

VARIATION IN SONG STRUCTURE WITHIN AND AMONG POPULATIONS OF AUSTRALIAN ZEBRA FINCHES

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ABSTRACT.—Zebra Finch (*Taeniopygia guttata castanotis*) songs from 33 colonies in two geographic zones of Australia (central and southeastern) were investigated in order to describe variation from macrogeographic to microgeographic levels. Canonical discrimination classified songs according to 31 measurements of the song phrase and clearly distinguished those from the two zones. Songs from regions within the southeastern zone fell into two groups on element sequence and frequency of element types. The two song groups came from habitats that differ in aridity and tree cover; both factors affect dispersal. Song variation within and among colonies in a region occurred in the frequency of "labile" elements. Movements of birds among colonies are extensive, but patterns are still far from clear. Despite resemblance in song structure between sons and their fathers, dispersal to and from colonies prevents the formation of colony-specific versions of the song. Received 9 March 1992, accepted 30 November 1992.

YOUNG ZEBRA FINCHES (*Taeniopygia guttata castanotis*), like other oscines, learn their songs from males they encounter, but are unusual in that they learn the song very early in life and reproduce it in the crystalized form by the end of the third month; this holds for wild birds (Zann 1990), as well as domesticated ones (Immelmann 1969, Slater et al. 1988). Furthermore, the majority of wild birds have songs that resemble those of their fathers (Zann 1990). If Zebra Finches are sedentary and breed in the colony of their birth, one would expect each colony to develop its own specific song type as the tradition would be handed down from father to son so that micro- and macrogeographic variants would form. However, if dispersal is high, colony-specific songs would be eroded as immigrants produced sons that sang a different song and, thus, diluted the local variant. Song type within a colony might reflect the immediate dispersal history of the males within it.

My purpose was to determine in wild Australian Zebra Finches: (1) how the song varies across the distribution of the subspecies, encompassing comparisons of songs from different geographic sites ranging from those at the coarse-grain, macrogeographic level, where sites were over 1,700 km apart, down to fine-grain, microgeographic comparisons with sites separated by only a few kilometers; (2) how song varies over the course of several years within a study site; and (3) whether the pattern of temporal and geographic variation in song can per-

mit inferences about patterns of dispersal in this species.

METHODS

Sampling.—I recorded song phrases from 402 males from 33 breeding colonies in the central and southeastern zones of Australia from 1976 through 1989 (Fig. 1a). Recordings were made during long-term behavioral and ecological studies at specific colonies, or opportunistically at other sites; as a consequence, there was a great range in sample sizes across colonies and geographic coverage was fairly uneven. For some analyses, I pooled colonies into regions if they were within 40 km of one another. Recordings from the central Australia zone were made at the CSIRO research station at Alice Springs in 1986 (colony As); habitat details are described in Burley et al. (1989). Songs from the southeastern zone were recorded at 31 colonies along the alluvial plains north and south of a 450 km stretch of the Murray River that separates the states of Victoria and New South Wales (Fig. 1b). Further habitat details are given in Zann and Straw (1984). Two colonies were also sampled away from the Murray River: You Yangs (region 11), 60 km southwest of Melbourne; and Inverell (region 12) in the far northern portion of the State of New South Wales. The You Yangs colony is the most southern in the range and one of the most isolated.

Recordings from colonies in region 1 (Fig. 1c), which was the principal focus for ecological and behavioral studies, were obtained during two periods, 1976-1982 and 1985-1988; I recorded 156 and 117 males, respectively. Colony Da in region 1 was the site of a detailed color-banding study, and 99 songs were recorded from this focal colony.

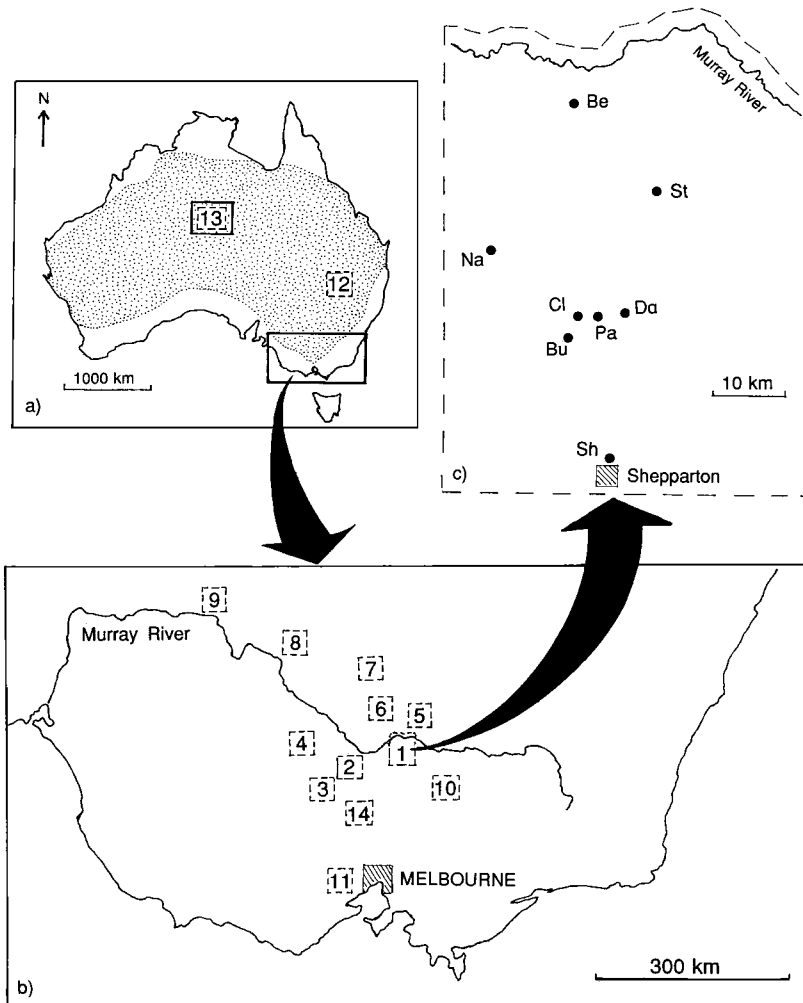


Fig. 1. Zebra Finch distribution in Australia showing: (a) two geographic zones (boxes) where songs recorded; (b) regions (dashed boxes) where colonies located in southeastern zone; and (c) colonies in region 1. Songs recorded from 33 colonies: (region 1) 8 colonies, 273 individuals; (2) 2 colonies, 17 individuals; (3) 1 colony, 3 individuals; (4) 8 colonies, 16 individuals; (5) 1 colony, 5 individuals; (6) 3 colonies, 21 individuals; (7) 2 colonies, 7 individuals; (8) 1 colony, 1 individual; (9) 2 colonies, 8 individuals; (10) 1 colony, 3 individuals; (11) 1 colony, 4 individuals; (12) 1 colony, 3 individuals; (13) 1 colony, 40 individuals; (14) 1 colony, 1 individual.

Song variables and analysis.—The components of the song phrase and their sequence have been described in a companion paper (Zann 1993). I analyzed at least three phrases from each male with a sonograph to determine precisely what constituted the phrase, then scored the phrase for 31 variables (Table 1): number of elements, including repeats, sung per phrase; speed of singing expressed as number of elements/s; number of elements belonging to 14 distinct types (Fig. 2) sung by Zebra Finches with an additional category for elements that could not be classified to type; number of sequence pairs and trios of elements that formed the start (four sequence types), middle (five sequenc-

es) and end (five sequences) of the phrase (this provided a crude measure of element sequence in phrase). Identification data on the singer's geographic region, colony and year of recording completed the data set.

I used canonical discrimination (CANDISC procedure; SAS Institute 1985) to see if these variables could separate phrases in a manner that might reflect the geographic origin of the singers. The procedure is a combination of principal-components and discriminant analysis, and assumes the data are at the interval level and normally distributed, which was not the case with most variables in the study. However, the technique was useful in this instance as a first ex-

TABLE 1. Loadings of Zebra Finch song phrase variables on first two axes generated by canonical-discriminant analysis of (a) all populations studied, (b) populations from southeastern zone, and (c) populations within region 1 in the southeastern zone.

Variable	All populations		Southeastern zone		Region 1	
	I	II	I	II	I	II
1 Number of elements	0.04	-0.13	-0.08	0.09	-0.30	0.00
2 Elements/second	-0.17	0.01	0.11	0.07	0.19	-0.03
Element types						
3 Introductory (<i>I</i>)	-0.05	0.00	0.01	0.01	-0.11	0.01
4 Introductory Diad (<i>II</i>)	0.12	0.05	-0.02	0.20	0.16	-0.13
5 Noise-structure (<i>NS</i>)	-0.14	0.18	0.12	0.15	0.26	-0.12
6 Noise-structure Distance-call (<i>NSDC</i>)	-0.20	0.20	0.18	0.16	-0.15	0.36
7 Noise-structure Tone (<i>NST</i>)	0.37	0.00	-0.77	0.31	-0.06	0.11
8 Distance-call (<i>DC</i>)	-0.19	-0.09	-0.03	0.01	0.06	-0.07
9 Noise-noise Distance-call (<i>NNDC</i>)	-0.09	0.09	0.06	0.00	-0.24	0.01
10 Ladder-noise (<i>LN</i>)	-0.19	0.20	0.17	0.18	0.42	0.01
11 Tone (<i>TO</i>)	-0.01	0.07	0.07	-0.01	-0.05	0.16
12 Tone-noise (<i>TON</i>)	-0.20	0.19	0.17	0.16	-0.11	0.50
13 High (<i>H</i>)	0.13	-0.19	-0.11	-0.03	-0.56	0.19
14 Noise-noise (<i>NN</i>)	0.44	-0.23	-0.16	-0.13	-0.25	-0.51
15 Down-slur (<i>DS</i>)	-0.13	-0.80	-0.10	-0.62	-0.04	-0.11
16 Stack (<i>S</i>)	0.11	-0.09	-0.09	-0.04	-0.10	0.00
17 Unclassifiable	0.05	0.07	0.01	0.09	-0.26	-0.27
Sequence of elements at phrase start						
18 (<i>I + TON + H</i>)	-0.14	0.14	0.13	0.12	-0.17	0.54
19 (<i>I + NN + H</i>)	0.41	-0.03	-0.12	0.01	-0.23	-0.30
20 (<i>I + LN + H</i>)	-0.10	0.10	0.06	0.11	0.08	0.19
21 (<i>I + S</i>)	0.08	0.09	-0.08	0.13	0.01	-0.08
Sequence of elements at phrase middle						
22 (<i>NN + H + NST/NNT</i>)	0.77	-0.13	-0.48	0.24	-0.09	-0.19
23 (<i>H + NSDC + ?</i>) ^a	-0.13	0.13	0.13	0.10	-0.23	0.28
24 (<i>H + NST + ?</i>)	0.44	-0.05	-0.42	0.31	-0.06	0.11
25 (<i>H + NS + ?</i>)	-0.08	0.10	0.11	0.09	-0.07	-0.02
26 (<i>H + ?</i>)	0.04	0.07	-0.19	0.10	-0.15	0.16
Sequence of elements at phrase end						
27 no <i>DC</i> or <i>S</i>	0.02	0.11	-0.15	0.10	-0.10	0.03
28 (<i>NS + ? + ?</i>)	-0.09	0.11	0.11	0.09	0.22	-0.06
29 (<i>I + ? + ?</i>)	0.02	-0.11	0.01	-0.13	0.01	-0.02
30 (<i>DC + ? + ?</i>)	-0.07	0.09	0.03	0.05	0.01	0.04
31 (<i>H + ? + ?</i>)	0.04	0.09	0.03	0.12	-0.18	-0.07

^a?, unspecified element.

ploratory step in pattern recognition and classification (Dillon and Goldstein 1984). A complementary nonparametric technique, CART (Breiman et al. 1984), was also used to classify song phrases. The technique, which makes no assumptions about the data, constructs binary trees based on classification of the variables in each song phrase; however, it is sensitive to unequal sample sizes. Each branch point of the tree is a division of the song phrases into two subgroups that are more homogeneous with respect to the variables measured than the parent group. The classes in this analysis were the geographic regions and colonies where songs were recorded and, hence, are known. The procedure was used to test the prediction that the song phrases would be classified in a pattern

that corresponded to that of the geographic distribution of recording sites. The technique also determines which variables give essential information on each binary split and, thus, provides a type of nonparametric variable reduction; the same variable may enter the classification several times at different levels of the tree.

Nearest-neighbor discriminant analysis (PROC NEIGHBOUR; SAS Institute 1985), which does not require multivariate normal distributions, was also used to classify song phrases, and stepwise variable reduction was used to determine which variables were the most important in the classification. Univariate procedures were taken from SAS Institute (1990, 1991), and all tests were two-tailed.

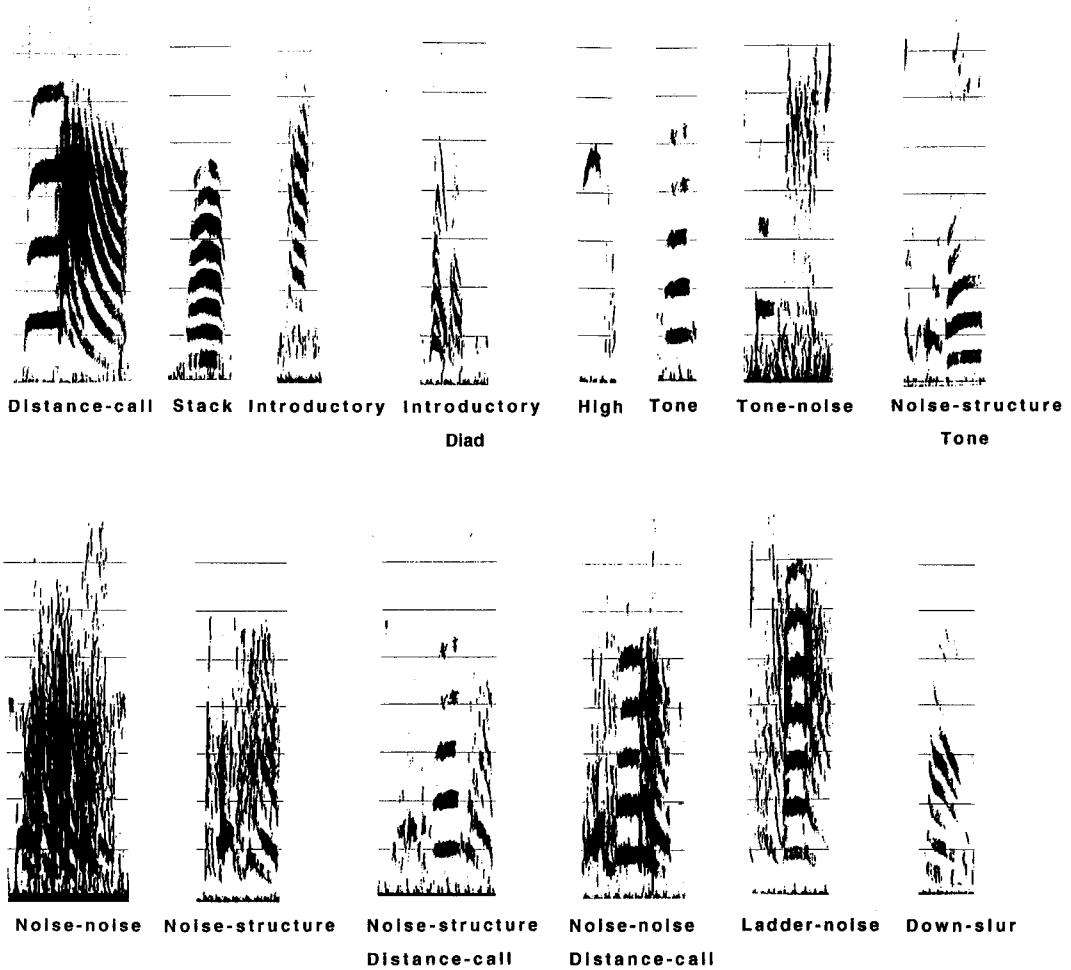


Fig. 2. Fourteen types of song elements sung by wild Zebra Finches used in canonical-discriminant analysis. Horizontal calibration marks at 1-kHz interval.

RESULTS

Variation between geographic zones.—Canonical discrimination of all 402 phrases in the sample using 31 variables accounted for 93% of the variance in the first two axes, and produced a pattern (Fig. 3) that broadly matched the geographic dispersion of the sampled populations (Fig. 1a and 1b). Means with 95% confidence circles that do not overlap imply that there is separation of geographically distinct groups. The first canonical axis represents element sequence and separated the southeastern and central geographic zones, although there was some overlap between the two. The variables with the highest loadings that produced this division were all sequences of pairs and triplets of elements that

characterized the start and middle of the stereotyped phrases of birds from central Australia: $I + NN + H$ (0.41); $NN + H + NST/NNT$ (0.77); $H + NST$ (0.44; Table 1). The frequency of the element Noise-structure Tone (0.37) also had a substantial loading. A rare element, the Down-slur (−0.80), was the only variable that loaded the second canonical axis to any significant extent; it occurred in all four males sampled in the most southern population (region 11) and separated it from the other regions in the southeastern zone. The most northern region sampled (12) aligned with those sampled along the Murray River some 850 km to the south.

The nearest-neighbor analysis on the same data gave a somewhat similar picture; 50% of

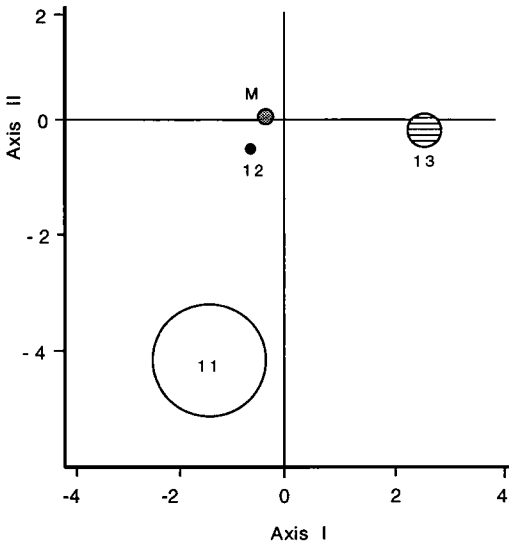


Fig. 3. Canonical-discriminant analysis of 402 song phrases from all song regions, with 95% confidence circles around means for four groups of regions: (M) Murray (regions 1-10 and 14, $n = 355$); (region 11) You Yangs ($n = 4$); (region 12) Inverell ($n = 3$); (region 13) Alice Springs ($n = 40$). The first two canonical axes account for 93% of variance.

the central Australian phrases and 95% of those from the southeastern zone were classified successfully. Two types of elements were used in this classification: Introductory Elements were more numerous and Distance-call Elements less numerous in the central Australian zone. Four sequences were also used to classify the two zones: $NN + H + NST/NNT$; $I + TON + H$; $I + S$; and $H + NS$.

In sum, between-zone differences exist principally in the middle section of the phrase, where specific sequences of noncall-like elements are diagnostic of birds from central Australia. Furthermore, these birds had more Introductory Elements in the song and sang at a faster tempo than did the southeastern birds (Zann 1993:table 1).

Variation among regions in southeastern zone.—Phrases of 359 males from all 12 regions in the southeastern zone (Fig. 1b) were subjected to canonical-discriminant analysis in which the first two canonical axes accounted for 74% of the variance in the data. Canonical axis I made a division between the sampling regions roughly coinciding with the Murray River, thus separating regions north of the river from those south of the river (Fig. 4). Regions 3 and 4,

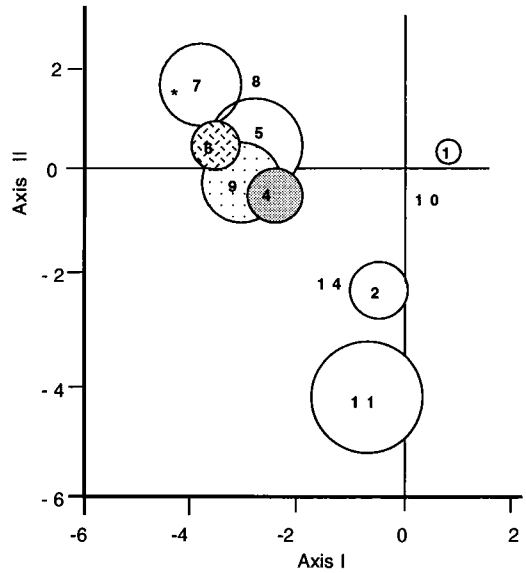
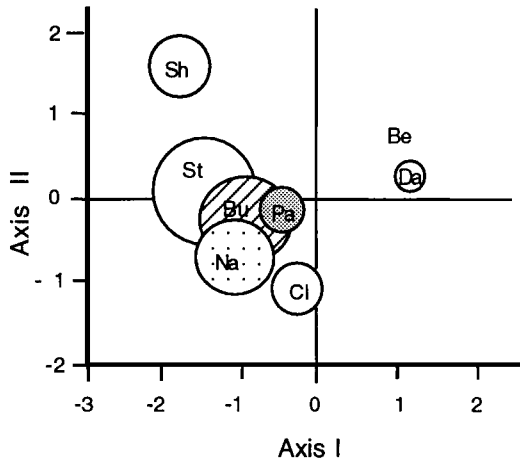


Fig. 4. Canonical-discriminant analysis of 359 phrases from 12 recording regions in southeastern zone of distribution along and south of the Murray River. Axes I and II account for 74% of variance. Number of each recording region is located at position of group means, and circles give the 95% confidence limits for regions where sample sizes greater than 3. Regions 5-9 located north of the Murray River (Fig. 1). An asterisk (*) denotes region 3.

located south of the river, were classified with the northern ones. Regions north of the Murray River were not separated clearly by canonical axis II, although the regions south of the Murray were more distinct. Only five variables contributed significantly to the loadings (Table 1). On canonical axis I the Noise-structure Tone Element (-0.77) and the sequences $NN + H + NST/NNT$ (-0.48) and $H + NST$ (-0.42) were significant; the Noise-structure Tone Element (0.31) and the Down-slur Element (-0.61) loaded axis II.

Variation among colonies in region 1.—Canonical-discriminant analysis was run on phrases of all 273 males recorded from 1976-1988 in region 1 (south of the Murray River; Fig. 1c) and classified according to the eight colonies sampled; the first two axes accounted for 67% of the variance. Canonical axis I separated colony Da from the seven remaining colonies (Fig. 5a); this colony was distinguished by the high representation of the Ladder-noise Element (loading 0.42), the low representation of the High Element (-0.56) and the small number of elements

a)



b)

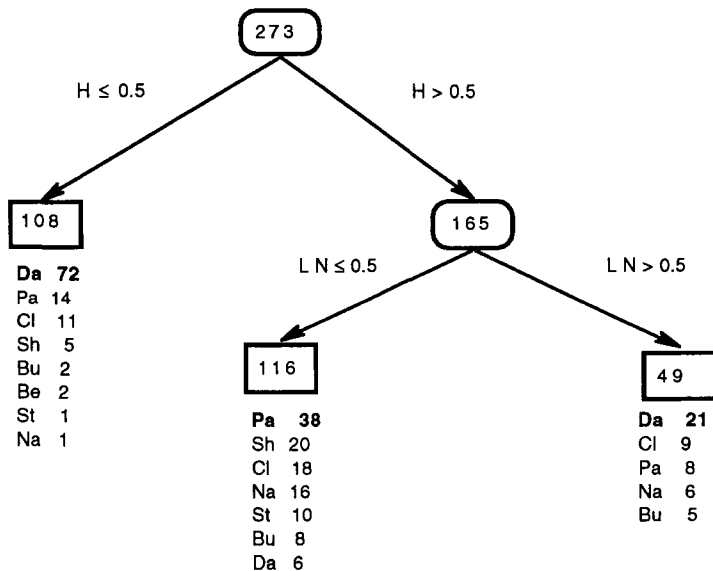


Fig. 5. Analysis of 273 song phrases in region 1 by colony using (a) canonical discrimination, and (b) CART. Circles in (a) are 95% confidence limits about mean for each colony. In CART binary tree, breakdown of each terminal node by colony is given together with song variable used at each split. Colony abbreviations and sample sizes are: (Da) Danaher, 99; (Bu) Bunbartha, 15; (Pa) Padgett, 60; (Cl) Cloverlea, 38; (Sh) Shepparton, 25; (Na) Nathalia, 23; (St) Strathmerton, 11; (Be) Bearii, 2.

per phrase (-0.30; Table 1). The separation of Da songs is not so clear-cut when the data points rather than the confidence circles are plotted; there is some spread to the other colonies of those songs that have the High Element. Axis II separated colony Sh from the remainder on the basis of the high representation of the Noise-

noise Element (-0.50), and the low representation of the Tone-noise Element (0.50) and the sequence $I + TON + H$ (0.54).

The binary tree constructed by CART (Fig. 5b), which attempts to account for all the variance in the data, identifies groups that are similar to those found through canonical analysis.

The variables CART used to make the first two binary divisions are the same variables that the canonical discrimination loaded onto axis I: the frequency of the High Element and the Ladder-noise Element. The CART variable for the best "surrogate split" was Element Number, the same variable that loaded significantly on canonical axis I. CART first separates the 108 songs that had no High Element; most (72) were from colony Da because the element was rare in the first two study seasons (1985–1986, present in 19% of males; 1986–1987, 12%). The 165 songs with High Elements were partitioned into two groups: those predominantly from colony Da that also had the Ladder-noise Element; and those from the remaining colonies that did not.

It is possible that differences between colonies actually reflect differences in the year of recording rather than geographic differences. Therefore, the canonical discrimination and CART were rerun on a subset of 156 birds recorded from 1976–1982. The first two canonical axes accounted for 60% of the variance and the variables with the highest loadings—the Noise-structure Element and the Noise-noise Element—were the same two variables CART used in its first two binary splits of the data. The CART surrogate variable for the first split was the *H + NS* sequence, which also loaded significantly on axis II in the canonical analysis. In both analyses the southernmost colony, Sh, was clearly separated from the rest by the low representation of the Noise-structure Element and the high representation of the Noise-noise Element.

To further reduce the effect of time of recording on differences between colonies, two of the closest (6.5 km apart) colonies in the region (Da and Cl; Fig. 1c) recorded only 6 to 12 months apart were compared. Banding data showed that movements between them were very rare, but there was considerable immigration to both from unknown sources (Zann and Runciman in press). The two colonies differed in the frequency of two elements: the Noise-structure Distance-call Element (Fisher's exact test, $P = 0.004$, $n = 74$); and the High Element ($G = 10.862$, $df = 37$, $P = 0.001$). Thus, these two closely adjacent colonies have song phrases significantly different in two parameters and to some extent this is due to lack of interchange between them.

Temporal variation within colonies.—Three colonies, studied over a number of years, provided

an opportunity to analyze changes over time: Cloverlea (Cl), 1981–1982 (20 songs) and 1988–1989 (18); Danaher (Da), 1985–1986 (36), 1986–1987 (17), and 1987–1988 (46); and Padgett (Pa), 1978–1979 (14), 1979–1980 (25), 1980–1981 (4), and 1981–1982 (17).

The large number of variables and the smaller sample sizes per colony precluded canonical-discriminant correlations for colonies Da and Cl, but criteria were acceptable for colony Pa. However, the number of Noise-structure Distance-call Elements (0.48) was the only significant variable that loaded the canonical axes and separated phrases recorded in 1981–1982 from the rest.

I used univariate methods to compare phrases between years in colonies Cl and Da. In colony Cl there was a significant difference in elements sung per second ($F_{1,36} = 7.99$, $P = 0.007$), but not phrase duration ($F_{1,36} = 2.01$, $P = 0.17$). Furthermore, the occurrence of three elements differed significantly between the two periods: the Noise-structure (Fisher's exact test, $P = 0.021$, $n = 38$), Ladder-noise ($G = 11.76$, $df = 1$, $P = 0.003$), and Tone-noise ($G = 6.85$, $df = 1$, $P = 0.009$) elements. However, there was no significant difference with the remaining elements (Introductory, Noise-structure Distance-call, Distance-call, High, and Stack). When the three significantly different elements were used in a log-linear model using maximum-likelihood estimates (CATMOD procedure; SAS Institute 1985) with year as the response effect, there were interactions between them. This was evident when the elements were fed into the model in pairs in order to maintain cell size requirements. Noise-structure Elements and Tone-noise Elements did not differ between sampling periods when in combination with Ladder-noise Elements, suggesting that these three variables were not orthogonal to one another and overlapped in some combinations.

In colony Da there was no significant difference in phrase duration ($F_{2,96} = 0.85$, $P = 0.43$) or elements sung per second ($F_{2,96} = 0.84$, $P = 0.43$) over the three seasons. The frequency of four elements was significantly different (Noise-structure Element, $G = 8.48$, $df = 2$, $P = 0.013$, $n = 99$; Noise-structure Distance-call Element, $G = 12.29$, $P = 0.002$; Ladder-noise Element, $G = 9.10$, $P = 0.012$; and High Element, $G = 6.66$, $P = 0.036$), but not the remainder (Introductory Element, Distance-call Element, Stack Element). When the four significantly different elements

were used in a log-linear model using maximum-likelihood estimates with year as the response effect, again there were significant interactions among the elements. To satisfy class-size requirements the four elements were fed into the model in triplets with the result that the significance of each element varied according to others in the triplet; consequently, the elements interacted with one another and were not orthogonal, so that they overlap in some way when used in different combinations. Greater sample sizes would allow the model to be run in four dimensions and specify the nature of the interactions with more clarity than has been possible here.

Of the 99 singers recorded in Da over three years, 52 were hatched in the colony and 47 were immigrants, most arriving as adults. Thus, about one-half were hatched in the colony and unpublished pedigree data showed that only 25% of these had fathers that were also hatched in the colony; this pattern was consistent for each year (Table 2). Unpublished banding data showed that only 23% of birds breeding in this colony were hatched there. However, my song sample was biased towards colony-hatched males because I needed their songs for a separate study on song learning (Zann 1990). There were significant differences in phrase duration in 1987-1988 ($F_{1,44} = 7.71$, $P = 0.008$) and element number ($G = 10.87$, $df = 4$, $P = 0.028$; SAS Institute 1991), but no differences for the other years or when the data were pooled across years. Immigrants of that season may have come from a different source to that of previous years.

Immigrants in colony Da in the 1987-1988 season differed in only one element from their closest neighbors (colony Cl) recorded in the 1988-1989 season. The High Element was rarer in the former ($G = 4.2$, $df = 37$, $P = 0.042$). In contrast, colony-hatched birds in Da differed in three elements from their neighbors in Cl (High Element, $G = 13.33$, $df = 45$, $P = 0.001$; Tone-noise Element, Fisher's exact test, $df = 45$, $P = 0.045$; and Noise-structure Distance-call Element, Fisher's exact test, $df = 45$, $P = 0.045$). Furthermore, the phrase was significantly shorter in the colony-hatched birds of Da ($F_{1,43} = 0.38$, $P = 0.0007$). Thus, the immigrants that arrive in colony Da do not come from Cl (thus, confirming the banding data), but from other sources that may or may not be shared by the two colonies. The characteristically low representation of the High Element in Da colony-

TABLE 2. Singers in colony Da by year and origin.

	Immigrants ^a	Colony born ^b	Total
1985-1986	17 (8)	19 (2)	36
1986-1987	11 (6)	8 (3)	19
1987-1988	19 (4)	25 (8)	44
Total	47 (18)	52 (13)	99

^a Numbers in parentheses show minimum numbers of immigrants that became fathers of sons in colony.

^b Numbers in parentheses show number of colony-hatched males whose fathers were also born in colony.

hatched birds clearly is a feature that was transmitted from one year to the next and was not rapidly diluted by subsequent immigrants.

DISCUSSION

The correspondence between song classifications produced by the canonical discrimination and the positions of colonies at the macrogeographic scale do not appear to be artifacts of the method since the nonparametric classification, CART, which made few assumptions about the data, arrived at similar patterns. Specifications for the song phrase in the wild Zebra Finches sampled here appear to be conservative. There was little variation in the duration and tempo of the phrase, the number of elements, and their syntax. Price (1979) found that the temporal organization of domesticated Zebra Finch song is resistant to effects of social isolation and deafening, and concluded that "neuromotor constraints" were responsible. However, recent experiments by Nordeen and Nordeen (1992) showed that deafening affected song performance several months after surgery. Hence, hearing is necessary to maintain the integrity of element production, timing and sequence. In cross-fostering experiments of Zebra Finch subspecies, Clayton (1990b) found in semidomesticated stocks that differences in phrase duration, element number, and fundamental frequency were macrostructural features of each subspecies that were unresponsive to learning. Presumably, variation in these parameters among populations within either subspecies would be due, predominantly, to genetic variation. In *T. guttata castanotis* studied here, I found that duration did not differ significantly between the remote colonies of Da and As, even though they were 1,700 km apart. However, the number of elements and tempo did differ significantly (Zann 1993:table 1), probably as a consequence of the genetic dif-

ferences between the populations. However, tempo is affected by motivation (Sossinka and Böhner 1980, Bischof et al. 1981) and hormonal status (Walters et al. 1990), neither of which were controlled in the present study.

Although the design of each call-like element in start and end sections of the song (Introductory, Stack and Distance-call elements) was stereotyped and conservative in my wild populations, there were minor differences in structural detail such that elements between the two geographic zones differed in fundamental frequency, duration, and degree of frequency modulation (Zann 1993). Experiments are in progress to test whether females can discriminate between songs from different zones using the methods developed by Clayton and Pröve (1989).

Variation across years within colonies was due to variation in six noncall-like elements that comprised the middle section of the song: Ladder-noise, Noise-noise, Noise-structure, High, Noise-structure Distance-call and Tone-noise. These elements were also important in distinguishing colonies within regions and must be considered, with the exception of the High Element, the least stereotyped of elements sung by wild Zebra Finches; of course, their limited spectral structure makes them difficult to measure. Variation in emphasis on the tonal component of the Ladder-noise Element causes transitions to the Noise-noise Element (Zann 1993:fig. 3); these variations can occur in transition from father to son and grandson (Zann 1990). In studies on song learning, most investigators (Böhner 1983, 1990, Eales 1985, Slater et al. 1988, Clayton 1990a, b, Williams 1990, Zann 1990, ten Cate and Slater 1991) compare songs of two birds for evidence of learning by matching each element in the phrase and giving a final score in which each element is given equal value. However, Introductory and Stack elements, in particular, vary little in gross structure across populations, whereas others are highly variable within and among populations (Zann 1993), which suggests that the value of matches should be weighted according to the probability of chance matching of the element type.

In a previous study on a wild population of Australian Zebra Finches, I found that some 60% of males in a colony (Da) had song phrases that strongly resembled those of their fathers and that this resemblance was not due to chance,

but probably due to learning from the father during the second month of life (Zann 1990). This phenomenon has been demonstrated in the laboratory a number of times with domesticated birds (e.g. Immelmann 1969, Böhner 1990), although Williams (1990), in a seminaturalistic study of captive birds, found sons had songs different from those of their fathers but which strongly resembled those of unrelated adult males that provided them with high levels of parental care. In Zebra Finches, parental care to nonoffspring is probably an artifact of domestication and/or captivity, since it has never been reported in wild birds, nor did I observe it during six years of fieldwork that included a specific study of fledglings for two breeding seasons. Therefore, Williams' findings are unlikely to be representative of the situation in the wild. Slater and Mann (1990) also mentioned the results of a seminatural aviary experiment, as yet unpublished, where they found that about 50% of sons learned their father's song. Thus, my findings on wild populations and theirs agree on the fact that at least one-half of all sons have songs that strongly resemble those of their fathers. Therefore, the potential exists for a song tradition within a family and this could lead to the formation of colony-specific song types if members of families were fairly sedentary.

Slater and Mann (1990) have correctly pointed out that there is no direct proof that a wild Zebra Finch learns its song from its father; it may have learned it from an unrelated male that happened to sing a song that resembles that of the father. Evidence for this possibility comes from experiments with domesticated laboratory Zebra Finches, which can learn songs of other males if they are isolated from their fathers during the sensitive phase (e.g. Eales 1985, Slater et al. 1988, Williams 1990). When given a choice of tutors, Clayton (1987) found that these young males prefer to copy the individual whose song most resembles the father's. This could conceivably happen in the wild as well, but is impossible to verify. Nevertheless, it is unlikely to hold in my study population since the chance probability of another unrelated bird matching the father's song is less than 2.5% (Zann 1990). This low probability is a consequence of the high level of annual immigration where almost one-half the singers recorded in this study were immigrants (Table 2); even this is an underestimate since banding data show that about 77%

of breeding pairs were immigrants each season (Zann and Runciman in press). Differences between immigrants and colony-hatched singers were not large in my study because measurements were much less sensitive than those used in the song-learning study. Nevertheless, there were significant differences in the 1987-1988 season. In the song-learning study, in contrast, a detailed comparison of the morphology of variants within the same element type was made and, in the case of the Distance-call Elements, the fundamentals were measured. In sum, therefore, the simplest explanation for the close resemblance of songs between fathers and their sons is that the latter learned them from the former. I have made the same conclusion about Distance Calls where 80% of sons have calls identical to those of their fathers (Zann 1990).

Patterns of dispersal among colonies are still not clear. However, banding and song data within and among colonies in region 1, the most intensively studied region, suggest that dispersal is the key factor that erodes the formation of colony-specific song types, and that the differences between geographic zones simply reflect reduced dispersal on a macrogeographic scale. In the southeastern zone the Murray River is a boundary that divides the more arid and open habitats to its north from the more mesic and wooded habits to the south. Zebra Finches avoid heavily-wooded areas; consequently, there are fewer barriers to dispersal north of the Murray and more to the south. Furthermore, drought is more prevalent north of the river and less so to the south. Consequently, there are more environmental pressures for dispersal north of the river. These differences in prevalence of dispersal are reflected in the greater overlap of songs from regions north of the Murray. Following European settlement, the clearing of forested areas in the less-arid habitats south of the Murray probably led to some differences arising between regions as a consequence of uneven and limited immigration from the north and the temporary isolation of colonies in these new habitats. With further clearing of woodlands, barriers to dispersal will diminish so that differences in songs across colonies will lessen.

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