

VARIATION IN THE STRUCTURE OF FEMALE BROWN-HEADED COWBIRD VOCALIZATIONS AND ITS RELATION TO VOCAL FUNCTION AND DEVELOPMENT¹

KRIS BURNELL AND STEPHEN I. ROTHSTEIN

Department of Biological Sciences, University of California, Santa Barbara, CA 93106

Abstract. Female Brown-headed Cowbirds (*Molothrus ater*) are unusual among temperate zone songbirds in that they possess a distinctive and loud call, known as "chatter" and consisting of a series of brief chevron-shaped syllables. Unlike the high-amplitude vocalizations commonly given by males, which show extreme macrogeographic and microgeographic (i.e., dialect) variation, chatter shows no apparent qualitative variation throughout North America. Quantitative variation in frequency and temporal parameters was assessed by measuring 40 variables on chatter calls given by 45 females from the three recognized cowbird subspecies. Univariate and multivariate (principle components) analyses showed only minor macrogeographic differences among the subspecies and gave no indication that local microgeographic variation or dialects exist. Despite the near lack of spatial variation, analysis of variance demonstrated that nearly every variable shows significant individual variation within each subspecies. This is probably sufficient to allow cowbirds to recognize individual females. Chatter is used in diverse contexts and in communication with both males and other females. Its quantitative features may vary according to context, but this was not investigated because all calls in this study were given in the same context.

Key words: *Brown-headed Cowbird; female vocalizations; vocal function; individual variation; subspecific variation.*

INTRODUCTION

The function and development of avian vocalizations have been the subjects of numerous studies. A species that has played a central role in this research is the brood parasitic Brown-headed Cowbird (*Molothrus ater*) (West et al. 1981a, 1981b; King and West 1983a; Rothstein and Fleischer 1987a; O'Loughlen and Rothstein 1993). Since it has little or no early contact with conspecifics, the cowbird's vocal development raises especially interesting ontogenetic questions (West et al. 1981a). Contrary to initial expectations, cowbirds show complex developmental processes (West and King 1985; Rothstein and Fleischer 1987a, 1987b; King and West 1989; O'Loughlen and Rothstein 1993) and considerable individual and geographic variation in some of their vocalizations (King and West 1983b, Dufty 1985, Rothstein and Fleischer 1987a).

However, this previous work has involved only male vocalizations. Female cowbirds are unusual because they possess a loud vocalization, called chatter or rattle, that is often used in broadcast fashion (Friedmann 1929). Here, we present a

continent-wide study of variation in this female vocalization which is used infrequently by males and is the only loud vocalization given by females (Friedmann 1929).

The purpose of this study was to quantify the amount of variation in the female chatter vocalization within and among all three subspecies of Brown-headed Cowbirds (*M. a. ater*, *M. a. artemisiae*, *M. a. obscurus*). There are morphological (Grinnell 1909, Rothstein 1978, Fleischer and Rothstein 1988) and genetic (Fleischer et al. 1991) differences among these subspecies and they also provide pre-determined and meaningful geographic sampling units. Studies of variation in male cowbird vocalizations have also assessed results at the subspecies level (King and West 1983b, Rothstein et al. 1988).

Female chatter is used in three contexts. (1) It is directed to nearby (< 1-2 m) or distant females. Chatter in this context is clearly aggressive as it is interspersed with head-up displays (Dufty 1982a, Rothstein et al. 1986, Yokel 1989), a standard threat display of icterines (Orians and Christman 1968). (2) It is given in response to nearby males directing "perched songs" (Rothstein et al. 1988) to females. This is also aggressive as it is again used with head up displays and often accompanied by pecks directed at the sing-

¹ Received 19 October 1993. Accepted 7 March 1994.

ing male (West and King 1985, Yokel 1989). (3) It is given in response to distant male "flight whistle songs" (Rothstein et al. 1988; Ortega and Rothstein, unpubl. manuscript). This is likely a "friendly" response because a female reveals her position and males quickly fly towards the source of chatter calls (Rothstein et al. 1988).

To better understand variation in chatter calls, we addressed five questions. (1) Is there variation among the three subspecies in quantitative aspects of the call? To the human ear, chatter always seems recognizable as a species-specific vocalization, but perhaps there are subtle differences among the subspecies. This question was addressed by measuring a suite of 40 temporal and frequency parameters. (2) Are there any general qualitative trends or patterns in the chatter vocalizations and do they differ among subspecies? If the patterns do not differ among subspecies, it might be because chatter development is constrained so as to always follow some set of acoustic rules as is the case with one type of male song (West and King 1986). (3) Regardless of the patterns of variation among the subspecies, is there microgeographic variation, as in male flight whistles (Rothstein and Fleischer 1987a), i.e., does female chatter show dialects? (4) Is variation among individual females within a subspecies sufficient to allow individual recognition? We addressed this question by determining whether the variation in the chatter calls of single individuals is less than that among the calls of different individuals. (5) Do the general features of chatter elucidate its functions and proximate causation? Chatter is especially interesting because it consists of a series "chevron" shaped notes similar to those given by many species of birds and mammals (Morton 1975).

METHODS

Recordings were made in the field by SIR between 1982 and 1988 with a Sennheiser ME-80 microphone on a Marantz Superscope CD 320, 340, or Sony Professional Walkman WM-D6 cassette recorder. All recordings of chatter calls were of free-ranging female cowbirds attracted to playbacks of female chatter. Playbacks were done in what appeared to be suitable cowbird habitat and were begun regardless of whether a female was known to be present. Chatter playback elicits strong approach and vocal responses by females (Dufty 1982a, Yokel 1989). There were two chatter sequences used in playbacks,

one from *M. a. obscurus* and one from *M. a. artemisiae* and these were played at random as in Rothstein et al. (1988). We found no indication that females responded differently to conspecific and heterospecific chatter playbacks. Most analyses subdivided the overall data along subspecies lines. We selected recordings for analysis to cover as much of the geographic range of each subspecies as possible. Recording localities are listed in Appendix 1. Only females for which two or more good quality vocalizations were recorded were used for analysis. Sonograms of each vocalization were produced using a Digital Sona-Graph 7800 Dual Channel Spectrograph and a Sona-Graph 7900 Printer (Kay Electronics Corp., Pine Brook, NJ) with the 16 Hz scale and a narrow-band filter.

Quantitative variation was assessed by measuring 15 frequency and 24 temporal variables (Fig. 1 and Table 1) chosen to detect the greatest range of potential differences within and among subspecies. Measurements were made directly on sonograms using digital calipers and were later converted to hertz (frequency variables) and seconds (temporal variables). In addition, we analyzed variation in the number of syllables within each chatter call (SYLNUM, Table 1).

We analyzed vocalizations from 15 individuals from each of the three subspecies. Each of the 45 individuals was represented by 2–11 vocalizations (mean = 4.02, median = 3 vocalizations per female). Means and variances for each variable for each individual were calculated and, for analyses among subspecies, the mean of each female was used as the sample value from that female.

Variation within and among subspecies was analyzed using Kruskal-Wallis analysis of variance. Because many of the measured variables are highly correlated, a principal components analysis was also done for comparisons among subspecies. This produced three principle components that represented most (64%) of the variation in the original variables. Principle components 1 (PC1), 2 (PC2), and 3 (PC3) were then subjected to Kruskal-Wallis analyses of variance.

To address the question of whether female chatter shows dialects, we tested for correlations between the geographic distance between each pair of females and the difference in the principle component scores for that pair. In addition, we assessed the overall variation among females by calculating PC123, the mean point in euclidean

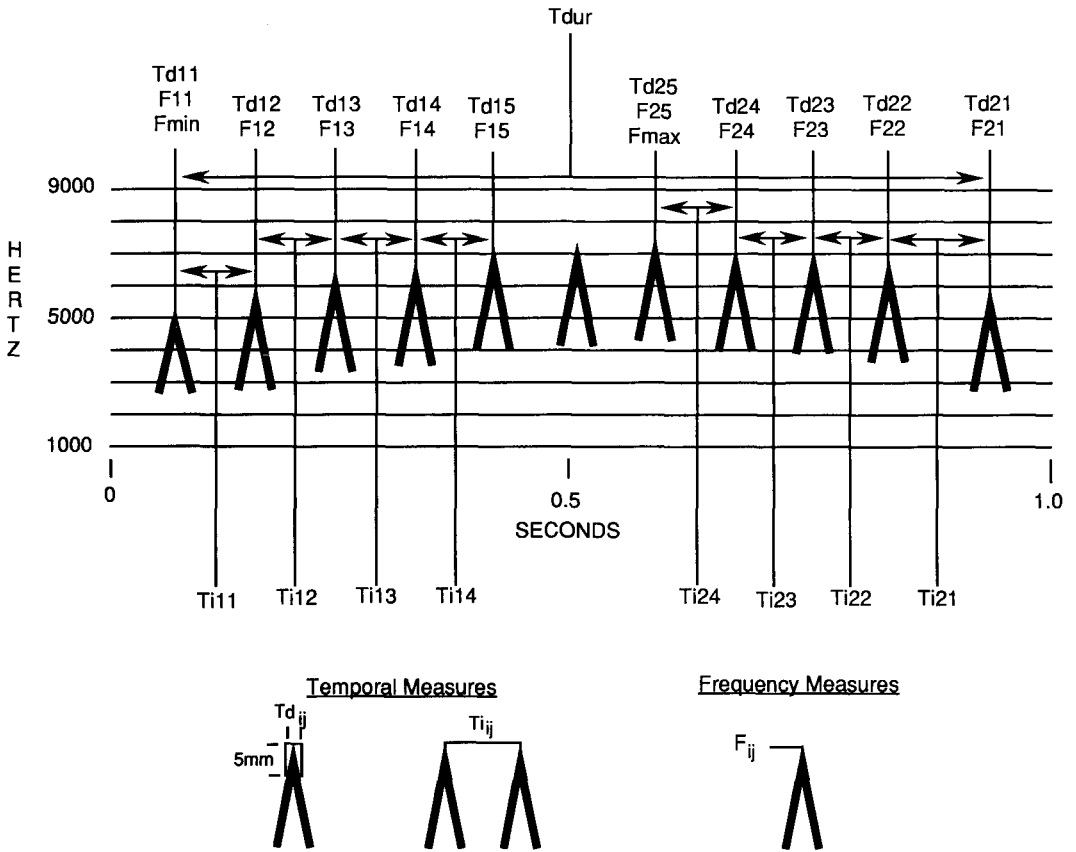


FIGURE 1. Representative chatter vocalization. Measured variables are indicated with abbreviations. All "T" variables represent temporal measures where "Ti" variables measure the duration of intervals between syllables and "Td" variables measure the duration of individual syllables. "T" variables are measured in seconds. All "F" variables represent frequency variables and are measured in hertz.

space from PCs 1, 2, and 3. Each of the four analyses of PC scores (PC1, 2, 3, and 123) and distances between paired females was run separately for each of the three subspecies, resulting in 12 analyses overall. If variation among individuals within a subspecies is due to dialects, the geographic distances between pairs of females should be correlated with differences in PC values, i.e., females recorded at nearby localities should show smaller differences than females recorded far apart.

RESULTS

QUALITATIVE CHARACTERIZATION OF CHATTER VOCALIZATIONS

Several general trends were observed in female chatter. Chatter was always a series of brief, rap-

idly modulated chevron-shaped syllables (see Figs. 1 and 2). It typically began with syllables that were relatively low in both amplitude and frequency, but that then rose in a step-like fashion for the first two to four syllables. The first syllable was lower in frequency than all other syllables in 35 of the 45 birds sampled and was lowest in amplitude in 37 of the 45 birds. Because the first syllable was often so low in amplitude that it was barely noticeable on sonograms, we could not always measure its duration. Thus we deleted this variable (Td11, Table 1) from our analyses, thereby reducing the variables from 40 to 39. After the first two or three syllables, amplitude and frequency were maintained at fairly constant levels for the rest of the vocalization. The maximum frequency of syllables tended to show a slight rise after the middle of the call (Fig.

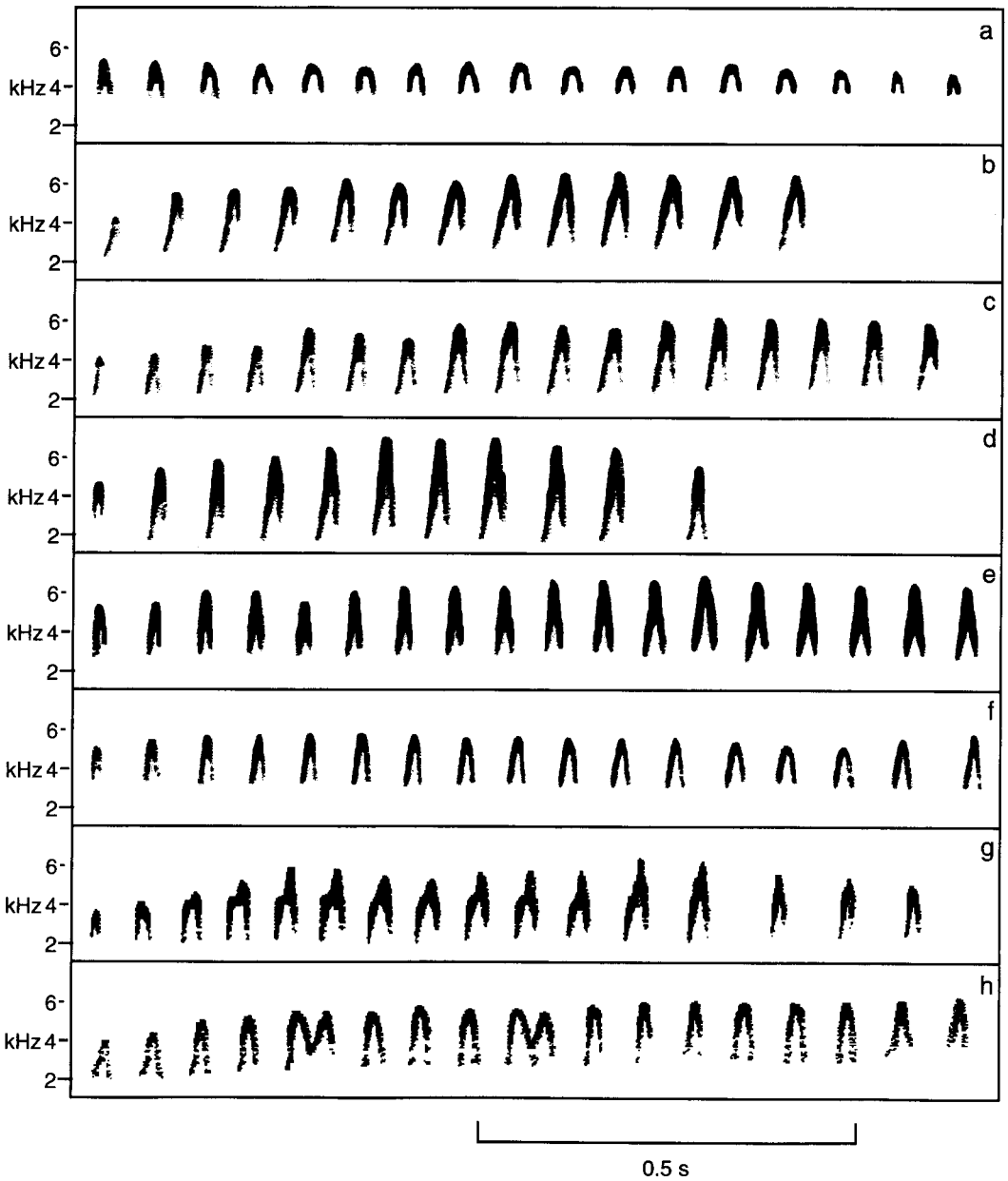


FIGURE 2. Sonograms of actual chatters from different individuals. Frequency is measured in kilohertz (kHz) and duration in seconds (sec). Panels a–f show typical chatters from each subspecies; a and b are from *ater* females, c and d from *obscurus* and e and f from *artemisiae*. Panels g (from an *artemisiae* female) and h (*obscurus*) show the relatively rare “double-humped” syllables discussed in the text.

2) and the highest frequency syllable occurred in the last half of the chatter in 30 of the 45 birds sampled. The maximum peak frequency (MAX) of individual syllables ranged from 3,380 to 7,360 hertz, although the majority (29 of 45) of females

had a maximum frequency between 5,000 to 6,500 Hz. The total number of syllables in a chatter fell between 10 and 25 in 39 of the 45 females sampled. And finally, the average total duration of chatter across all 45 females sampled

TABLE 1. Variables measured and their definitions (see also Fig. 1).

Variable ¹	Definition
Ti11 ²	Duration of the interval between syllables 1 and 2
Ti12	Duration of the interval between syllables 2 and 3
Ti13	Duration of the interval between syllables 3 and 4
Ti14	Duration of the interval between syllables 4 and 5
Ti1	Mean of Ti11–Ti14
Ti21	Duration of the interval between last and 2nd to last syllables
Ti22	Duration of the interval between 2nd and 3rd to last syllables
Ti23	Duration of the interval between 3rd and 4th to last syllables
Ti24	Duration of the interval between 4th and 5th to last syllables
Ti2	Mean of Ti21–Ti24
Td12	Duration of syllable 2 ³
Td13	Duration of syllable 3
Td14	Duration of syllable 4
Td15	Duration of syllable 5
Td1	Mean of Td12–Td15
Td21	Duration of last syllable
Td22	Duration of 2nd to last syllable
Td23	Duration of 3rd to last syllable
Td24	Duration of 4th to last syllable
Td25	Duration of 5th to last syllable
Td2	Mean of Td21–Td25
Tdur	Total duration of chatter
Tmint	Total mean interval between frequency peaks of syllables = Tdur/SYLNUM-1
F11	Maximum frequency point of syllable 1
F12	Maximum frequency point of syllable 2
F13	Maximum frequency point of syllable 3
F14	Maximum frequency point of syllable 4
F15	Maximum frequency point of syllable 5

ranged from 0.52–2.26 sec with an average of 1.25 sec.

Although these patterns were generally consistent across all individuals some deviations occurred. For example, six of the 45 females had “double-humped” syllables, i.e., syllables that had two frequency peaks instead of just one (Fig. 2h) or one distinct peak and a lesser peak or “plateau” (Fig. 2g). Four of those six birds used only one or two “double-humped” syllables within a chatter comprised of approximately 15 syllables

TABLE 1. Continued.

Variable ¹	Definition
F1	Mean of F11–F15
F21	Maximum frequency point of last syllable
F22	Maximum frequency point of 2nd to last syllable
F23	Maximum frequency point of 3rd to last syllable
F24	Maximum frequency point of 4th to last syllable
F25	Maximum frequency point of 5th to last syllable
F2	Mean of F21–F25
Fmax	Peak frequency of highest frequency syllable
Fmin	Peak frequency of lowest frequency syllable
Fdiff	Frequency difference within chatter = Fmax – Fmin
SYLNUM	Total number of syllables in chatter

¹ All “T” variables represent temporal measures where “Ti” variables measure the duration of intervals between syllables and “Td” variables measure the duration of individual syllables. “T” variables are measured in seconds. All “F” variables represent frequency variables and are measured in hertz.

² All Ti variables measured the time between frequency peaks of consecutive syllables.

³ Durations were measured 5 mm (830 Hz) from the frequency peak. Duration of syllable 1 was not used in analyses because it often was emitted at too low an amplitude to be accurately measured.

(Fig. 2h). In the other two birds, approximately one-half of the syllables were “double-humped” syllables (Fig. 2g). These “double-humped” syllables occurred in all three subspecies and appeared to occur randomly within the vocalization. Thus, although some individuals deviate from general qualitative trends, chatter usually conforms to certain structural rules.

QUANTITATIVE VARIATION AMONG THE SUBSPECIES IN THE CHATTER VOCALIZATION

The recordings that were analyzed covered a major part of the cowbird’s enormous range. Recordings of *M. a. obscurus* were from the southern half of California; those of *M. a. artemisiae* were from the eastern two thirds of Washington and adjacent Idaho; and those of *M. a. ater* were from areas along and near the East Coast between North Carolina and New York (see Appendix 1).

The Kruskal-Wallis analyses of variance showed that eight of the 39 analyzed variables differed significantly among subspecies ($\chi^2 = 5.99-11.40, P = 0.05-0.002$ [Table 2]). Of those eight, six were temporal measures. However, many of the 39 original variables were not independent. Considering variables that measured similar characters (i.e., frequency, interval between

TABLE 2. Descriptive statistics for variables significantly different among the subspecies via analysis of variance and for syllable number.

Variable ¹		Subspecies			<i>P</i> ²
		<i>ater</i> ³	<i>artemisiae</i> ³	<i>obscurus</i> ³	
Ti13	Mean (SE)	0.075 (0.003) ^f	0.069 (0.002) ^{f,g}	0.073 (0.002) ^g	0.04
	Range	0.057–0.130	0.058–0.074	0.053–0.103	
	Median	0.071	0.063	0.070	
Ti1	Mean (SE)	0.076 (0.003) ^f	0.071 (0.002) ^f	0.074 (0.002)	0.03
	Range	0.062–0.115	0.051–0.118	0.054–0.123	
	Median	0.073	0.070	0.071	
Ti21	Mean (SE)	0.099 (0.008)	0.088 (0.004) ^e	0.101 (0.0075) ^e	0.03
	Range	0.072–0.203	0.067–0.123	0.071–0.228	
	Median	0.091	0.086	0.093	
Ti22	Mean (SE)	0.085 (0.004) ^e	0.076 (0.002) ^{e,b}	0.085 (0.004) ^b	0.003
	Range	0.070–0.134	0.064–0.107	0.067–0.143	
	Median	0.080	0.075	0.081	
Ti2	Mean (SE)	0.084 (0.003) ^f	0.078 (0.002) ^{f,d}	0.087 (0.004) ^d	0.01
	Range	0.072–0.119	0.064–0.102	0.069–0.132	
	Median	0.083	0.076	0.081	
Tmint	Mean (SE)	0.070 (0.002) ^a	0.070 (0.0002) ^{a,b}	0.076 (0.002) ^b	0.002
	Range	0.069–0.098	0.065–0.079	0.068–0.098	
	Median	0.075	0.069	0.076	
F22	Mean (SE)	4,740 (150) ^f	5,040 (160)	5,390 (200) ^f	0.05
	Range	3,810–6,440	3,690–6,400	4,040–7,160	
	Median	4,690	5,000	5,180	
F23	Mean (SE)	4,740 (150) ^d	5,000 (160)	5,470 (200) ^d	0.02
	Range	3,670–6,330	3,750–6,420	4,060–7,360	
	Median	4,700	4,970	5,380	
SYLNUM	Mean (SE)	16.6 (1.70)	18.5 (1.15)	18.9 (1.25)	NS
	Range	7.3–33.3	12.5–27.5	10.6–26.0	
	Median	15.0	18.3	19.7	
	<i>n</i>	15	15	15	

¹ "T" variables are measured in seconds, "F" variables are measured in hertz.

² *P* values from Kruskal-Wallis Analysis of Variance.

³ Letters indicate significant differences between pairs using pairwise Kruskal-Wallis tests. *P* values for each letter are: a = 0.001, b = 0.003, c = 0.004, d = 0.007, e = 0.008, f = 0.02, g = 0.05.

syllables, etc.) as just one variable results in only four variables that are likely to be independent. These variables consist of intervals between syllables (the 10 Ti variables in Table 1 plus Tmint and Tdur), the duration of individual syllables (the 11 Td variables plus Tdur), the frequency of syllables (the 12 F variables plus Fmax, Fmin, and Fdiff), and the total number of syllables in the chatter (SYLNUM). Considering only these four variables, it is likely that interval variables do differ among the subspecies as six of 11 interval variables resulted in significant ANOVAs (Table 2). It is possible that there are frequency differences as well but here only two of 15 variables were significant (Table 2).

The principle components (PC) analysis was performed to help control for the lack of inde-

pendence among the 39 variables used in our analyses. The PC analysis generated three principal components which accounted for 64% of the total variation in the original data set (Table 3). PC1 explained 29% of the variation, consisted predominantly of frequency measures, and was not significantly different among subspecies (Kruskal-Wallis analysis). PC2 explained 18% of the variation, consisted predominantly of those temporal variables measuring intervals between syllables, and the Kruskal-Wallis analysis of variance showed statistically significant differences among subspecies ($\chi^2 = 9.7$, $P < 0.008$). PC3 explained 17% of the variation, consisted primarily of temporal measures (both interval and duration measures), and was not significantly different among subspecies. There was,

therefore, minor variation among the subspecies mainly in temporal characteristics that measured intervals. This is consistent with the indications from the univariate analyses that measures of intervals between syllables are those most likely to vary among subspecies. Inspection of the means and medians (Table 2) shows that *artemisiae* females had the shortest intervals in each of the seven sets of interval data that were significant with Kruskal-Wallis tests. In addition, the two other subspecies had no significant paired comparisons for any of these interval variables, while *artemisiae* was significantly different from one or both of the other two subspecies in all seven cases. It is apparent that the significant differences among the subspecies are due largely or solely to *artemisiae* having relatively short intervals between syllables. Nevertheless, the three subspecies show extensive overlap in these interval measures as indicated by the ranges in Table 2.

VARIATION AMONG FEMALES WITHIN A SUBSPECIES

We found no significant correlations for the differences between PC1, PC2, PC3, and PC123 for each pair of females within a subspecies and their geographic distance from each other. The correlation coefficients (Pearson Product-moment r^2) for the 12 plots (PC1 vs. geographic distance, PC2 vs. distance, PC3 vs. distance, PC123 vs. distance for each of the 3 subspecies) range from $r^2 = 0.00002$, $P > 0.9$ (PC2 vs. distance in *ater*) to $r^2 = 0.039$, $P > 0.5$ (PC3 vs. distance in *obscurus*). Even in the plot with the highest r^2 value (Fig. 3), females from nearby localities (<50 km apart) showed differences that were as great as females recorded hundreds of km apart. This is strong evidence that local chatter dialects do not exist. Although we did not test for normality in this data set, we used a parametric test because it provided a more powerful test of correlation than a non-parametric test (Siegel and Castellan 1988). Thus, the lack of statistically significant results in all 12 tests shows reliably that the differences between the PC scores of pairs of females and the geographic distances between them are not correlated.

The Kruskal-Wallis analyses of variance for differences among individuals within each subspecies produced statistically significant results in *obscurus* females for 14 of the 15 frequency

TABLE 3. The eigenvectors and the percentage of the total variance explained by principal components 1, 2, and 3 (PC1, PC2, PC3).

Variable	Eigenvectors		
	PC1	PC2	PC3
Ti11	-0.027	-0.189	0.047
Ti12	-0.005	-0.239	0.179
Ti13	-0.009	-0.284	0.159
Ti14	-0.006	-0.274	0.171
Ti1	-0.016	-0.280	0.147
Ti21	0.053	-0.132	0.139
Ti22	0.038	-0.212	0.211
Ti23	0.010	-0.201	0.202
Ti24	0.049	-0.225	0.228
Ti2	0.049	-0.219	0.223
Td12	-0.077	0.119	0.250
Td13	-0.076	0.132	0.285
Td14	-0.076	0.122	0.287
Td15	-0.086	0.159	0.272
Td1	-0.093	0.135	0.263
Td21	-0.170	0.127	0.169
Td22	-0.154	0.170	0.169
Td23	-0.145	0.198	0.187
Td24	-0.123	0.171	0.158
Td25	-0.111	0.227	0.199
Td2	-0.141	0.211	0.195
Tdur	0.048	0.050	0.032
Tmint	0.007	-0.291	0.211
F11	0.216	0.058	0.033
F12	0.253	0.047	0.035
F13	0.259	0.034	0.052
F14	0.259	0.025	0.051
F15	0.242	0.029	0.038
F1	0.264	0.042	0.044
F21	0.228	0.106	0.069
F22	0.234	0.101	0.079
F23	0.236	0.084	0.090
F24	0.243	0.073	0.109
F25	0.240	0.069	0.112
F2	0.248	0.090	0.095
Fmax	0.258	0.106	0.088
Fmin	0.222	0.076	0.040
Fdiff	-0.034	0.006	0.031
SYLNUM	0.045	0.103	-0.024
% of variance	29%	18%	17%

measures and 21 of the 23 temporal measures (Table 4). Thus, there was significantly more variation among the calls of different females than among the calls of the same female. For females of the subspecies *artemisiae*, 14 of 15 frequency and 15 of 23 temporal measures were significant. Lastly, significance occurred among *ater* females in 14 of 15 frequency and 12 of 23 temporal variables. The only variable that measured neither frequency nor temporal aspects, syllable number (SYLNUM), did not differ significantly among females in all three subspecies.

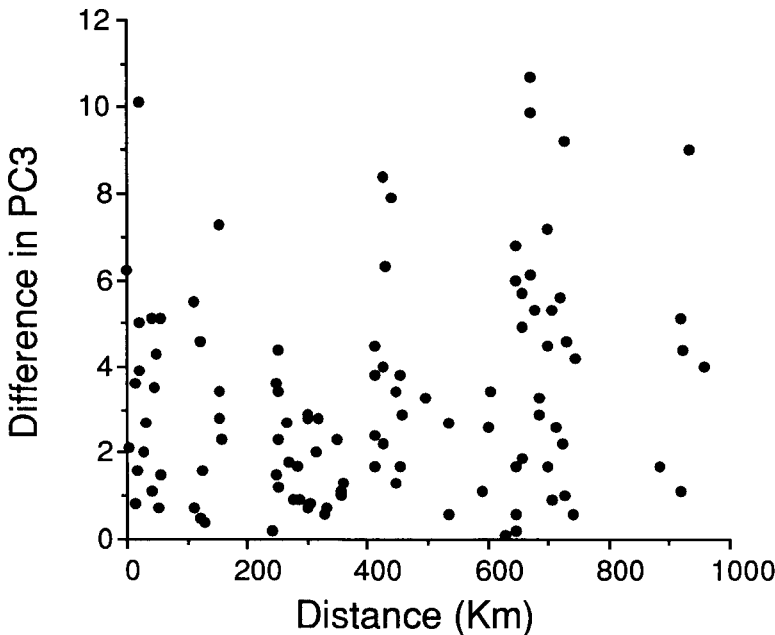


FIGURE 3. Plot of the differences in principle component 3 vs. the geographic distance among all females within the subspecies *obscurus*. This plot had the largest r^2 out of all the 12 plots and is being used to illustrate the lack of correlation between PCs 1, 2, 3, and 123 with geographic distance.

The much smaller P values for *obscurus* females (Table 4) probably do not reflect greater variation among individuals in that subspecies than in the two other subspecies because sample sizes differed. Among *obscurus* females, an average of 6.3 chatters/female were analyzed, whereas among *artemisiae* and *ater*, an average of 3.1 and 2.7 chatters/female, respectively, were analyzed. These sample size differences alone could have resulted in lower P values. Regardless, these results suggest that there is a large amount of variation among individuals of the same subspecies and that this variation lies most consistently in frequency characteristics. As with the univariate comparisons among the three subspecies, the analyses in Table 4 are not all independent. However, as nearly all of the analyses were significant, it is clear that chatter calls of different individuals actually differ.

The Kruskal-Wallis analyses do not reveal whether significant results were due to only a few or to most females having divergent chatter calls. Rather than analyze randomly paired females, we analyzed the amount of variation between all pairs of females that were recorded close enough (<1.6 km) to come into contact with each other (see Appendix 1). Each of the 39 variables was

compared (Mann-Whitney U tests) for each of three pairs of *obscurus* females and most (71%) of the 117 (3 times 39) comparisons were significant. Thus, we conclude that even if minor microgeographic (i.e., dialect) variation occurs in chatter calls (and the previous section showed no indication of this), females that are likely to come into contact with one another have individually distinct chatters.

DISCUSSION

VARIATION AMONG SUBSPECIES

We found only slight macrogeographic (subspecific) variation in quantitative characteristics of the chatter call and no clear qualitative variation. In agreement with this structural similarity across the subspecies, Rothstein et al. (1988) found that western (*M. a. obscurus* and *M. a. artemisiae*) and eastern (*M. a. ater*) male cowbirds responded similarly to the chatter calls of western females. However, this functional similarity is based on only two series of chatter calls and may therefore be due to pseudoreplication (Kroodsmas 1989). Furthermore, the playback result does not preclude structural differences between eastern and western chatter calls (and therefore the necessity

of our study) because male cowbirds outnumber females (Rothstein et al. 1986) and therefore might not be selective in attempts to interact with females; i.e., they may always be responsive to female-like calls. The low variation in the female chatter call is unique among cowbird vocalizations and contrasts greatly with the vocalizations given by male cowbirds which are highly variable on both macro- and microgeographic scales (King and West 1983b, Rothstein and Fleischer 1987a, Rothstein et al. 1988). Consistent with its lack of strong intraspecific variation, Brown-headed Cowbird chatter is very similar to that given by the congeneric Shiny Cowbird, *M. bonariensis*, (Friedmann 1929; Rothstein, pers. observ.) and to a lesser extent by other icterines (Red-winged Blackbirds, *Agelaius phoeniceus* [Beletsky 1983, Orians and Christman 1968]). The similarity between the chatter calls of Brown-headed and Shiny Cowbirds is so great that males and females of the latter species are attracted to playback of the other species in Uruguay and Argentina (S. I. Rothstein, pers. observ.) and in Puerto Rico (B. Woodworth, pers. observ.).

The consistent nature of chatter within all three subspecies and even among closely related species, suggests that chatter development may be genetically based or constrained. Indeed, chatter is similar to the first vocalization that cowbirds develop, their begging call. Begging appears at an age of three days (Friedmann 1929) which is before nestling songbirds have well-developed hearing (Aleksandrov and Dmitrieva 1992) and before song acquisition and learning typically begin (Marler 1970, Marler and Peters 1987). Both begging and chatter consist of series of chevron-shaped syllables, although those in begging are higher in frequency (Broughton et al. 1987). Thus, begging may be the ontogenetic precursor of adult chatter. Unlike what appears to be the case for chatter, the two male song types, flight whistles and perched song, are both highly variable and highly modifiable by learning (West and King 1985, Rothstein and Fleischer 1987b, O'Loughlen and Rothstein 1993). Furthermore, neither has any likely precursor in the vocalizations of juvenile cowbirds which lack the pure tone notes characteristic of most male songs.

VARIATION AMONG FEMALES WITHIN A SUBSPECIES

The Kruskal-Wallis analysis of variance tests showed statistical significance within each subspecies for the majority of variables we measured

TABLE 4. P values from Kruskal-Wallis analysis of variance among females within a subspecies.

Variable	Subspecies		
	<i>obscurus</i>	<i>artemisiae</i>	<i>ater</i>
Ti11	ns*	ns	ns
Ti12	0.001	ns	ns
Ti13	0.0001	0.03	ns
Ti14	0.0001	0.03	0.01
Ti1	0.0003	ns	ns
Ti21	0.0001	ns	ns
Ti22	0.0001	ns	ns
Ti23	0.0001	0.03	ns
Ti24	0.0001	0.05	ns
Ti2	0.0001	ns	ns
Td12	0.0009	0.04	ns
Td13	0.0004	0.01	0.03
Td14	0.0009	0.001	0.02
Td15	0.0009	0.002	0.03
Td1	0.0001	0.001	0.009
Td21	0.0001	ns	0.03
Td22	0.0001	0.04	0.01
Td23	0.0001	0.009	0.004
Td24	0.0001	0.01	0.002
Td25	0.0001	0.002	0.005
Td2	0.0001	0.002	0.002
Tdur	0.0001	0.004	0.005
Tmint	ns	ns	ns
F11	0.0001	0.03	0.003
F12	0.0001	0.02	0.001
F13	0.0001	0.004	0.001
F14	0.0001	0.0005	0.003
F15	0.0001	0.004	0.002
F1	0.0001	0.006	0.001
F21	0.0001	0.005	0.02
F22	0.0001	0.01	0.02
F23	0.0001	0.001	0.008
F24	0.0001	0.002	0.004
F25	0.0001	0.009	0.004
F2	0.0001	0.002	0.004
Fmax	0.0001	0.0008	0.006
Fmin	0.0001	0.02	0.002
Fdiff	ns	ns	ns
SYLNUM	ns	ns	ns

* ns = not significant.

and thus chatter meets a necessary, but not sufficient, requirement for an individual recognition cue. Indeed, we found considerably more variation among individuals within each subspecies than we found among the subspecies. Our discovery of individual variation is not unexpected, as some females give chatter calls that are noticeably different to our unaided ears.

It has been suggested that frequency characteristics of vocalizations are more useful in individual recognition than are temporal characteristics (Goldman 1973; Brooks and Falls 1975; Falls 1982; Davis 1986; Nelson 1988, 1989; Weary 1990; Loesche et al. 1992). In accord with

this suggestion, 14 of the 15 frequency variables (see Table 4) were significantly different among females within each subspecies whereas temporal characteristics showed fewer significant results. But can cowbirds detect the frequency differences that occur in chatter calls? Cowbirds can discriminate about a 1% change in frequency at 4,000 Hz and about a 2% change at 8,000 Hz (Table 2 in Sinnott et al. 1980, Fig. 5 in Dooling 1982). This equals a 45 to 55 Hz change within the frequency range covered by chatter. As frequency differences for identical variables ranged over more than 2,000 Hz within subspecies (Table 2), it is likely that cowbirds can detect differences among the chatter calls of different females. In addition, Medvin et al. (1993) suggest that repetitive frequency modulation and variation in frequency differences are important for enhancing individual recognition in Cliff Swallows (*Hirundo pyrrhonota*). Cowbird chatter conforms to these parameters in that syllables are repeated, are frequency modulated, and there is variation among females in the frequency peaks within a chatter vocalization.

Individual identification could be of value to females. Most studies of cowbird mating systems show monogamy (Darley 1982, Dufty 1982b, Yokel 1986) and females may benefit from enabling their mates to identify them at long distances. Individual identification via chatter may be beneficial in female-female interactions because it allows females to determine that another female is a familiar individual with whom dominance and spatial relationships have been determined. Thus female cowbirds, like many male songbirds (Stoddard et al. 1990), may respond more strongly to vocalizations of strangers than to those of familiar individuals since female cowbirds show some indications of territoriality (Rothstein et al. 1986).

Individual variation is not necessarily incompatible with our view that chatter development is genetically programmed. It is unlikely that there is a single "chatter gene." It is more likely that a behavior as complex as chatter is affected by numerous genes even ones as seemingly removed as those that affect body size. Small birds have higher frequency voices than larger ones, which may explain why *obscurus*, the smallest race (Grinnell 1909), has the highest frequencies (Table 2). Furthermore, even a behavior that can be expressed in the absence of a conspecific role model (chatter develops in isolate reared females

[E. Gorney and S. I. Rothstein, unpubl. data] and females reared with no exposure to natural cowbird vocalizations [M. J. West, pers. comm.]) is likely to be influenced by the vagaries of an individual's overall physical and behavioral development.

Our inferences regarding chatter and individual recognition are tentative because we do not know if the individual differences we found are stable over time. (Females were represented by calls recorded over a short period, usually of 5 min or less.) However, we can reject the possibility that individual differences occurred because chatter parameters change according to context. Regardless of whether there are context specific changes, all recordings were made in the same situation, i.e., when females were responding agonistically to playback of chatter.

FUNCTIONS OF FEMALE CHATTER

Morton (1975) discussed a set of motivational-structural (MS) rules that describe the physical structure of sounds used in close contact communication. Based on these rules, he suggested that sounds having a chevron shape communicate an intermediate level of fear/appeasement and hostility (Fig. 1 in Morton 1975). The chevron shape of female cowbird chatter fits this scheme. Although it is primarily aggressive, female chatter in response to other females and to nearby males doing perched songs may represent conflict because a chattering female may also be fearful of other females and males. However, the remaining context in which females give chatter—a friendly response to the flight whistle of distant males—seems to involve little or no conflict. Why, then, do not females have two distinct vocalizations to match the aggressive and friendly contexts in which chatter is given? There may be unknown constraints to vocal repertoire size in females and, since MS rules apply primarily to close proximity communication, female chatter may be adapted to aggressive contexts and is used secondarily when a female attracts a distant male.

In addition, although we have found no obvious qualitative variation in chatter according to different contexts, there may be quantitative variation in accord with MS rules. For example, chatter used as a friendly response to male flight whistles may show relatively little frequency modulation. That is, one or both arms of the chevron may be reduced in length or slope.

ACKNOWLEDGMENTS

Field work was supported by NSF grants BNS 82-16778 and BNS 86-16922, a grant from the National Zoological Park (Smithsonian Institution), and U.C. Faculty Research Grants to SIR. KB was supported by a U.C. Regents Fellowship during preparation of the manuscript. We thank Eugene S. Morton, Adrian O'Loughlen, Robert Slotow, and two anonymous reviewers for their many helpful comments.

LITERATURE CITED

- ALEKSANDROV, L. I., AND L. P. DMITRIEVA. 1992. Development of auditory sensitivity of altricial birds: absolute thresholds of the generation of evoked potentials. *Neurosci. Behav. Physiol.* 22:132-136.
- BELETSKY, L. D. 1983. Aggressive and pair-bond maintenance songs of female Red-winged Blackbirds (*Agelaius phoeniceus*). *Z. Tierpsychol.* 62: 47-54.
- BROOKS, R. J., AND J. B. FALLS. 1975. Individual recognition by song in White-crowned Sparrows. III. Song features used in individual recognition. *Can. J. Zool.* 53:1749-1761.
- BROUGHTON, K. E., A. L. A. MIDDLETON, AND E. D. BAILEY. 1987. Early vocalizations of the Brown-headed Cowbird and three host species. *Bird Behav.* 7:27-30.
- DARLEY, J. A. 1982. Territoriality and mating behavior of the male Brown-headed Cowbird. *Condor* 84:15-21.
- DAVIS, W. J. 1986. Acoustic recognition in the Belted Kingfisher: cardiac response to playback vocalizations. *Condor* 88:505-512.
- DOOLING, R. J. 1982. Auditory perception in birds, p. 95-130. *In* D. E. Kroodsma and E. H. Miller [eds.], *Acoustic communication in birds*, Vol. 1. Academic Press, New York.
- DUFTY, A. M., JR. 1982a. Response of Brown-headed Cowbirds to simulated conspecific intruders. *Anim. Behav.* 30:1043-1052.
- DUFTY, A. M., JR. 1982b. Movements and activities of radio-tracked Brown-headed Cowbirds. *Auk* 99: 319-327.
- DUFTY, A. M., JR. 1985. Song sharing in the Brown-headed Cowbird (*Molothrus ater*). *Z. Tierpsychol.* 69:177-190.
- FALLS, J. B. 1982. Individual recognition by sounds in birds, p. 237-278. *In* D. E. Kroodsma and E. H. Miller [eds.], *Acoustic communication in birds*, vol. 2. Academic Press, New York.
- FLEISCHER, R. C., AND S. I. ROTHSTEIN. 1988. Known secondary contact and rapid gene flow among subspecies and dialects in the Brown-headed Cowbird. *Evol.* 42:1146-1158.
- FLEISCHER, R. C., S. I. ROTHSTEIN, AND L. S. MILLER. 1991. Mitochondrial DNA variation indicated gene flow across a zone of known secondary contact between two subspecies of the Brown-headed Cowbird. *Condor* 93:185-189.
- FRIEDMANN, H. 1929. The cowbirds, a study in the biology of social parasitism. C. C. Thomas, Springfield, IL.
- GOLDMAN, P. 1973. Song recognition by Field Sparrows. *Auk* 90:106-113.
- GRINNELL, J. 1909. A new cowbird of the genus *Molothrus*, with a note on the probable genetic relationships of the North American forms. *Univ. Calif. Publ. Zool.* 5:275-281.
- KING, A. P., AND M. J. WEST. 1983a. Epigenesis of cowbird song—a joint endeavour of males and females. *Nature* 305:704-706.
- KING, A. P., AND M. J. WEST. 1983b. Dissecting cowbird song potency: assessing a song's geographic identity and relative appeal. *Z. Tierpsychol.* 63: 37-50.
- KING, A. P., AND M. J. WEST. 1989. Presence of female cowbirds affects vocal imitation and improvisation in males. *J. Comp. Psychol.* 103:39-44.
- KROODSMA, D. E. 1989. Suggested experimental designs for song playbacks. *Anim. Behav.* 37:600-609.
- LOESCHE, P., M. D. BEECHER, AND P. K. STODDARD. 1992. Perception of Cliff Swallow calls by birds and humans. *J. Comp. Psychol.* 106:239-247.
- MARLER, P. 1970. A comparative approach to vocal learning: song development in White-crowned Sparrows. *J. Comp. Physiol. Psychol. Mono.* 71: 1-25.
- MARLER, P. AND S. PETERS. 1987. A sensitive period for song acquisition in the Song Sparrow, *Melospiza melodia*: a case of age-limited learning. *Ethology* 76:89-100.
- MEDVIN, M. B., P. K. STODDARD, AND M. D. BEECHER. 1993. Signals for parent-offspring recognition: a comparative analysis of the begging calls of Cliff Swallows and Barn Swallows. *Anim. Behav.* 45: 841-850.
- MORTON, E. S. 1975. Ecological sources of selection on avian sounds. *Am. Nat.* 108:17-34.
- NELSON, D. A. 1988. Feature weighting in species song recognition by the Field Sparrow (*Spizella pusilla*). *Behaviour* 106:158-182.
- NELSON, D. A. 1989. Song frequency as a cue for recognition of species and individuals in the Field Sparrow (*Spizella pusilla*). *J. Comp. Psychol.* 103: 171-176.
- O'LOUGHLEN, A. L., AND S. I. ROTHSTEIN. 1993. An extreme example of delayed vocal development: song learning in a population of wild Brown-headed Cowbirds. *Anim. Behav.* 46:293-304.
- ORIAN, G. H., AND G. M. CHRISTMAN. 1968. A comparative study of the behavior of Red-winged, Tricolored, and Yellow-headed Blackbirds. *Univ. Calif. Publ. Zool.* 84:1-81.
- ROTHSTEIN, S. I. 1978. Geographical variation in the nestling coloration of parasitic cowbirds. *Auk* 95: 152-160.
- ROTHSTEIN, S. I., AND R. C. FLEISCHER. 1987a. Vocal dialects and their possible relation to honest status signalling in the Brown-headed Cowbird. *Condor* 89:1-23.
- ROTHSTEIN, S. I., AND R. C. FLEISCHER. 1987b. Brown-headed Cowbirds learn flight whistles after the juvenile period. *Auk* 104:513-516.
- ROTHSTEIN, S. I., D. A. YOKEL, AND R. C. FLEISCHER.

1986. Social dominance, mating and spacing systems, female fecundity, and vocal dialects in captive and free-ranging Brown-headed Cowbirds. *Current Ornithology* 3:127-185.
- ROTHSTEIN, S. I., D. A. YOKEL, AND R. C. FLEISCHER. 1988. The agonistic and sexual functions of vocalizations of male Brown-headed Cowbirds, *Molothrus ater*. *Anim. Behav.* 36:73-86.
- SIEGEL, S., AND N. J. CASTELLAN, JR. 1988. Non-parametric statistics for the behavioral sciences, 2nd ed. McGraw-Hill, Singapore.
- SINNOTT, J. M., M. B. SACHS, AND R. D. HEINZ. 1980. Aspects of frequency discrimination in passerine birds and pigeons. *J. Comp. Physiol. Psychol.* 94:401-415.
- STODDARD, P. K., M. D. BEECHER, C. L. HORNING, AND M. S. WILLIS. 1990. Strong neighbor-stranger discrimination in Song Sparrows. *Condor* 92:1051-1056.
- WEARY, D. M. 1990. Categorization of song notes in Great Tits: which acoustic features are used and why? *Anim. Behav.* 39:450-457.
- WEST, M. J., AND A. P. KING. 1985. Social guidance of vocal learning by female cowbirds: validating its functional significance. *Z. Tierpsychol.* 70:225-235.
- WEST, M. J., AND A. P. KING. 1986. Song repertoire development in male cowbirds (*Molothrus ater*): its relation to female assessment of song potency. *J. Comp. Psychol.* 100:296-303.
- WEST, M. J., A. P. KING, AND D. H. EASTZER. 1981a. The cowbird: reflections on development from an unlikely source. *Am. Scient.* 69:56-66.
- WEST, M. J., A. P. KING, AND D. H. EASTZER. 1981b. Validating the female bioassay of cowbird song: relating differences in song potency to mating success. *Anim. Behav.* 29:490-501.
- YOKEL, D. A. 1986. Monogamy and brood parasitism: an unlikely pair. *Anim. Behav.* 34:1348-1358.
- YOKEL, D. A. 1989. Intrasexual aggression and the mating behavior of Brown-headed Cowbirds: their relation to population densities and sex ratios. *Condor* 91:43-51.

APPENDIX 1. Date recorded and locality of vocalizations analyzed.

Female	Date	Locality
ATER-A	6/6/84	Rockville, Montgomery Co., MD
ATER-B	6/10/84	Richmond, Chesterfield Co., VA
ATER-C	6/13/84	Jct. Rtes 798 & 54, Ashland, Chesterfield Co., VA
ATER-D	6/14/84	Jct. Rtes 40 & 695, Baltimore, Baltimore Co., MD
ATER-E	6/14/84	Odenton, Anne Arundel Co., MD
ATER-F	6/15/84	Pocohontas State Park, Chesterfield Co., VA
ATER-G	6/16/84	Chapel Hill, Orange Co., NC
ATER-H	4/9/88	Cambridge Springs, Crawford Co., PA
ATER-I	4/10/88	Cambridge Springs, Crawford Co., PA
ATER-J	4/15/88	Grave Ranch Road, Kent Island, Queen Annes Co., MD
ATER-K	4/15/88	Bennett Point Rd., Kent Island, Queen Annes Co., MD
ATER-L	4/16/88	Tilghman Neck Rd., Kent Island, Queen Annes Co., MD
ATER-M	4/18/88	Rockefeller Univ., Millbrook, Dutchess Co., NY
ATER-N	4/19/88	Jct Hwy 343 & Rt 82, Millbrook, Dutchess Co., NY
ATER-O	4/19/88	Jct Hwy 23 & 343, Millbrook, Dutchess Co., NY
ART-A	6/4/85	Rte 12, Walla Walla, Walla Walla Co., WA
ART-B	6/4/85	Rte 12 & Cummins Road, Walla Walla Co., WA
ART-C	6/3/85	Julietta, Latah Co., ID
ART-D	6/5/85	Auburn, King Co., WA
ART-E	6/4/85	Rte 12 & Last Chance Rd, Walla Walla Co., WA
ART-F	5/31/85	Othello, Adams Co., WA
ART-G	5/30/85	Yakima, Kittitas Co., WA
ART-H	5/30/85	Hwy 821 & I-90, Kittitas Co., WA
ART-I	5/30/85	Jct. Rte 10 & Yakima Rd, Kittitas Co., WA
ART-J	5/31/85	Othello, Adams Co., WA
ART-K	5/31/85	Lake Lenore, Grant Co., WA
ART-L	5/31/85	Potholes Reservoir Dam, Grant Co., WA
ART-M	6/2/85	Turnbull Refuge, Spokane Co., WA
ART-N	6/2/85	Rock Lake Rd & Cheney Plaza Rd, Spokane Co., WA
ART-O	6/3/85	McGee Park, Pullman, Whitman Co., WA
OBS-A ¹	5/18/83	Finney Lake, Imperial Co., CA
OBS-B ¹	5/18/83	Finney Lake, Imperial Co., CA
OBS-C	4/19/83	Blythe, Riverside Co., CA
OBS-D	5/20/83	Otay Rd & Beyer Way, San Diego, San Diego Co., CA
OBS-E	6/21/83	Camino Cielo, Santa Barbara, Santa Barbara Co., CA
OBS-F ²	4/16/82	Union Cemetery, Bakersfield, Kern Co., CA
OBS-G ³	5/9/82	Carpenter Ave, Modesto, Stanislaus Co., CA
OBS-H ³	5/9/82	Jennings Rd, Modesto, Stanislaus Co., CA
OBS-I	5/6/82	Dickinson Ferry Rd., Merced Co., CA
OBS-J	5/5/82	Merced, Merced Co., CA
OBS-K ²	4/15/82	Bakersfield, Kern Co., CA
OBS-L	5/6/82	Hatfield State Recreation Area, Merced Co., CA
OBS-M	5/8/82	River Rd & Big Chico Creek, Butte Co., CA
OBS-N	5/19/83	Alamo Rd & Rte 98, Imperial Co., CA
OBS-O	5/19/83	Alamo Rd & Harris Rd, Imperial Co., CA

^{1,2,3} Females of the same subspecies that were recorded within 1.6 km of each other.