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THE DISTANCE CALL OF DOMESTICATED ZEBRA FINCHES (*POEPHILA GUTTATA*)

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ABSTRACT: Wild zebra finches use distance calls in a wide variety of contexts including flight, mild alarm, perching, and courtship. The call is also thought to allow paired males and females to maintain contact in large flocks. The purpose of this study is to compare the acoustic structure of distance calls of wild and domesticated zebra finches. We analyzed distance calls from our own colony and combined the results of this analysis with the findings from two other published studies on distance calls of domesticated finches. The results from these studies were compared to earlier research on the distance calls of wild zebra finches.

Overall, domesticated male and female zebra finches produce calls that have longer duration, lower fundamental frequency, and higher frequency of maximum amplitude than those of wild zebra finches. These differences were generally consistent across different domesticated populations. Domesticated males produce distance calls in which the frequency modulation of the noise element is substantially different from the noise element of wild males. Furthermore, there was little consistency in the structure and location of the male's noise element across different domesticated populations. It remains to be demonstrated whether these changes have altered the function of this call in domesticated finches.

INTRODUCTION

According to Immelmann (1965), zebra finches have three basic calls: the loud identity call, the low communication call, and an aggressive call. Unfortunately, different researchers have used different names to denote these calls. For example, the loud identity call has been referred to as the distance call (Zann, 1984, 1985), the lost call

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(Immelmann, 1965), the long call (Price, 1979; Simpson & Vicario, 1990), and the lure call (Lombardi & Curio, 1985). The low communication call has been referred to as the tack call (Lombardi & Curio, 1985), and the short call or medium call (Price, 1979). Although researchers have performed numerous studies on song and song development in zebra finches (See Slater et al., 1989 for a review), they have expressed nowhere near this level of interest in the zebra finch's calls. This is somewhat surprising since male finches incorporate a number of these calls into their song (Price, 1979; Zann, 1990).

The loud identity call, or distance call, is the only call that has been subjected to detailed analysis. Zann (1984, 1985) performed two studies on wild zebra finches in which he described the acoustic features of the distance call and examined the experiential factors that were important in its development. Okanoya et al. (1993) examined the acoustic properties of this call in three different populations of domesticated zebra finches. In addition, Okanoya and Dooling (1991 a, b) and Dooling et al. (1992) used distance calls to investigate species-typical auditory processes across a number of species. Finally, Simpson and Vicario (1990) used distance calls to examine the neural pathways that controlled the production of learned vocalizations. Interestingly, the function of this call has not been examined in an experimental setting.

The distance call is produced by both males and females in a wide variety of contexts including flight, mild alarm, perching, and courtship (Zann, 1984). The call is thought to allow paired males and females to maintain contact (Zann, 1984). Most males learn their distance calls from the distance calls and song of their father (Zann, 1990). Females, on the other hand, do not need to hear species-typical distance calls in order to develop normal distance calls themselves (Zann, 1985). Males incorporate the distance calls of their father and other males into their song. Those portions of song that resemble distance calls are referred to as distance call elements. A male may have distance call elements in his song that do not resemble his distance call, but that do, nonetheless, look like distance calls on a sound spectrogram (Zann, 1990).

Most researchers who study zebra finches use domesticated finches as subjects. Domestication has resulted in a number of behavioral, developmental, and morphological changes (Sossinka, 1982; Carr & Zann, 1986). Domesticated zebra finches from European collections tend to be larger, less active, exhibit a greater variety of color morphs, undergo slower gonadal maturation, and engage in lower levels of courtship than their wild counterparts. Slater and Clayton (1991) found a number of subtle differences between the song of wild and domesticated finches. They found that domesticated males were likely to have faster song tempo, shorter phrase length, and fewer distance call elements in their song. In addition, Zann (1990) stated that the distance call element is absent or distorted beyond recognition in the song of domesticated zebra finches.

There is evidence that domesticated zebra finches also produce distance calls that are different from those of wild finches. Sound spectrograms of distance calls of domesticated finches reported by Price (1979), Okanoya and Dooling (1991 a, b), Dooling et al. (1992), Okanoya et al. (1993), and Simpson and Vicario (1990) are quite different from those of wild finches (Zann, 1984, 1985). Furthermore, there are also striking differences in the acoustic structure of distance calls of domesticated finches reported by these researchers.

Distance calls play an important role in the social interactions of wild male and female zebra finches. Before any studies on the function of this call among domesticated finches are undertaken, it is important to understand the extent to which distance calls of domesticated zebra finches differ from the calls of wild finches, and the extent to which such changes are consistent across domesticated populations. The purpose of this study was to compare the acoustic properties of distance calls of wild and domesticated zebra finches. To accomplish this we analysed distance calls from our population of domesticated finches and examined previous research on distance calls of domesticated finches by Okanoya et al. (1993) and Simpson and Vicario (1990). We compared these findings to Zann's (1984) work on distance calls of wild finches.

METHOD

Subjects

We used 26 adult domesticated zebra finches (15 males and 11 females) that were either purchased from local breeders or bred in our aviary (6.1 x 6.1 x 2.5 m). Normally, there were 25–30 birds in the aviary. They were fed and watered *ad libitum*. Their diet consisted of commercial finch food, grit, and vitamin supplements. Lights in the aviary were on a 14 h: 10 h light/dark cycle. The birds also received sunlight through a window near the side of the aviary. Thus, daylength varied throughout the year.

Okanoya et al. (1993) used two populations of domesticated finches. One population (ANR–American normal reared) was obtained from breeders in Maryland, and a second population (JNR–Japanese normal reared) was obtained from Japanese breeders. We did not include

Okanoya et al.'s findings on finches that were foster reared by Bengalese finches. Simpson and Vicario (1990) obtained their domesticated finches from a local supplier in New York or from their own breeding colony.

Recording Procedure

We used the same procedure that Zann (1984, 1985) used to evoke and record distance calls from wild birds. We captured birds with either a mist net or a bait trap. They were banded and placed in a small (.35 x .35x .35 m) cage. The cage was removed from the aviary and placed behind a barrier approximately 2 m from the aviary. Thus, the bird in the cage could hear but not see the birds in the aviary. To reduce background noise, we placed the cage in a foam-lined enclosure (.75 x .5 x .64 m) that was open on the top and the side facing the aviary. An AKG C 568 EB directional microphone was placed approximately 5 cm from the cage. The microphone was connected to a Crown PH-1a phantom power supply which in turn was connected to a Marantz 221 PMD cassette recorder. After the cage was placed in the foam-lined enclosure, the cassette recorder was turned on, and all personnel left the room. One hour later, we returned and collected the tape. Only experimentally naive birds were recorded. Okanoya et al. (1993) and Simpson and Vicario (1990) used similar methods to record distance calls.

We reviewed the tape and located the distance calls. Distance calls are the loudest and longest calls that zebra finches produce in this context, and they are easily recognizable (Zann, 1984). We analyzed the first 10 calls that were not distorted by movement or the bird's position in the cage. Distance calls were digitized using Audiomedia digitizing hardware and software on a Macintosh IIci (Apple Computer, Inc.). We used a sampling rate of 44.1 kHz with 16 bit resolution. We used this sampling rate when we made spectrograms. To give better frequency resolution at low frequencies, all calls were desampled to 20 kHz and 12 bits for the analyses outlined below. This causes the spectrogram to extend over a smaller range of frequency and thereby show each band in greater detail.

Acoustic Analysis

All analyses were performed using a commercial software package called Signalyze 2.47 (Keller 1992) that employs Fast Fourier Transform (FFT) to perform spectral analyses. The wild male's distance call consists of a stack of harmonics with an initial frequency modulated (FM) upsweep, followed by a period in which the bands have little FM. In the second half of the call, the bands rapidly descend. (Zann, 1984, 1985). The part of the call in which FM is low is called the tonal element. The portion of the call with rapidly descending FM is called the noise element. The wild female's call closely resembles the tonal element of the wild male's call. The wild female's call does not contain a noise element (see Fig. 1).

We measured the same acoustic features that Zann (1984, 1985) used to analyze the distance calls of wild finches. The measures were as follows:

a) Frequency of Maximum Amplitude (FMA): The frequency component of a call that, on average, had the greatest amplitude. This was measured by having Signalyze compute an average spectrum using a 512 point FFT with an effective resolution of 40 Hz. The average spectrum provides a measure of the average relative amplitude of the frequency components of a signal. We measured the amplitude of each peak by placing a cursor on the peak. The peak with the greatest amplitude was the FMA.

b) Call Duration: The duration of a call measured on an amplitude by time plot. The duration was measured and automatically calculated by highlighting the call with a cursor. The effective temporal resolution was 5 ms.

c) Tonal Element Duration: The duration of the tonal element was measured on a spectrogram. The tonal element is easy to discern on a spectrogram because its FM qualities are distinct from those of the noise element. Duration was measured using the technique described above. The spectrogram was made using a 512 point FFT, with an effective resolution of 40 Hz. In our population, only males produced calls which do not consist exclusively of an unmodulated tonal element.

d) Fundamental Frequency (F_0): The lowest band of energy present in a call. This was determined by finding the lowest peak in a sound spectrum that could be divided evenly into the higher peaks. The spectrum was taken in the middle of a call using a 1024 point FFT. The effective resolution of the spectrum was 20 Hz.

e) Location of the Noise Element: Whether the noise element was located before, after, or both before and after the tonal element. This was determined by viewing a spectrogram of a call. The spectrogram was made using a 256 point FFT with an effective resolution of 80 Hz. Only males produce calls with noise elements. Okanoya et al. refer to the noise element as the auxiliary element and Simpson and Vicario refer it as fast frequency modulation.

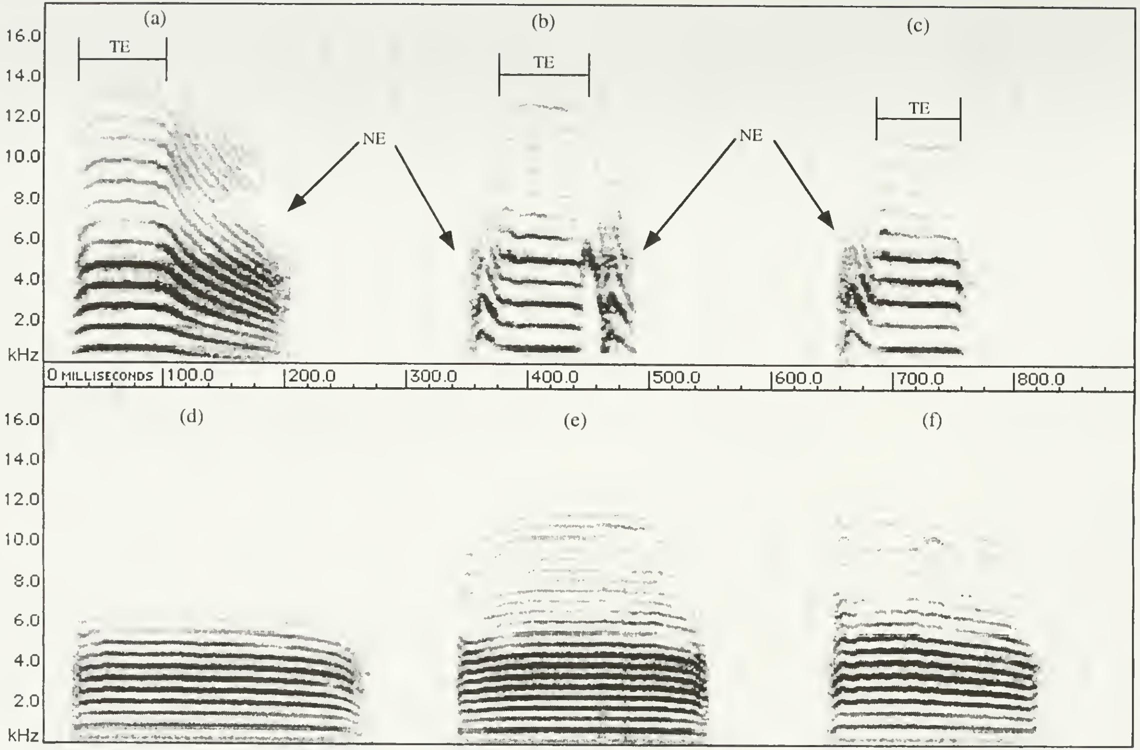

Figure 1. Spectrograms of the distance calls of three different males (a)-(c) and three different females (d)-(f). Note that each male has a noise element (NE) in a different location with respect to the tonal element (TE). Only male (a) has a distance call similar to that of wild zebra finches. These spectrograms were produced with SoundEdit Pro (Macromind-Paracomp, Inc.)

Okanoya et al. (1993) and Simpson and Vicario (1990) used similar digital techniques to analyze distance calls. Zann used a Kay Spectrum Analyzer to analyze the calls he recorded. To insure that any differences we found between distance calls of domesticated and wild finches did not result from different analytic techniques, we analyzed a number of distance calls using both FFT and a Kay Spectrum Analyzer similar to the one that Zann used. The results were similar. Measures of FMA differed, on average, by 26 Hz and measures of F_0 differed, on average, by 22 Hz. Our measurements of F_0 by FFT were always lower than measures of F_0 on the Kay.

Statistical Analyses

Zann (1984) provided means and standard deviations for call duration, tonal element duration, FMA, and F_0 of wild male and female zebra finches. For domesticated finches, Okanoya et al. analyzed the same acoustic features as Zann, and Simpson and Vicario analyzed call duration, F_0, and gave some information about noise element location. Simpson and Vicario did not provide precise information about the standard deviation of each acoustic feature. Okanoya et al. measured only one call per bird.

To assess the degree to which distance calls have changed during domestication, we compared Okanoya et al.'s , Simpson and Vicario's, and our findings on domesticated birds to Zann's research on wild finches. We computed 95% confidence intervals for each acoustic feature that Zann measured using the method described by Jaccard and Becker (1990) for determining confidence intervals when the population value of the standard error of the mean is unknown. If the domesticated finches' mean call duration, tonal element duration, FMA, or F_0 fell outside the 95% confidence interval for that feature, we considered the difference to be statistically significant. We used two-tailed t-tests to determine whether there were any sex differences in note duration, FMA, and F_0 in our population. O'Brien's test was used to determine whether variances across groups were unequal. If there was a significant difference in variance across groups we used an unequal variance t-test.

Finally, like Zann (1984), we assessed the degree to which individual's calls were stereotyped by computing the coefficient of variation (standard deviation divided by the mean) for each bird on each acoustic feature. Neither Okanoya et al. nor Simpson and Vicario performed this measure. All statistical analyses were performed using JMP 2.0 (SAS Institute 1989).

RESULTS

Call Duration

In general, domesticated zebra finches produce distance calls that are longer than the calls of their wild counterparts (Table 1). Only one domesticated population, Okanoya et al.'s JNR females, produced calls that were approximately the same duration as those of wild females. Zann found that wild females produced longer distance calls than wild males. This was also true in three of the four domesticated populations. Female domesticated finches in Okanoya et al.'s ANR finches, Simpson and Vicario, and our population (t (255) = 11.9, $p < .0001$) produced distance calls that were significantly longer than those produced by males. The magnitude of the sex difference was approximately the same across the wild population and the three domesticated populations. Only Okanoya et al.'s JNR finches did not exhibit a sex difference in call duration.

Fundamental Frequency (F_0)

Domesticated finches produce distance calls that, on average, have lower F_0 than distance calls produced by wild finches (Table 2). This change is consistent with the fact that domesticated zebra finches tend to be larger than their wild couterparts (Sossinka, 1982; Carr & Zann, 1986). Zann found that wild females produce calls with lower F_0 than wild males. Domesticated females also produced calls with lower F_0 in three of four domesticated populations. In our population the difference was significant at $p < .0001$ (t (255) = 13.8). However, the difference in the F_0 of distance calls produced by males and females is smaller in domesticated populations than it is in wild populations.

Frequency of Maximum Amplitude (FMA)

In two of three domesticated populations in which FMA was measured, domesticated finches produced distance calls with higher FMA than wild finches. In addition, there were no sex-differences in FMA (Table 3). Zann found that wild males produce distance calls with significantly higher FMA than wild females. However, it is not clear to what extent the lack of sexual dimorphism in FMA among domesticated finches actually differs from Zann's findings on wild finches. First, wild finches from one of the two colonies Zann examined did not exhibit a sex difference in FMA. Second, the sex-difference in FMA in Okanoya et al.'s colonies is at least as large as the difference that Zann found.

Table 1. The average (± SD) call duration (ms) of wild and domestic zebra finches, * indicates that the value for domestic finches exceeded the 95% confidence limits for the wild population (same sex)

Population Type	Study	Males	Females
Wild	Zann	140±20	190 ± 30
Domestic	Blaich et al.	159 ± 38*	218 ± 41*
	Okanoya et al. (ANR)	188 ± 39*	242 ± 48*
	Okanoya et al. (JNR)	195 ± 54*	188 ± 61
	Simpson and Vicario	178*	268*

Table 2. The average (± SD) F_0 (Hz) of wild and domestic zebra finches, * indicates that the value for domestic finches exceeded the 95% confidence limits for the wild population (same sex)

Population Type	Study	Males	Females
Wild	Zann	1110 ± 210	620 ± 65
Domestic	Blaich et al.	892 ± 234*	575 ± 41*
	Okanoya et al. (ANR)	700 ± 206*	581 ± 56*
	Okanoya et al. (JNR)	969 ± 389*	540 ± 55*
	Simpson and Vicario	804*	568*

Okanoya et al. probably did not find this difference to be significant because they found more variability, and because they used a more conservative statistical test. Finally, it should be noted that the upward shift in FMA among domesticated finches may not reflect a change in the resonant quality of the domesticated zebra finches vocal tract. Rather, such changes may simply result from the alteration in the domesticated finch's F_0 that we noted in the previous section. (See Nowicki (1987) for a discussion of vocal tract resonance in oscines.)

Table 3. The average (± SD) FMA (Hz) of wild and domestic zebra finches, * indicates that the value for domestic finches exceeded the 95% confidence limits for the wild population (same sex)

Population Type	Study	Males	Females
Wild	Zann	3750 ± 560	3540 ± 330
Domestic	Blaich et al.	4102 ± 741*	3983 ± 672*
	Okanoya et al. (ANR)	3833 ± 403	3608 ± 325
	Okanoya et al. (JNR)	4262 ± 806*	3700 ± 731*

Table 4. The average (± SD) tonal element duration (ms) of wild and domestic zebra finches, * indicates that the value for domestic finches exceeded the 95% confidence limits for the wild population (same sex)

Population Type	Study	Males
Wild	Zann	45 ± 20
Domestic	Blaich et al.	109 ± 42*
	Okanoya et al. (ANR)	147 ± 48*
	Okanoya et al. (JNR)	182 ± 75*

Noise Elements and Frequency Modulation

Domesticated males produce distance calls in which the noise element is shorter than the wild males' noise element. This is consistent with our finding that tonal element duration (the remaining portion of the male's call) is much longer in calls produced by domesticated males (Table 4). Zann (1985) reported that the duration of the tonal element is normally 1/4–1/2 of the call duration (See Fig. 1, bird (a)). Most domesticated males produce calls in which tonal element duration is about 1/2–2/3 of the call duration (see Fig. 1, birds (b) and (c)).

Zann (1984) reported that 99% of wild males produce distance calls in which the tonal element is followed by a noise element. This pattern was far less frequent among domesticated males. Indeed, there is little consistency in the location of the noise element across domesticated populations. Instead, the noise element may be found before the tonal element, before and after the tonal element, in the middle of the tonal element, or entirely absent. (For examples see Fig. 1, birds (a)-(c).) In three of the domesticated populations (Okanoya et. al. [ANR], 1993; Simpson & Vicario, 1990) the noise element was most often located at the beginning of a call. In our population at least, individual males placed their noise elements in the same location every time they called. This is consistent with the pattern exhibited by wild males.

The frequency modulation of domesticated males' noise elements were also quite different from those of wild males. A number of our birds displayed noise elements with sharply ascending and then descending FM. On a spectrogram these noise elements resembled inverted "V"s (see Fig. 1, birds (b) and (c)). In wild finches, the FM of the noise element typically descends only, and the change in frequency is more gradual (see Zann, 1984, 1985). Only one of our domesticated males produced a distance call whose noise element resembled that of a wild male (Fig. 1, bird a). Generally, domesticated males produced noise elements in which the rapidly descending FM portion appeared to be cut off relative to the noise elements of wild males.

Otherwise, the FM of both the male's tonal element and of the entire female's call appeared to be similar to the FM of calls produced by wild finches. Spectrograms of the distance calls of domesticated females (see Fig. 1, birds (d)-(f) appear to be virtually identical to those Zann (1984, 1985) published of wild females.

Call Stereotypy

One area in which the calls of domesticated males did not differ from those of wild males was in the degree of call stereotypy. Domesticated males in our population showed levels of within-subject variability on call duration, tonal element duration, and F_0 comparable to those of wild finches (see Table 5). However, there was far more within-bird variability in FMA. Thus, while the spectral characteristics of distance calls produced by domesticated males in our population were quite different from those of wild males, the degree of call stereotypy was not. Distance calls of domesticated and wild females showed comparably low levels of within-bird variability on F_0. However, domesticated females had higher coefficients of variation on call duration and FMA (Table 5).

Table 5. Median coefficient of variation for call duration, tonal element duration, FMA, and F_0 of domestic male, wild male, domestic female, and wild female zebra finches. The median coefficients of variation for wild birds were calculated from Zann's (1984) results.

	Domestic males	Wild males	Domestic females	Wild females
Call duration	.036	.038	.104	.046
Tonal element duration	.063	.065	n/a	n/a
FMA	.108	.015	.124	.019
F_0	.022	.015	.016	.019

DISCUSSION

According to Lickliter and Ness (1990) domestication, "...refers to the process by which organisms change in terms of morphology, physiology, or behavior as a result of the human control of their breeding, feeding, and care (p. 211)" (See also Hale, 1969; Miller, 1977). It is evident that the different forms of human control outlined by Lickliter and Ness have changed the distance calls that domesticated zebra finches produce. In general domesticated males and females produce calls that have longer duration, lower F_0, and higher FMA. However, it should also be noted that these changes are quite subtle. In some cases the differences between some domesticated and wild populations were smaller than the differences among domesticated populations.

The males' noise element is the most obvious acoustic feature that has changed as a result of domestication. The frequency modulation of noise elements produced by domesticated males often differed dramatically from those produced by wild males. This change should not be surprising. There is clear evidence that young males model their noise element on those that they hear during development (Zann, 1985; 1990). Given this degree of developmental plasticity, cultural changes alone may account to a large extent for the different noise elements that domesticated and wild males incorporate into their distance calls. Yet, as obvious as the change in the structure of the noise element is, it should be noted that the role of this acoustic feature in the function of the distance call is not clear. Thus, changes that have occurred during domestication in the structure of the noise element may have little or no effect on the function of the call.

We believe that the remaining changes in the distance call that have occurred across domesticated populations, as subtle as they are, are not due solely to changes in the calls that domesticated zebra finches hear when they develop. With the exception of the noise element, the development of most features of the distance call do not change when young finches are reared in an abnormal acoustic environment. Zann (1985) cross-fostered zebra finches using Bengalese finches as parents. Although the noise element of foster-reared males developed abnormally, there was no difference in the FMA, F_0, and call duration of foster reared and normally reared males. Foster-reared females had slightly higher F_0 than normally reared finches (by 30 Hz), but their calls did not differ in FMA, call duration, or frequency modulation.

Some authors have argued that male and female zebra finches differ in the degree to which the development of their distance calls is altered by experience. For example, Simpson and Vicario (1990) stated that three features of the male's distance call are learned from external models: high F_0, call duration, and the noise element. They also state that the development of distance calls among females is not altered by external models. We believe that the evidence supports a more subtle interpretation. Although the development of the males' noise element is clearly altered by experience, it is not clear how to relate this finding to call development in females since females don't use noise elements in their calls. Furthermore, Zann's (1985) findings on the effects of cross-fostering on the remaining acoustic features of distance calls don't point to a large sex difference in developmental malliability.

Okanoya et al. (1993) argue that sexual dimorphism in the acoustic structure of the zebra finches' distance call is gradually disappearing during domesticatedation. Our findings are generally consistent with their claim. First, the reduction in the size of the male's noise element, and consequent enlargement of the their tonal element, has reduced the sex difference in the frequency modulation of the distance call. Second, the difference in F_0 is smaller among domesticated finches than it is among wild finches. The difference in FMA also appears to have decreased. However, this change should be treated with some caution since Zann (1984) did not find a consistent sex-difference in FMA among wild populations that he studied. Thus, it is not clear to what degree a consistent sex difference in FMA exists in wild zebra finches.

Zann (1984) hypothesized that the primary function of the distance call in the wild is to allow breeding pairs to maintain contact in large flocks. Despite changes that have occurred in the structure of the distance call during domestication, we believe that there may be sufficient inter-individual variability and intra-individual stereotypy to allow this function to be retained in domesticated birds. Dooling et al. (1992) have shown that domesticated finches can distinguish distance calls of different individuals. However, their paradigm required zebra finches to differentiate four different calls from four different birds. The task of distinguishing the distance calls of a mate from those of other finches in a large flock is probably more difficult. Thus, it remains to be experimentally demonstrated that domesticated zebra finches can use distance calls to recognize their mates.

A number of researchers have used domesticated zebra finches as models to investigate the physiological and acoustical basis of call production and perception (Dooling et al., 1992; Okanoya & Dooling, 1987, 1991 a, 1991b; Okanoya et al.,1993; Simpson & Vicario, 1990). Despite this fact, there is no research on the functional significance of the various calls that zebra finches produce. We believe that such work will be important not only for a greater understanding of the natural history of zebra finches, but also to understand how the production and perceptual capacities that have been so carefully studied play a role in the behavior of this species.

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