Hailman 1982) and are not merely the result of individuals being reared in different environments.

The gross difference in neural tissue volume could be due to a variety of factors such as neuronal number or size, amount of neuropil, glial number or size, or even the degree of vascularization (Canady et al. 1984). The increase in size of song control centers in western birds could be due to something as simple as neonatal steroid hormone levels; appropriate administration of estradiol and dihydrotestosterone to female Zebra Finch (*Poephila guttata*) chicks influences the size and number of song-center neurons in adults (Gurney and

Konishi 1980, Gurney 1981). The increased size also could be a result of adult hormone levels. In Common Canaries (*Serinus canaria*), steroid hormones do cause adult female song nuclei to increase in volume with the concurrent expression of malelike song. The increase in the volume of RA in those birds is at least partly explained by an increase in the length and degree of branching of the major neuronal cell class in that nucleus (DeVoogd and Nottebohm 1981).

Because the cell number and size seem to be so easily manipulated by hormone (see also Nottebohm 1981), this is a conceivable mechanism for increasing the size of song control nuclei in the western birds. However, we have no evidence for this, and it seems just as likely that selection may have favored an increase in the number of cells in song control centers of western birds by controlling the number of cells produced at an early embryonic stage. It is also possible that western males, by practicing and singing more songs, would thereby develop larger song control centers. We do not know whether western males have larger song control centers because they sing more song types, or whether they have larger song repertoires because their innately larger song control centers enable those larger repertoires. Further experiments will be necessary before we can understand the genetic bases for these population differences.

Over evolutionary time, environmental differences undoubtedly have played a key role in establishing population-typical behaviors. In San Francisco, for example, the wrens are year-round residents, while the New York wrens are migratory. Partly as a result, the duration of the singing and breeding season in the western wrens is nearly twice that of the eastern wrens (Welter 1935, Kale 1965, Verner 1965). This may offer a longer period during which young can hear and learn songs during their first summer.

The territories of the western males also tend to be much smaller, averaging perhaps one-third the size of those in the New York population (Kroodsma unpubl. data). More frequent encounters and countersinging duels with neighboring males on these smaller territories throughout a longer season could place a premium on both the diversity of songs used and a stimulating style of singing that presents

many contrasting song types over a short period of time. Song playbacks have demonstrated, for example, that increased variety in songs tends to be more stimulating to a territorial male (Krebs 1976, Yasukawa 1981). Furthermore, both within species and among closely related species, song repertoire sizes do appear positively correlated with conspecific density (Kroodsma 1983).

The mating system also is very likely to have played an important role in the evolution of these population differences. While as many as 50% of western males may be polygynous (Verner 1965), the level of polygyny is close to 5% in eastern populations (Welter 1935, Kale 1965). Marsh Wrens countersing in a complex fashion with each other (Verner 1975, Kroodsma 1979), and presumably these vocal duels play an important role in either territory acquisition or mate attraction, or both. A high variance in reproductive success among males would be a strong selective force on those vocal behaviors used to obtain a quality territory and, either directly or indirectly, a disproportionate share of the females (Emlen and Oring 1977).

There may be other factors involved in the evolution of these population differences, but the above three seem most consistent with our understanding of the function, ontogeny, and evolution of vocal behaviors in oscines. All three factors, including the duration of the breeding season, smaller territories, and polygynous mating systems, could select for larger repertoires in the western populations. Determining the relative roles of these or other factors in the evolution of Marsh Wren vocal behaviors will require careful selection of future study populations.

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The **North American Bluebird Society** announces the **third annual grants in aid** for ornithological research on cavity-nesting species of North America with emphasis on the genus *Sialia*. Presently, up to three awards totaling \$3,000 are made annually and include the Bluebird Research Grant, available to student, professional, or individual researchers for a research project focused on any of the three species from the genus *Sialia*; General Research Grant, available to student, professional, and individual researchers for a research project focused on a North American cavity-nesting species; and Student Research Grant, available to full-time college or university students for a research project focused on a North American cavity-nesting species. Guidelines and application materials are available from **Theodore W. Gutzke, Research Committee Chairman, P.O. Box 121, Kenmare, North Dakota 58746 USA**. Completed applications must be received by **31 January 1986**; decisions will be announced by 15 March 1986.

The **Hawk Mountain Sanctuary Association** is accepting applications for its **ninth annual award for raptor research**. To apply for the \$750 award, students should submit a brief description of their research program (5 pages maximum), a curriculum vitae, and two letters of recommendation by **30 September 1985** to **Stanley E. Senner, Executive Director, Hawk Mountain Sanctuary Association, Rte. 2, Kempton, Pennsylvania 19529 USA**. The Association's board of directors will make a final decision late in 1985. Only students enrolled in a degree-granting institution are eligible; both undergraduate and graduate students may apply. The award will be granted on the basis of a project's potential to improve understanding of raptor biology and its ultimate relevance to conservation of North American raptor populations.