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STRUCTURE, SEQUENCE AND EVOLUTION OF SONG ELEMENTS IN WILD AUSTRALIAN ZEBRA FINCHES

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ABSTRACT.—Songs from 402 Zebra Finches (*Taeniopygia guttata castanotis*) were sampled in order to describe the structure of the song phrase and the relationship of its elements to the call repertoire. The song of wild birds was also compared to that of 47 domesticated Zebra Finches from two European laboratories in order to examine the effects of domestication on song structure. The stereotyped phrase, which is the repetitive unit of the song, had a mean number of 6.75 elements and a mean duration of 0.86 s in wild birds. Elements were sung in sequence that defined three parts to the phrase—a start, a middle and an end. Fourteen types of elements were identified of which four were sung by the vast majority of males; three of these "primary" elements were "borrowed" unmodified from the call repertoire, and formed the start and end sections of the phrase. "Secondary" elements, which were less frequently represented across males, constituted the middle of the phrase and appeared to be modified versions of the Distance-call Element, the loudest element in the phrase. I tentatively conclude that Zebra Finch song may have evolved from the calls associated with flight intention and take-off. Domestication has led to changes in element morphology, frequency of occurrence, and rate of singing (elements/s), but not in number of elements per phrase. *Received 9 March 1992, accepted 30 November 1992.*

ALTHOUGH THE SONG of domesticated Zebra Finches (*Taeniopygia guttata castanotis*) has become a classical subject for laboratory-based studies of the development (Immelmann 1969, Slater et al. 1988, Williams 1990), control (Nottebohm et al. 1990), and function (Clayton 1990a, b, Clayton and Pröve 1989) of behavior, few studies have investigated the structural organization of the song itself, and little information about song of the species in the wild has been published. In order to make sense of the laboratory-based discoveries that detail the specifications and constraints on the mechanisms for song learning and its perception in the Zebra Finch, it is necessary, as a first step, to make a detailed descriptive study of the acoustic structure of the song itself and its relationship with other acoustic signals emitted by the species.

Cynx (1990) found that the elements or syllables—the smallest tracings on the sonagram that are temporally distinct from neighboring elements (Eales 1985)—are the functional units of song production in domesticated Zebra Finches. Consequently, they are the most basic unit of analysis in this study. Each male has, on average, seven different elements that he sings in a set order and together they constitute the phrase ("song-unit," Price 1979; "motif," Böhner 1990; "song," Cynx et al. 1990), which is repeated one or more times to form the song ("bout," Price 1979; "strophe," Böhner 1983, 1990). The first phrase of the song is preceded by several identical notes, the Introductory Elements, some of which are incorporated into the phrase pattern itself. Macrostructural features of song (number of elements per phrase, number of phrases per song, elements sung per second, and number of Introductory Elements per song) have been studied and found to differ: (1) between those songs sung in premating courtship and those undirected songs sung in noncourtship contexts (Sossinka and Böhner 1980, Bischof et al. 1981); and (2) between undirected songs of domesticated and wild birds (Slater and Clayton 1991). By contrast, there have been no studies of microstructural aspects of the song (namely, the song elements themselves, their acoustic structure and sequential organization within the phrase) in either domesticated or wild birds of the Australian (*T. g. castanotis*) or Timor (*T. g. guttata*) subspecies. Thus, my aim is to describe the structural features of song in wild Australian Zebra Finches and to draw contrasts between two focal colonies some 1,700 km apart in order to examine stereotypy in microstructure. Songs of wild birds will be compared with those of domesticated birds from Europe in order to determine what aspects of song change under domestication. Variation in more macrostructural features of song within and among 34 wild populations is the subject of a companion paper (Zann 1993).

Investigations into the evolutionary precursors of song and its elements have not received much attention from researchers in this or other species of songbirds, although Price (1979), while studying determinants of song development in domesticated Zebra Finches, noticed similarities between some elements of the song and certain calls from the vocal repertoire. However, I have shown that at least one call of wild-caught Zebra Finches, namely the male Distance Call, the loudest and most penetrating sound emitted, is actually learned from the father early in life, and aviary confinement and domestication affects this process so that the Distance Calls of almost all domesticated birds published to date are aberrant in structure by comparison with those of wild birds (Zann 1985). Consequently, a second aim is to compare the structure of the elements of the song phrase of wild (nondomesticated) birds with that of their calls in order to understand the possible derivation of the song.

METHODS

Songs from 402 males were recorded at breeding colonies in two geographically distant areas of Australia: the central arid zone at Alice Springs; and the semiarid southeastern corner bordering the Murray River some 1,700 km away. For comparison, large samples were taken from two focal colonies: 40 males from colony As (24°45′S, 133°52′E) in central Australia; and 99 males from colony Da (36°09′S, 145°26′E) in southeastern Australia. See Zann (1993:fig. 1) for further details on study sites.

I recorded songs using several recorders (Uher 4000 report L, Nagra 4.2 L, Marantz Superscope, Sony Walkman Professional and Sony TCD5 Pro) coupled with either a parabolic reflector (Sony PBR 330 with a Beyer M69 microphone), or a shotgun microphone (Sennheiser Electret or MKH 816 T). Most songs were the undirected type, but a few were directed at females during courtship. I recorded free-flying birds at their nesting or roosting bushes, but some males were temporarily confined to a portable aviary in order to obtain quality recordings. All birds were sexually mature when recorded. Each song included in the study was assumed to have originated from a different male; this certainly was the case where the birds were color banded or where a colony was visited only once. The possibility exists in one colony that some males recorded one year were rerecorded the next, but the high turnover among breeding birds (Zann and Runciman in press) makes this unlikely.

I analyzed songs on a Kay Sonagraph 7030A with the 150-Hz filter, which provided the most appropriate resolution for this study. Phrases were defined as the repetitive unit of the song, and at least three phrases of each male were analyzed from the onset of singing to establish which elements were repeated consistently and constituted the phrase. Successive phrases sometimes were separated by pauses or calls (e.g. Fig. 1c), but frequently were not (e.g. Fig. 1a). Song (bouts) varied considerably in duration and structure within individuals, but the single phrase, once learned, was fixed in structure and duration, making it an appropriate unit for analysis of song organization in this species (Zann 1990).

To determine the duration of the phrase the sonagram was measured with a ruler to the nearest millimeter (equivalent to 8 ms) from the start of the first element to the end of the last element. In order to characterize the types of elements sung by Zebra Finches, all of the elements from 20 males, each chosen at random from the focal colonies (Da and As), were measured for duration to the nearest millimeter. If an element had harmonic structure the distance between the first and second harmonic was measured to the nearest millimeter (equivalent to 80 Hz). Furthermore, the tone and noise components that constitute the Distance-call Element were measured separately (see Zann 1984).

I used visual inspection of sonagrams to classify elements in the phrases from songs of all 402 males in the sample into 14 different categories or types. Classification of acoustic signals by visual inspection of sonagrams is a reliable and proven method for defining natural categories and results can be comparable with objective numerical methods (Nowicki and Nelson 1990). Elements were first classified according to the presence or absence of tonal structure and those with tonal structure were further classified according to the morphology of the first or second harmonic. Duration of the element and the frequency of the fundamental were then taken into consideration. The majority of males had unique variants of each type of element (Zann 1990), but these were ignored in this study. Repeatability of element classification was tested in a replicated double-blind trial of 83 elements representing the 10 most common element types sung by Zebra Finches; elements in the trial were chosen haphazardly from a reference collection and presented randomly to the assessor. The Kappa coefficient of concordance (*K*; Lehner 1979) between the original classification and the classification in the blind trial over all element types was 0.93, with a range of 0.66 to 1.00, depending on the type of element.

To investigate amplitude of the song elements, I scored songs from a sample of five males each from the two focal colonies using the energy calculation option on a Kay CSL Computerized Speech Laboratory 4300 application (ver. 4.0). Recordings at both

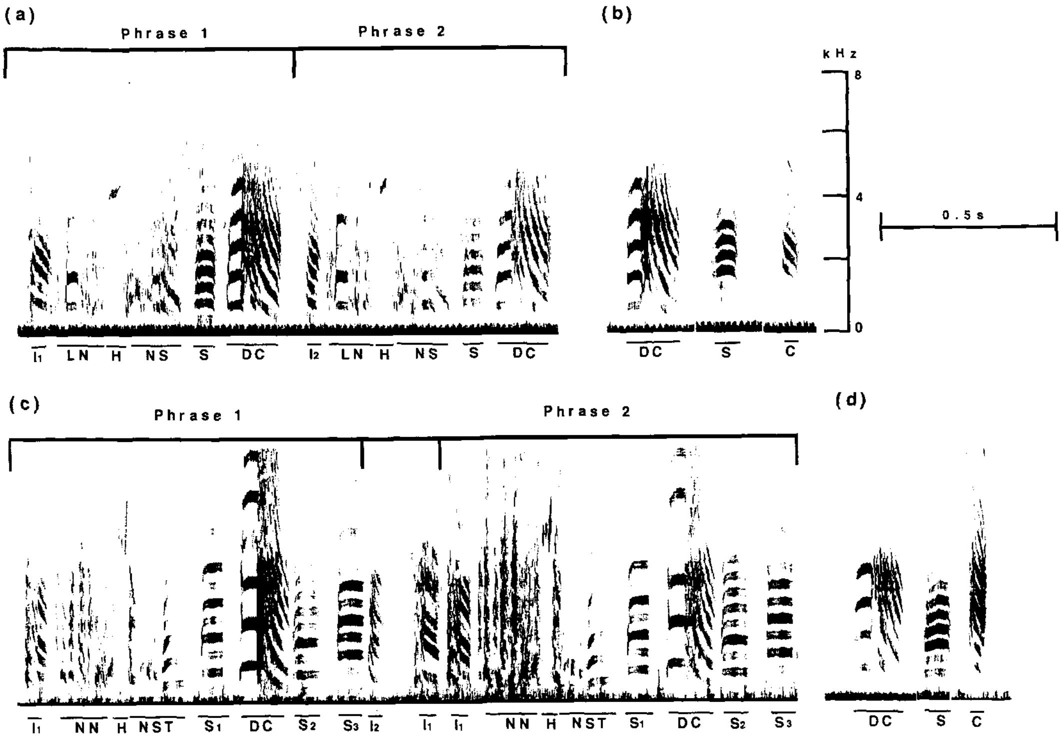

Fig. 1. Wide-band-filter (300-Hz) sonagrams of song phrases and calls of two wild Zebra Finches from different parts of range: (a and b) southeastern Australia; and (c and d) central Australia. Calls recorded between bouts of song: DC, Distance Call; S, Stack Call; C, Communication Call. Song elements: *I*, Introductory; *LN*, Ladder-noise; *NN*, Noise-noise; *NS*, Noise-structure; *NST*, Noise-structure Tone; *H*, High; *S*, Stack; *DC*, Distance-call. Different versions of same element type have numerical subscripts.

colonies were made with the same equipment under similar conditions; birds were held in an outdoor aviary and sang 25 to 30 cm from the microphone. I chose males at random and analyzed the elements of the five best-quality phrases of each. The cursor was moved through the amplitude envelope of each element analyzed on the screen and the loudest reading in dB (SPL) recorded. A mean was calculated for the five replicates of each type of element sung by each male. Data were analyzed with JMP (software for statistical visualization on the Apple Macintosh, ver. 2.04; SAS Institute 1991). Transformations of the data failed to produce equal variances so a nonparametric test was used (Kruskal-Wallis test).

Photocopies of sonagrams of undirected songs of 24 domesticated Zebra Finches from St. Andrews, United Kingdom, were provided by P. J. B. Slater and 22 from Bielefeld, Germany, were provided by N. S. Clayton (e.g. Fig. 2). Songs were recorded under similar conditions at the two laboratories and analyzed with similar settings. These 46 song phrases were subjected to the same measurements and element-classification procedures used on wild birds. The morphology of 152 elements (repeats omitted) from the songs of these domesticated birds were compared with a subsample of sonagrams of comparable quality from wild birds (22 songs from colony Da and 14 from colony As) that yielded 110 elements in total. Each element was cut from its sonagram sheet and any identifying marks removed. Single elements were drawn from the combined pool ($n = 262$) and classified according to type and origin (domesticated vs. wild) in a randomized blind trial.

RESULTS

Phrase macrostructure.—The number of elements per phrase ranged from 3 to 14, with a mean of 6.76; correspondingly, the duration ranged from 0.32 to 1.66 s, with a mean of 0.86 s (Table 1). The Pearson product-moment correlation between number of elements and phrase duration was 0.816 ($P < 0.0001$). The regression equation was

$$D = 0.167 + 0.1084E, \qquad (1)$$

where D is duration in seconds and E is element

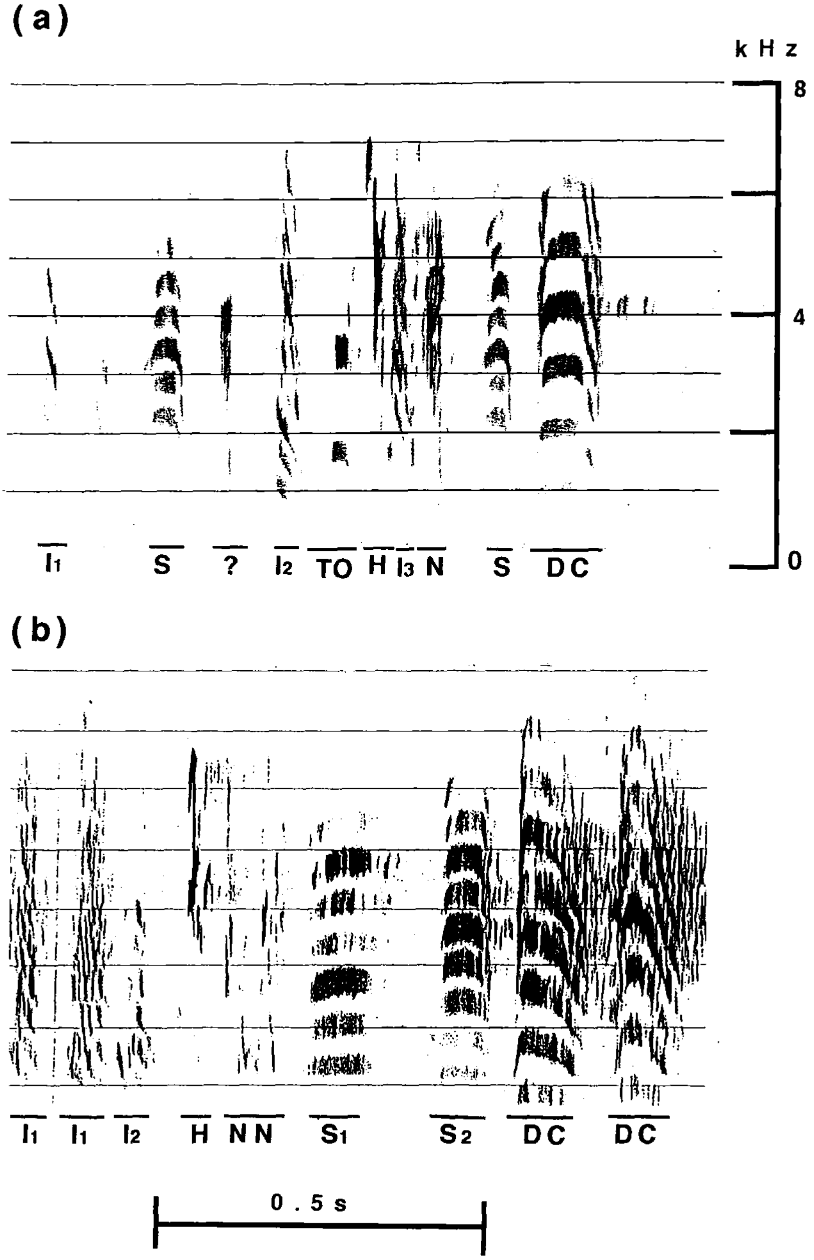

Fig. 2. Wide-band-filter (300-Hz) sonagrams of song phrases sung by two domesticated Zebra Finches from two European laboratories: (a) St. Andrews; (b) Bielefeld. Song elements: *I*, Introductory; *H*, High; *NN*, Noise-noise; *TO*, Tone; *S*, Stack; *DC*, Distance-call; ?, unclassifiable element.

number. The tempo ranged from 5.22 to 12.38 with a mean of 7.90 elements/s.

The duration of the phrase did not differ significantly between colony As and colony Da. However, birds from the former had significantly more elements per phrase and sang the phrases faster (Table 1).

Types of elements.—Based on morphology of spectral structure, 97.1% of all song elements (n = 2,711) from 402 males analyzed were successfully allocated to 14 categories or types; the remainder were unclassifiable (Table 2). Most elements fell into discrete categories, but a few graded from one to another via intermediates,

TABLE 1. Comparison of macrostructural parameters (medians and interquartile ranges) of song phrases from wild (Danaher and Alice Springs) and domesticated (Bielefeld and St. Andrews) colonies.

	Wild[a]			Domesticated[b]		
	All colonies	Colony Da	Colony As	Colony Bl	Colony Sa	P^c
Duration(s)	0.86 (0.71-0.97)	0.78 (0.69-0.91)	0.83 (0.70-0.99)	0.65 (0.56-0.77)	0.67 (0.53-0.80)	0.001
No. elements	7 (6-8)	6 (5-7)	7 (6-8)	6 (6-7)	5 (5.5-8)	0.003
Elements/s	7.9 (7.1-8.7)	7.4 (6.7-8.2)	8.5 (7.6-9.2)	10.1 (9.1-10.7)	9.9 (8.8-11.6)	0.001
No. distance-call elements	1 (1-1)	1 (1-1)	1 (1-1)	1 (0-1)	1 (0-1)	0.001
Repeats (percent of birds)	73	66	75	95	83	
n	402	99	40	22	24	

[a] Da vs. As (Wilcoxon two-sample test with continuity correction): duration, $P = 0.31$; number of elements, $P = 0.002$; elements/s, $P < 0.001$; distance calls, $P < 0.001$.

[b] Bl vs. Sa (Wilcoxon): duration, $P = 0.99$; number of elements, $P = 0.72$; elements/s, $P = 0.74$; distance calls, $P = 0.10$.

[c] Kruskal-Wallis test (chi-square approximation) across all colonies (SAS Institute 1990).

and their classification was less precise; the degree of ambiguity in classifying each element is given by the Kappa (K) coefficient of concordance listed below. I found that 73% of the phrases had "repeats" (i.e. two or more elements belonging to one type); however, these were usually different variants within the type and not exact replicates.

Measures of duration, frequency and rate of occurrence are given in Table 2 for a sample of all 14 element types, and in Table 3 quantitative comparisons of five of the most frequent elements are made for the two focal colonies. These are described below:

(1) Introductory Elements (*I*) are common elements that introduce the phrase. They are brief, soft, low-frequency sounds (Table 2) with multiple harmonics of a chevron-shape with a pronounced down-slur. Their classification was unambiguous ($K = 1.00$). In 60% of males there was only one variant of the Introductory Element, but 40% had two (e.g. Figs. 1a and c) or even three; these repeats often were sung in sequence. Introductory Elements did not differ significantly in duration, but the fundamental frequency of those from central Australia was significantly lower than those from southeastern Australia (Table 3).

(2) Introductory Diads (*II*) are Introductory Elements in context and configuration that oc-

TABLE 2. Frequency of occurrence of Zebra Finch song elements with measure of their acoustic structure. Sample of 2,711 elements from 402 males.

	Occurrence (%)			Duration (ms)		Frequency (kHz)[a]	
Element type	Elements	Males	n	Median	Interquartile range	Median	Interquartile range
Introductory (*I*)	23.9	90.0	40	54	46-52	0.40	0.32-0.48
Distance-call (*DC*)	16.4	87.1	40	155	139-163	1.04	0.90-1.36
Stack (*S*)	17.0	80.1	40	70	62-85	0.56	0.48-0.56
High (*H*)	10.1	66.6	40	8	8-29	6.40	5.30-6.72
Noise-noise (*NN*)	6.9	39.6	40	124	110-147	—	—
Ladder-noise (*LN*)	3.9	24.9	20	155	139-142	0.96	0.88-0.96
Noise Structure (*NS*)	3.6	23.9	20	155	141-168	—	—
Tone-noise (*TON*)	3.2	21.6	20	116	93-116	0.92	0.88-1.80
Noise-structure Distance-call (NSDC)	3.2	21.6	20	224	194-253	0.96	0.88-0.96
Noise-structure Tone (*NST*)	2.8	17.9	20	163	149-170	0.72	0.72-0.80
Down-slur (*DS*)	2.2	13.4	20	101	85-132	0.56	0.48-0.64
Introductory Dyad (*II*)	1.8	11.7	20	89	77-101	0.48	0.48-0.54
Tone (*TO*)	1.2	7.7	20	31	23-39	1.52	0.98-1.76
Noise-noise Distance-call (*NNDC*)	0.8	5.7	8	244	207-267	0.92	0.68-0.96
Unclassified	2.9	5.7					

[a] Fundamental frequency measured on 150 Hz filter sonagrams between first and second harmonics, except for H element, which had only one harmonic.

TABLE 3. Duration and frequency of five song-element types from two colonies (Da, southeastern Australia; and As, central Australia) 1,700 km apart ($n = 20$ for all measures).

Variable	Colony[a]		P[b]
	Da	As	
Introductory Element			
Duration (ms)	54 (46–70)	54 (46–52)	0.647
Frequency (kHz)	0.48 (0.48–0.48)	0.32 (0.24–0.32)	0.0001
Distance-call Element			
Duration (ms)	151 (139–168)	155 (139–163)	0.957
Frequency (kHz)	0.96 (0.88–1.16)	1.12 (1.00–1.36)	0.001
Tonal component of Distant-call Element			
Duration (ms)	35 (23–46)	58 (42–70)	0.001
Stack Element			
Duration (ms)	64 (64–78)	88 (72–96)	0.0005
Frequency (kHz)	0.48 (0.48–0.56)	0.56 (0.56–0.64)	0.0004
High Element			
Duration (ms)	27 (16-31)	8 (8–8)	0.0001
Frequency (kHz)	5.32 (3.12–5.80)	6.68 (6.48–7.08)	0.0001
Noise-noise Element			
Duration (ms)	112 (85–143)	135 (116–151)	0.031

[a] Median, with interquartile range in parentheses.

[b] Wilcoxon two-sample test with continuity correction of 0.5 (SAS Institute 1990).

cur in doublets; usually, both are different variants of Introductory Elements.

(3) Distance-call Elements (*DC*) are the loudest and one of the longest elements sung by Zebra Finches (Table 2). There is normally one Distant-call Element per phrase (Figs. 1a and c), but 13% have none and 20% have more than one; colony As had fewer than did colony Da (Table 1). The element is diagnostic ($K = 1.00$) because of two distinct parts to its structure: a tonal component of multiple harmonics with little frequency modulation that precedes a second part, the noise component, which has a sudden downward sweep in frequency of the harmonics (Figs. 1a and c). The proportions of the components vary greatly between individuals. The Distance-call Element is normally the ultimate (Fig. 1a) or penultimate element in the phrase. There were no significant differences in duration and fundamental frequency of Distance-call Elements between colonies Da and As, but duration of the tonal component was significantly longer in the latter (Table 3) and the noise component correspondingly shorter.

(4) Stack Elements (*S*; Figs. 1a and c) are similar to those calls given by birds when taking off (Figs. 1b and d). It is a brief sound with a lower fundamental frequency than the Distance-call Element and the multiple harmonic bands have little frequency modulation. The versions given by birds in central and southeastern Australia were significantly different in both duration and fundamental frequency (Table 3), but the visual classification was unambiguous ($K = 1.00$).

(5) High Elements (*H*) are the shortest and highest pitched of all Zebra Finch sounds (Table 2), and one of the most conspicuous on sonagrams, but too brief for humans to detect by ear ($K = 1.00$). The High Element in central Australia was significantly shorter in duration and the fundamental frequency was significantly higher than that in southeastern Australia (Table 3). The harmonic configuration also varied according to location. In central Australia, all 35 males had a straight, narrow vertical line on the sonagram and ranged from 1 to 2 kHz (Fig. 1c), whereas males from southeastern Australia had fundamentals with shapes ranging from a narrow vertical line to chevrons with several changes in frequency over a range of less than 1 kHz in most males (e.g. Fig. 1a).

(6) Noise-noise Elements (*NN*) have the energy more or less uniformly distributed over all frequencies without any spectral structure and resemble a band of white noise (Figs. 1c and 3). Birds from central Australia had a Noise-noise Element where amplitude modulation pro-

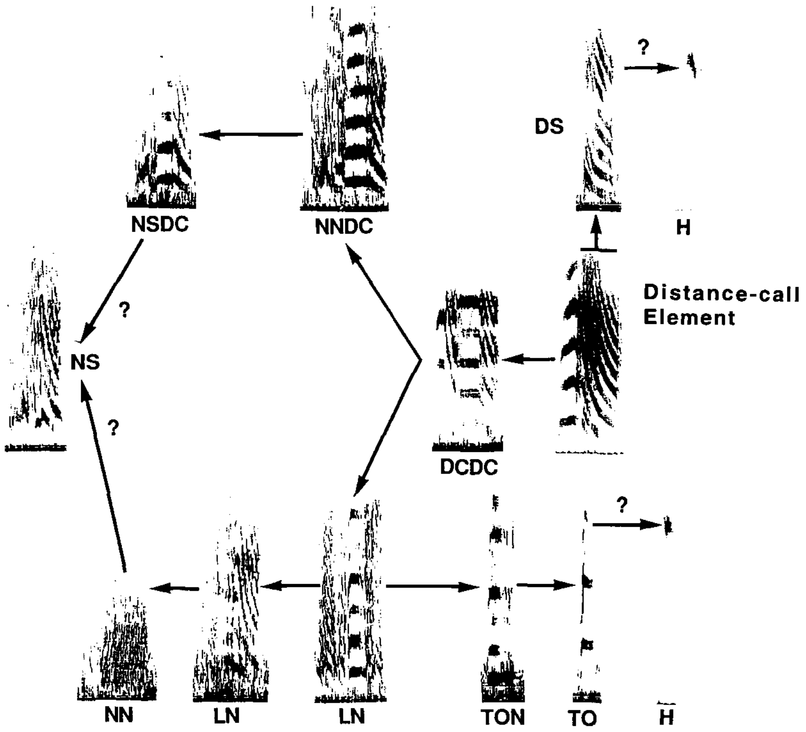

Fig. 3. Schema showing possible origins of eight song element types from Distance Call: *DC*, Distance-call; *DCDC*, Double Distance-call; *TON*, Tone-noise; *DS*, Down-slur; *H*, High; *NSDC*, Noise-structure Distance-call; *NNDC*, Noise-noise Distance-call; *NS*, Noise-structure; *NN*, Noise-noise; *LN*, Ladder-noise; *TO*, Tone.

duced three to four pulses of noise and were significantly longer than those from southeastern Australia (Table 3).

(7) Ladder-noise Elements (*LN*) are so called because horizontal harmonic bands sit between two vertical columns of unstructured noise, thus resembling a ladder (Figs. 1a and 3). The duration of the harmonics varied considerably between singers with gradations to Noise-noise Elements and Noise-structure Distance-call Elements (Fig. 3), producing some misclassifications ($K = 0.88$).

(8) Noise-structure Elements (*NS*) resemble Noise-noise Elements, but are significantly longer (Wilcoxon two-sample test, $z = 3.33$, $P = 0.001$, $n_1 = 20$, $n_2 = 40$; Table 2) and have several chevron-shaped fundamentals in the second half of the sound (Fig. 1a; $K = 0.93$).

(9) Tonal Elements (*TO*) are brief elements with a simple harmonic structure whose fundamental frequency is second only to that of the High Element (Table 2 and Fig. 3). Two of 18 were misclassified as brief Introductory Elements in the blind trials ($K = 0.75$).

(10) Noise-structure Tone Elements (*NST*) are formed from the fusion of the chevron-structured component of the Noise-structure Element with the Tone Element (Fig. 1c). One of 18 was misclassified as a Tone Element ($K = 0.94$).

(11) Tone-noise Elements (*TON*) are formed from the fusion of a Tonal Element and a short-duration Noise Element that lacks the downward sweep in frequency characteristic of the Distance-call Element (Fig. 3; $K = 1.00$).

(12) Noise-structure Distance-call Elements (*NSDC*) are formed from the union of two others: the structural component of the Noise-structure Element and a Distance-call Element. This is one of the two longest elements sung by Zebra Finches (Table 2). The amount of unstructured noise varies considerably between individuals and gradations occur with the Ladder-noise Element leading to misclassifications ($K = 0.66$); however, the latter is significantly shorter in duration (Wilcoxon two-sample test, $z = 4.37$, $P = 0.0001$, $n_1 = 20$, $n_2 = 20$; Table 2).

(13) Down-slur Elements (*DS*) are rare ele-

ments that resemble the noise component of Distance-call Elements, where there is a steep down-sweep in frequency (Fig. 3). Superficially, they resemble brief Noise-structure Elements, but are significantly shorter in duration (Wilcoxon two-sample test, $z = 4.71$, $P = 0.0001$, $n_1 = 20$, $n_2 = 20$; Table 2).

(14) Noise-noise Distance Calls (NNDC) are elements where the Distance Call component is preceded by a noise component to form one of the longest elements sung by Zebra Finches. They resemble Ladder-noise Elements, but are much longer such that the durations of the two elements do not overlap. Its rarity prevented sufficient samples being available for the classification trials.

Simple measurements could not encompass some fine details of element morphology that were hard to categorize and even harder to measure but, nevertheless, still might be diagnostic features of the phrases from colonies Da and As. In order to assess this possibility, I set up a trial in which sonagrams of song phrases from both colonies were assessed subjectively in a double-blind matching experiment. Phrases from 20 males, which were recorded with the same equipment under identical circumstances, were chosen at random from each colony and the sonagrams analyzed with the same settings. The task of the assessor was to sort sonagrams subjectively into two groups based on similarity of the detailed morphology of the elements. I ran two trials with different and independent assessors. Each trial was run such that there was random sampling with replacement between the 30 matching decisions so that each decision was independent of those that preceded it. The procedures allowed chance frequencies of the result to be calculated using the binomial distribution where the sample size was 30 and the probability 0.5. In each trial assessors allocated 27 out of 30 and 28 out of 30 matches correctly; the chance probabilities of such an outcome are less than 0.0001 in both instances. "Serrations" produced by rapid frequency modulation of the tonal parts of elements, in particular, Distance-call and Stack elements, were diagnostic of birds from central Australia.

Amplitude of elements.—Nine element types were analyzed, but only six were sung by more than six of the males investigated and included in the results. There was a significant difference in amplitude among the elements (Kruskal-Wallis test, $X^2 = 689.23$, df = 5, $P < 0.0001$). The median (interquartile range) amplitude of the Distance-call Element was 67.7 dB SPL (58.1–83.3), which was much higher than that of other elements: Noise-noise, 57.0 (55.0–59.9); High, 56.7 (50.1–62.6); Noise-structure Tone, 55.3 (52.8–58.6); Stack, 56.0 (52.6–61.9); Introductory 56.1 (52.6–59.1).

Phrase structure and element sequence.—Elements that form the Zebra Finch song phrase basically have a more or less defined location and order that divide the phrase into three parts—a start, a middle and an end (Table 4). The structure of the phrase can be best understood by first considering the pattern in the middle where the type of elements and their sequence is more determined than elsewhere. The middle consists of two types of elements: the conspicuous High Element; and various types of elements with unstructured noise (e.g. Figs. 1a and c). It is the presence and location of these two types of elements that divides the phrase into three parts in 95% of males. In 54% of males, the middle of the phrase had three elements, the High Element preceded and followed by elements with a significant noise component. In 29% of males, there were only two middle elements, most with a noise component; only 30% of these males had High Elements and they were placed in the second position (Table 4).

In colony As the three middle elements (Noise-noise, High, Noise-structure Tone) were identical in type and order for 35 of 40 birds sampled so that the three elements could almost be considered a one-element complex (Fig. 1c). Birds from colony Da were more variable in the type of noise elements (Ladder-noise, Tone-noise, Noise-structure), but the High Element was still in its central position (e.g. Fig. 1a) or the second position if only two middle elements were present.

Despite the pivotal nature of the High Element in the organization of the phrase, it was present in only 66.6% of 402 birds analyzed (Table 2). This value is biased by the large sample from colony Da where the High Element was present in only 27.2% of 99 males. The High Element was present in 79.3% of birds recorded from seven other colonies within 40 km of colony Da ($n = 174$). These proportions are significantly different ($G = 73.04$, df = 1, $P < 0.0001$).

The first and last sections of the phrase consist of three types of elements, the Introductory El-

TABLE 4. Main sequence of elements[a] in three sections that constitute song phrase of wild Zebra Finches ($n = 402$). Of males, 5% had phrases with no middle section, 5% had no start section, and 15% had no end section. Percentage frequency of main sequences within sections shown.

Start[b]				Middle[c]				End[d]			
1	2	3	Percent	1	2	3	Percent	1	2	3	Percent
I	—/I	—	53	NN	H	NST/NN	21	S	—/DC	—	28
I	S	I/S/DC	15	NN	H	NS/NSDC	7	S	DC	I/S/DC	8
I	DC	—	4	TON	H	NS/NSDC	14	DC	—	—	14
I	DC	I/S/DC	7	LN	H	NS/NSDC	5	DC	S	—	13
S	I/DC	I/S/DC	4	LN	NS/NN/H	—	9	DC	S	I/S/DC	5
DC	I/S	I/DC	5	NN	NS/NN/H	—	6	I	S/DC	—/DC/S	11

[a] Element abbreviations: I, Introductory; S, Stack; DC, Distance-call; H, High; NN, Noise-noise; NS, Noise-structure; NST, Noise-structure Tone; TON, Tone-noise; NSDC, Noise-structure distance-call; LN, Ladder-noise; —, no element; /, alternatives.

[b] 27% of starts had one element only, 36% two elements, 23% three elements, and 8% four elements.

[c] 10% of middles had one element only, 29% two elements, 54% three elements, and 4% four elements.

[d] 28% of ends had one element only, 41% two elements, 19% three elements, and 13% four elements.

ement, the Stack Element and the Distance-call Element; however, 80% of all Introductory Elements occur in the first section, and 81% of Stack Elements and 80% of Distance-call Elements occur in the last part of the phrase (Table 4). The Distance-call Element, which is the loudest in the phrase and most resistant to attenuation, appears to serve as a "coda" or "punctuation" separating one phrase from the next.

I found that 15% of males had songs that ended with elements characteristic of the middle section of the phrase, thus appearing to have no end section; however, in these cases there was a significantly greater number of elements in the first section of the phrase than those phrases where three sections were distinguishable (Wilcoxon two-sample test, $z = 6.76$, $P = 0.0001$, $n_1 = 52$, $n_2 = 321$). This suggests that the end section has not been omitted, but simply placed in the wrong order, thereby adding to similar element types found in the first part of the phrase.

Songs of domesticated Zebra Finches.—There were no significant differences in macrostructural features of song between the samples from Bielefeld and St. Andrews (Table 2), so they were pooled and compared to the whole sample ($n = 402$) of wild birds. There were no significant differences in the number of elements per phrase (Wilcoxon two-sample test, $P = 0.758$), but wild birds sang more slowly ($P = 0.0001$) and, hence, had a significantly longer ($P = 0.0001$) phrase than the domesticated birds (Table 1). Differences also existed in the rate of occurrence of different element types. Domesticated birds sang significantly more Introductory ($G = 9.95$, df $= 4$, $P = 0.041$) and High elements ($G = 20.95$, df $= 2$, $P < 0.001$), and more elements that could not be classified ($G = 26.48$, df $= 1$, $P < 0.001$; Fig. 2a). The latter were often new types formed by the fusion of High Elements with others, frequently, Introductory Elements (Figs. 2a and b). In contrast, wild birds sang more Distance-call Elements ($G = 34.61$, df $= 1$, $P < 0.001$), Stack Elements ($G = 7.90$, df $= 1$, $P = 0.005$) and Ladder Elements ($G = 17.56$, df $= 1$, $P < 0.001$).

In the subjective blind-matching trial, 85% of elements were classified correctly according to whether they originated from domestic stocks or wild colonies; there was no significant difference in the proportion of correct and incorrect classifications for the two categories of singers ($G = 1.12$, df $= 1$, $P = 0.29$). Thus, elements of the same type in wild and domesticated birds are distinct in detailed morphology. Incorrect classifications involved all element types but mainly Introductory, High and Noise-structure elements.

DISCUSSION

Fairly clear rules of song organization emerge from this analysis of the stereotyped song phrase of wild Zebra Finches: (a) song elements most similar to calls bracket the phrase; (b) two of these, the Stack Element and the very loud Distance-call Element often end the phrase; (c) another set of elements that are similar to soft calls begin the phrase; (d) the compound elements that make up the middle of the phrase and confer most of the variation to the phrase do not closely resemble any calls and could be considered the most "derived."

The Introductory Element, the Distance-call Element, and the Stack Element are the most frequently sung elements and are found in more than 80% of males. They appear to have been borrowed almost unchanged in structure from the most frequently uttered vocalizations in the call repertoire, namely the Communication Call, the Stack Call and the Distance Call, respectively. Except for colony Da, the High Element was also found in the songs of more than 80% of males sampled. It has no equivalent in the call repertoire and its derivation is problematical; it may have been modified from the tonal component of the Distance-call Element. Williams et al. (1989) believed that the High Element represents an extreme form of harmonic suppression in which the fundamental frequency and many lower harmonics are suppressed by the syrinx, but a higher one is emphasized. Variable degrees of harmonic suppression characterize the structure of many elements of Zebra Finch song and these can be perceived by both sexes (Cynx et al. 1990). The structure of the High Element is exceptional because it has a fundamental frequency five times greater than the next-highest-pitched element in the song; nevertheless, it is still in the range of frequencies to which Zebra Finches are most sensitive (Okanoya and Dooling 1987). I have termed these four frequent and widely sung elements the "primary elements" of the phrase because they do not appear to have been recently derived from other elements in the song.

The structure of the Introductory Elements strongly resembles that of the "Tet" Communication Calls first identified by Immelmann (1962). The call is not individually stereotyped in duration, but all harmonics have the same configuration; the briefest and most frequently uttered version (C in Fig. 1b) matched most Introductory Elements (e.g. I_2 in Fig. 1a), whereas other elements are longer (e.g. I_1 in Figs. 1a and b), but these also resemble longer versions of the call. Thus, the Introductory Elements are largely unmodified versions of those found among the Communication Calls. These soft calls, which are identical in structure between the sexes, accompany most nonflying movements and serve as a close contact signal between the partners. The Stack Element is identical to the Stack Call, which is uttered in the last second before take-off; the sustained harmonic structure shown in Figures 1b and d is normally distorted by rapid frequency modulation (ca. 60 Hz) at the moment of lift-off. This call, which is the same in both sexes, is invariably followed by one or more Distance Calls (see Zann 1984).

The Distance-call Element is identical to the sexually dimorphic Distance Call in about 50% of males (e.g. Figs. 1a and b), with the remainder having a slightly different variant (e.g. Figs. 1c and d; see Zann 1990). However, in two successive phrases of an Alice Springs individual, two distinct Distance-call Elements were sung, one of which was identical to his Distance Call.

Price (1979), while investigating song development in domesticated Zebra Finches, was the first to notice the strong resemblance between some song elements and three types of call notes, which he termed short, medium and long. These correspond to the Communication, Stack and Distance calls in the wild birds studied here; however, the harmonic modulation of the long call of the domesticated birds was completely different from that of the Distance Calls in: (a) omitting the noisy downward sweep component and, thus, resembling the female version of the call; or (b) placing it at the start of the call rather than at the end. These and other aberrations (e.g. Fig. 2b) are widespread in domesticated Zebra Finches and are associated with errors in the learning of this call in captivity (Zann 1984, 1990).

In contrast to the primary elements of the song phrase, the remaining 10 element types are sung far less frequently within and among males (Table 2), and it is difficult to find their exact counterparts in the call repertoire, but it is possible that these "secondary element" types may have been derived from them. The Introductory Diad is simply an association of two versions of the Communication Call, and the Noise-structure Tone Element appears to be a fusion of a noise component and the Tone Element.

It is possible that the remaining eight of these secondary elements originated from the Distance Call through systematic repetition, modification and omission of the spectral and noise components of the element (Fig. 3). Through omission of the tonal component it is possible to derive the Down-slur Element and, conceivably, through omission of the lower harmonics in the noisy down-slur component a version of the High Element could form. Other elements may have arisen from a rare "mistake" in the Distance Call (Zann 1984, 1985) and/or Distance-call Element, where two distinct but unusually brief Distance Calls have been fused to form a doublet with four components, tone-noise-tone-noise, the Double Distance-call Element (Fig. 3; DCDC); although the sample size is small, the doublet is only about 20% longer than the mean duration for a single Distance-call Element. Through progressive loss of the first tonal component and modification of the first noisy down-slur component, it is possible to derive the Ladder-noise Element, the Noise-noise Distance Call, and the Noise-structure Distance-call Element. The Ladder-noise Element may reduce then omit entirely the second tonal component so that it forms two contiguous noise components, the Noise-noise Element. The Tone-noise Element can be formed by the loss of the noisy down-slurs of the Ladder-noise Element, leaving the tonal part of the second Distance Call, and the loss of the second noise component forms the Tone Element, which may conceivably have produced a High Element with the loss of its lower harmonics. In the Noise-structure Distance-call Element the first tonal component is omitted and both noisy down-slurs have developed clear spectra with the first having a chevron-shaped fundamental. The origin of the Noise-structure Element is ambiguous; it may have arisen from spectra appearing in the Noise-noise Element or, conversely, it may have arisen from the loss of the spectral components or by the loss of all tonal features in the Ladder-noise Elements.

The Distance-call Element is not significantly different in duration from the Ladder-noise Element (Wilcoxon two-sample test, $z = 0.65$, $P = 0.51$), but the frequency of the tonal component is significantly higher ($z = 2.52$, $P = 0.01$). If the Ladder-noise Element is derived from the two very brief calls that constitute the Double Distance Call, one would expect it to be about 20% longer than a normal Distance Call. In contrast, the durations of the Noise-noise Distance Calls and the Noise-structure Distance Calls, the longest elements sung, are about 60% longer than the Distance-call Elements ($z = 4.31$, $P = 0.0001$, and $z = 5.75$, $P = 0.0001$, respectively), but not 20% longer as one might expect if they were derived from the Double Distance-call Element, or 100% longer if derived from the fusion of a Noise-noise/Noise-structure Element with a Distance-call Element.

The absence of matching of derived elements to the duration and frequency measures of the Double Distance-call Element may be due to drift or the extent of the evolutionary changes. Noise-noise Distance Calls, Noise-structure Distance Calls and the Down-slurs all have small, but significant ($P < 0.05$) negative correlations (Pearson product-moment correlations -0.15, -0.12, and -0.14, respectively) with the frequency of occurrence of the Distance-call Element. Conceivably, these three elements are more recently derived than other secondary elements that have no significant correlations with the Distance-call Element (Noise-structure, 0.12; Ladder-noise, 0.06; High, 0.04; Tone, 0.05; Tone-noise, 0.05; Noise-structure Tone, 0.02; Noise-noise, 0.00). Further clarification of the derivation of song elements may be possible with studies of song development.

The sequence of primary elements in the song, namely Introductory, Stack and Distance-call elements, follows the sequence of call notes given by birds just before and during take-off, whereby with increasing arousal the soft series of Communication Calls switch over to the Stack Calls that are followed by the very loud Distance Calls just after take-off. All three calls are not given at every take-off, but the sequence is the same. The sequence within the song phrase is not as stereotyped: 88% of songs have the Introductory Element preceding the Stack and Distance-call elements, but only 60% of songs have the Stack Element preceding the Distance-call Element.

Structuring of the song phrase into subsections in which call-like elements precede and follow a sequence of secondary or noncall-like elements has a functional basis. Young domesticated males learn their songs in "chunks" or blocks of elements (Williams and Staples 1992), and experimental disruption to the production of song in adults results in loss and recovery of chunks of elements (Williams and McKibben 1992). It is significant that these chunks correspond to sections of call-like and noncall-like elements that have been identified in this study of wild Zebra Finch song.

It is possible that the ancestral song of Zebra Finches simply consisted of three types of call notes given in a stereotyped sequence, since most elements in the phrase clearly have their origins in the call notes. The primitive ancestral song may have been derived unmodified in structure and sequence from the calls associated with preflight and take-off. Subsequent evolution involved the addition of sounds unique to the song by systematic modifications to the Distance-call Element and their incorporation into the sequence positioned between the Communication Calls and the Stack Call. These characteristics of song structure are not evident in the Timor subspecies *T. guttata guttata* nor have they occurred in related Australian estrildines. The Timor Zebra Finch does not incorporate Distance Calls into its song phrase (Clayton et al. 1991), nor is there any pronounced sexual dimorphism in these calls (Zann 1984). *Poephila acuticauda, P. cinta* and *P. personata,* close relatives of the Zebra Finch, do not have sexually dimorphic Distance Calls (Zann 1975), nor do they incorporate them into their songs (Zann 1976). I conclude that the evolutionary changes that have led to song organization in the Australian Zebra Finch are relatively recent.

The Distance Call appears to have had a unique role in the evolution of Zebra Finch song. It not only appears to serve as a source for new song elements, but has a similar developmental program to that of song (Zann 1985) and shares the same neural pathways (Simpson and Vicario 1990). Cross-fostering experiments with offspring of wild-caught Zebra Finches have shown that the information required for the development of the sexually specific features of the male Distance Call are acquired from the father before 40 days of age. This information provides for the masculinization of its much simpler, juvenile, and more feminine precursor between 40 to 60 days of age. The masculinization leads to sex differences in call duration, fundamental frequency and modulation (Zann 1985). Only about 30% of laboratory males copy the father's Distance Call exactly, but the remainder develop calls that show a strong resemblance. Females do not learn the Distance Call from the mother, but retain the juvenile version, more or less. The structure of the Distance Call can convey, potentially, information about the subspecies, sex, colony, family and individual (Zann 1984). In about 80% of free-living males the song's Distance-call Element matches that of the father's Distance Call or his Distance-call Element (Zann 1990) and, presumably, this is due to learning from the father.

According to Simpson and Vicario (1990), there are important sex differences in Zebra Finches in the neural control of Distance Calls. Distance Calls in females are controlled by an evolutionarily primitive pathway, found widely in both passerines and nonpasserines, whereby a structure in the brain stem governs the respiratory patterning necessary for the production of the call. In contrast, male Zebra Finches have an additional pathway superimposed on the primitive one, whereby complex syringeal control is provided for production of the Distance Call. This second pathway includes the same neural structures involved in control of Zebra Finch song, namely the telencephalic nuclei (HVC and RA) and the tracheosyringeal nerves innervating the syrinx, which allow complex vocalizations to be produced and imitated. When Simpson and Vicario (1990) disrupted this pathway by nerve section and lesion, they removed all the learned features of the male call, leaving a basic call characteristic of the female.

The primitive, ancestral song phrase probably consisted of the unlearned call notes after which the undifferentiated, bisexual Distance Call was subjected to sexual selection to produce the dimorphic male call under the additional control of the higher vocal centers. Subsequent selection may have been responsible for the modification of the Distance Call during development with reference to an external model provided by the father's Distance Call. At a later stage all calls in the primitive song phrase may have been brought under the neural control of the higher centers so that they too could be copied as a set from the father's song or some external model. The Distance-call Element remains the most evolutionarily labile of elements in the phrase, possibly having given rise to at least eight secondary elements in wild birds. Its open developmental program has produced versions of the call in domesticated birds that are almost unrecognizable but for their greater amplitude and duration relative to those of other elements (Simpson and Vicario 1990, Zann 1985, 1990).

Songs of wild Zebra Finches investigated here are distinct from domesticated stocks in duration, tempo and frequency of some element types, but not in number of elements in the phrase. These findings contrast with those of Slater and Clayton (1991), who found no differences between songs of wild birds ($n = 18$) and domesticated birds from Bielefeld ($n = 20$); birds from both locations differed from domesticated birds from St. Andrews ($n = 20$). Sample sizes for the domesticated stocks are similar to those in the present study. Consequently, I conclude that: (a) samples of this size are not adequate; and/or (b) important methodological differences exist in the scoring of sonagrams. Problems may arise in defining where one element starts and another stops; Cynx (1990) found that about 6% of elements in his sample had silent intervals of less than 10 ms, which is equivalent to about 1 mm, the limit of effective measurement, on a standard Kay sonagram using the 300-Hz filter. Slater and Clayton's (1991) samples of wild birds were probably not large enough (12/99 from colony Da and 6/40 from colony As), since they found no significant differences between them, whereas my larger samples differed in all but the number of elements (Table 2). Clearly, large samples are needed for comparisons of songs between populations, and methodological procedures for measuring sonagrams need to be standardized across studies. Differences in song between wild and domesticated birds are not necessarily due to domestication processes per se but may be a consequence of the number of wild birds that founded the colony and its subsequent isolation from other populations.

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