COMPARATIVE ANALYSIS OF PERCH-COO VOCALIZATIONS IN *STREPTOPELIA* DOVES

HANS SLABBEKOORN,[1] SELVINO DE KORT, AND CAREL TEN CATE

Behavioral Biology, Institute of Evolutionary and Ecological Sciences, Leiden University, P.O. Box 9516, 2300 RA Leiden, The Netherlands

ABSTRACT.—Some of the 16 dove species in the genus *Streptopelia* are very similar with respect to plumage pattern, but all seem to produce species-specific "perch-coo" vocalizations. Here, we describe variation in perch-coo recordings of all 16 species. All individuals could be correctly classified by species in a discriminant function analysis, which means that the overlap in inter- and intraspecific variation was limited for the total set of acoustic parameters. Interspecific similarity in acoustic parameters was compared with taxonomic classification, based upon qualitative morphological characteristics and geographic distribution (Goodwin 1983). The clustering of species using the acoustic data set showed little congruence with taxonomic clustering. This indicates that differentiation in plumage pattern does not necessarily coincide with differentiation in acoustic characteristics. However, our analysis did not completely contradict the subdivision into four taxonomic groups based on morphology and distribution. Two of the four putative groups differed significantly from the other groups in one of the components of a principal components analysis. Vocal differentiation in *Streptopelia* doves was strongest in temporal components, which is in line with expectations based on the evolutionarily conservative syringeal constraints. *Received 29 September 1997, accepted 4 January 1999.*

DIFFERENT SPECIES of a particular taxonomic group of birds often share vocal characteristics. At the same time, some vocal characteristics serve as accurate indicators of species status. For this reason, song comparisons have been widely used to evaluate relationships among species (see Payne 1986). Comparative analyses of vocalizations have been used to evaluate intra- and interspecific variation in several avian genera (e.g. Zann 1974, Miller 1978, Collins and Goldsmith 1998) and have led to suggestions for taxonomic subdivisions within some genera of doves (*Geopelia*, Harrison 1969; *Zenaida*, Baptista et al. 1983). Other studies have evaluated vocal variation among species in the context of phylogenetic reconstruction (e.g. Güttinger 1970, Miller et al. 1988, Islam and Crawford 1996, Miller 1996, McCracken and Sheldon 1997). In this study, we use a comparative approach to match vocal similarity among *Streptopelia* doves with their taxonomic classification. We used phenetic analyses of the "perch-coo" vocalization, and, as our taxonomic reference, we used a clustering suggested by Goodwin (1983), based on the qualitative interpretations of differences among species in morphology and distribution.

Perch-coo vocalizations of doves are regarded as functionally similar to advertising songs in songbirds; they serve in male-male conflict and for female attraction (Jackson and Basket 1964; Davies 1970, 1974; Goodwin 1983; Cramp 1985; Baptista 1996). Sexual selection may lead to intraspecific expansion of variance in the acoustic parameters of such a signal. However, the same signal also may serve in species recognition (Becker 1982, Nelson 1989). In this context, the negative consequences of hybridization may lead to intraspecific contraction of variance and interspecific divergence (see Miller 1982). Sexual selection may shape acoustic parameters such as frequency range or repetition pattern of vocalizations, but acoustic limits are affected by environmental and phylogenetic constraints (Ryan and Brenowitz 1985). Phylogenetic constraints make it likely that closely related species are more similar in vocal parameters than are distantly related species. Features like body size (Wallschläger 1980, Tubaro and Mahler 1998) and syrinx morphology (Gaunt 1988, Podos 1997) may impose limitations on sound production, and the auditory sensitivity of receivers may restrict the characteristics of communicative sounds to those of the species-specific hearing range (Dooling 1982, Ryan et al. 1990). In addition, the evolu-

[1] E-mail: slabbekoorn@rulsfb.leidenuniv.nl

tionary and ontogenetic flexibility of the neural pathways involved in vocal control and auditory processing may play an important role, potentially affecting acoustic character divergence and convergence via constraints on sound production and perception (Bass and Baker 1991, Smith 1994).

For selection to act on behavioral traits, variance in the traits must have a heritable basis. Doves develop vocal characters independent of learning (Nottebohm and Nottebohm 1971). Darwin (1868) reported that Rock Doves (*Columba livia*) could be artificially selected for temporal qualities of their coos (see also Baptista and Abs 1983). Vocalizations of hybrids of various *Streptopelia* doves either resembled one parental type, were intermediate between the parents, or resembled neither of the parents; the degree of disruption in coo characteristics increased as the relatedness of the parental forms decreased (Lade and Thorpe 1964, Davies 1970, Baptista 1996).

The aim of this paper is to examine a representative set of recordings for all 16 species of *Streptopelia* doves and to give a descriptive overview of their perch-coo characteristics. The coos of *Streptopelia* are relatively simple and well suited for extensive quantitative analyses, as was shown for *S. decaocto* (ten Cate 1992; ten Cate and Ballintijn 1996; Ballintijn and ten Cate 1997a, b). Species of *Streptopelia* show little divergence in allometry, and their syrinx appears to be anatomically restricted in producing variation in frequency range or frequency modulation patterns (Warner 1972, Ballintijn et al. 1995). Gaunt (1988) remarked that even birds with a relatively simple syrinx morphology can produce rather differently structured vocalizations by varying the rate and pattern of airflow. If this has affected vocal evolution in *Streptopelia* species, then one might expect vocal differentiation in temporal features in particular.

We compared interspecific similarity in perch-coos with the taxonomic clustering provided by Goodwin (1983). This is the prime reference for the taxonomy of doves (Howard and Moore 1991, Baptista et al. 1997) and is based on the qualitative interpretation of morphological characteristics and geographic distribution (see Fig. 1). Phenetic classifications, like those based on plumage pattern (Goodwin 1983) or acoustic characteristics (this study), need not
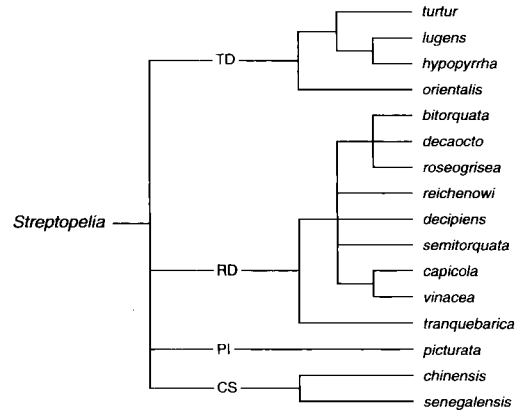

FIG. 1. Dendrogram reconstructed after Goodwin (1983) on the classification of 16 *Streptopelia* species. The classification is based upon qualitative morphological and distributional characteristics. TD = turtle-dove group, RD = ringed dove group, PI = *S. picturata*, and CS = *S. chinensis / S. senegalensis* group.

necessarily reflect common ancestry, but it is of interest to see whether they show the same pattern of clustering. Insight into how evolutionary pathways led to the similarities and dissimilarities in such features has to await a phylogenetic analysis of the genus *Streptopelia* based on an independent data set.

METHODS

Subjects.—The 16 species of *Streptopelia*, commonly referred to as "turtle-doves," are slender, relatively long-tailed, gray or brown pigeons (Goodwin 1983). Neck or collar patterns are the most conspicuous external plumage characteristics. The turtle doves are native to temperate and tropical regions of Europe, Asia, and Africa. Some of the species are expanding their distribution in Pacific, Australian, and Nearctic regions where they were introduced relatively recently. Most species inhabit open woodlands and a wide range of human settlements. They feed mainly on grains and seeds, although the forest-dwelling species frequently eat berries and other small fruits. *Streptopelia* doves are usually abundant within their range. They are territorial but often form large foraging or sleeping groups, particularly outside of the breeding season. All species are strong fliers, and some are long-distance migrants.

Goodwin (1983) divided the 16 species into four groups based on appearance and geographic distribution (see Table 1). The four species of typical "turtle doves" are darker than the other species and have a mottled pattern on the back of their wings and either a black-and-white striped patch or a completely

TABLE 1.   Overview of the genus *Streptopelia*. A description of the neck pattern is given because it is the most conspicuous field characteristic. We also list brief descriptions of geographic distribution based on Goodwin (1983) and Howard and Moore (1991).

Species	Group[a]	Size[b]	Neck pattern	Distribution
S. turtur	TD	26 to 28	Striped patch	Europe, W Asia, N Africa
S. lugens	TD	28 to 31	Black patch	E Africa, SW Arabia
S. hypopyrrha	TD	29 to 31	Black patch	E Nigeria, W Cameroon
S. orientalis	TD	33 to 35	Striped patch	Central to E India
S. bitorquata	RD	29 to 31	Black collar	Philippines, Indonesia
S. decaocto	RD	31 to 33	Black collar	Europe to E China, India
S. roseogrisea	RD	29 to 30	Black collar	Sahelian Africa
S. reichenowi	RD	26 to 28	Black collar	S. Somalia, NE Kenya
S. decipiens	RD	28 to 30	Black collar	Africa S of Sahara
S. semitorquata	RD	33 to 36	Black collar	Africa S of Sahara
S. capicola	RD	25 to 28	Black collar	S and E Africa
S. vinacea	RD	24 to 26	Black collar	Africa S of Sahara and N of equator
S. tranquebarica	RD	22 to 24	Black collar	SE Asia
S. picturata	PI	27 to 33	Side spots	Madagascar
S. chinensis	CS	27 to 33	Spotted patch	SE Asia
S. senegalensis	CS	25 to 27	Throat spots	Africa, Middle East, SW Asia

[a] TD = turtle-dove group, RD = ringed dove group, PI = *S. picturata*, and CS = *S. chinensis/S. senegalensis* group. Based on Goodwin (1983).
[b] Head-to-tail length (cm).

black patch at either side of their neck. The largest group within the genus, the "ring-necked turtle doves" (or "ring doves"), consists of nine species, each of which has a more or less uniform gray plumage and a characteristic black collar around the neck. The other two groups consist of, respectively, one species (*S. picturata*, Madagascar Turtle-Dove) and two species (*S. chinensis* [Spotted Dove] and *S. senegalensis* [Laughing Dove]). These species differ in several morphological features such as plumage pattern and relative length of the tail and wings. Goodwin (1983) also suggested that within the turtle-dove group, *S. lugens* and *S. hypopyrrha* are the product of the most recent species split, and they may be more closely related to *S. turtur* than to *S. orientalis*. In the ringed group, *S. vinacea* and *S. capicola* are assumed to be monophyletic, as are *S. bitorquata*, *S. decaocto*, and *S. roseogrisea*.

Recordings.—Most of the recordings were made in private aviaries and zoological gardens in the Netherlands and Belgium. These were supplemented by recordings of free-living doves in the Netherlands, Thailand, Uganda, Cameroon, and Ghana. The final collection was completed with some recordings from the National Sound Archive in London. The recordings of doves in aviaries were made with a Sennheiser MKH P48 microphone and a Sony TC-D5 Pro recorder, using TDK AD90 tapes. Some of the recordings of free-living doves were made with the same equipment, and some with a Sony F-V9 microphone with a Sony TCM-S66V recorder. We assumed that all individuals recorded were males, because males are the most vocal sex, and females produce distinctive coos that differ from those of males in various ways (Goodwin 1983, Cramp 1985, Ballintijn and ten Cate

1997a). Variation in the perch-coo of individual Eurasian Collared-Doves (*S. decaocto*) is less than that between individuals (ten Cate 1992), and differences between individuals are consistent for the same adult males over time (Ballintijn and ten Cate 1997b).

Coo assignment.—A "coo" bout consists of a series of sound elements that vary in frequency and in temporal and structural features. In such a bout, we defined a species-specific coo as the smallest stereotypic repetition of similar element sequences. Additional criteria were (1) pauses between coos typically are longer than pauses within coos; (2) the first element of a bout is likely to be the first element of a coo; and (3) the last element of a bout is likely to be the last element of a coo. These criteria were not always applicable simultaneously, e.g. because the bout ended in the middle of a coo, leading to contradicting criteria. However, all dubious coo assignments were resolved after analyses of multiple bouts and multiple individuals per species. One coo in the middle of a bout was chosen for detailed measurements. This is the least-variable part of a bout in *S. decaocto*, for which the perch-coo has been studied extensively (M. R. Ballintijn pers. comm.).

Measurements.—The recordings were digitized at a sample rate of 11 kHz using Canary 1.1 software on a MacIntosh computer. We applied Fast Fourier transformations to create sonagrams for quantitative measurements with a temporal resolution of 1.44 ms and a frequency resolution of 10.87 Hz. First, the number of coos in a bout and the number of elements in a coo were determined. Deviations in general bout structure were marked. Duration was determined for all elements (E1, E2, E3, etc.) and pauses between elements (P1, P2, P3, etc.). Other temporal measure-
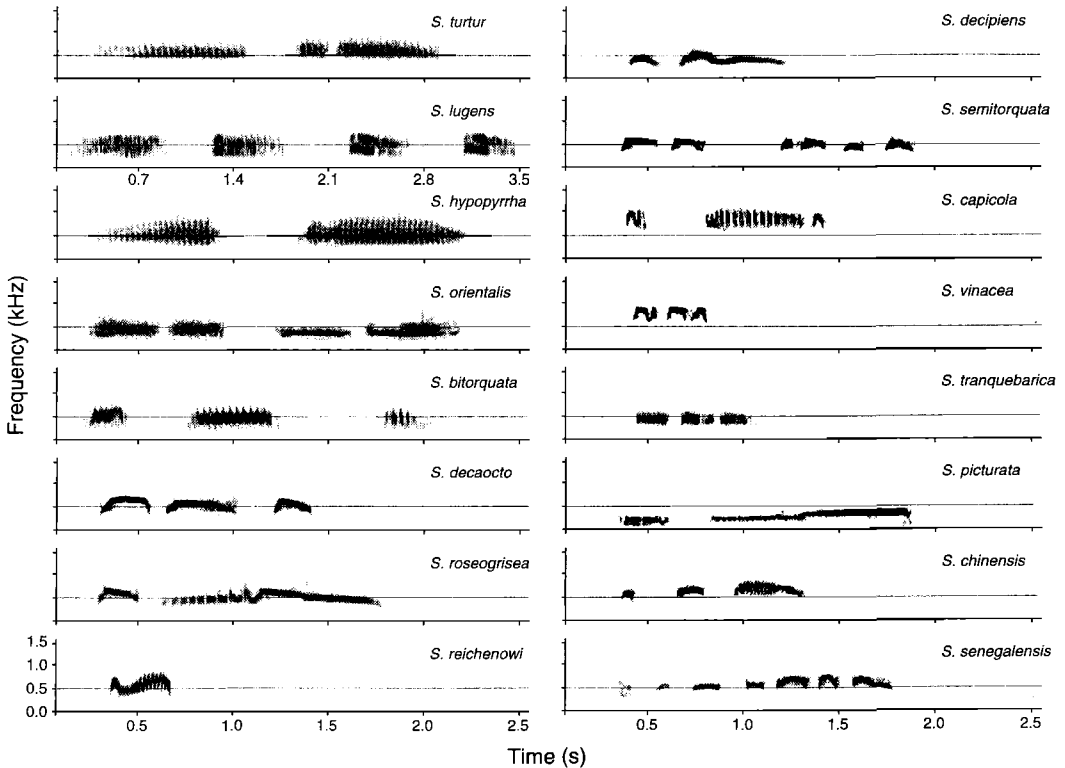
FIG. 2. Sonagrams of an example of one perch-coo for each species. The sonagrams were generated by Fast Fourier Transformations using Canary 1.1 software. The frequency resolution is 10.87 Hz and the temporal resolution is 1.4 ms.

ments were: total coo length (COLE), defined as the duration from the start of the first element (E1) to the end of the final element (EX); coo interval (INT), defined as the duration from the end of EX to the start of the next E1; and sound percentage (SOPE), defined as the summed duration of the separate elements divided by COLE. Frequency measurements included overall peak frequency (PEFR), which is the frequency with the highest amplitude in the coo; maximum frequency (MAFR), which is the highest frequency present in the coo; minimum frequency (MIFR), which is the lowest frequency present; and peak frequencies for the individual elements (PF1, PF2, PF3, etc.). Furthermore, the structure of the elements of a coo was categorized as a "bow," "noise," or "trill" type. A "bow" structure was defined as a relatively tonal element with a gradual increase in frequency in the first half and a gradual decrease in frequency in the second half of the element (see S. decaocto in Fig. 2). A "noise" structure was defined as an irregular pattern of intensity changes in a relatively broad frequency range, which leads to a hoarse sound (S. orientalis in Fig. 2). A "trill" structure was defined as a regular pattern of rapidly alternating phases of high and low amplitude for a relatively broad fre-

quency range (S. turtur in Fig. 2). The absolute amplitude was not used as a parameter because of variation in recording distance and orientation toward the microphone.

Statistical analyses.—Phenetic analyses comprise methods to form groups based upon overall similarity among entities, in contrast to phylogenetic analysis that are based on evolutionary relationships (see Felsenstein 1982, Sokal 1986, de Queiroz and Good 1997). The methods in use for phenetic analyses can be classified into ordination and cluster analysis. Ordination arranges entities in a continuous multidimensional space defined by the measured parameters, and cluster analysis assigns entities to groups (see James and McCulloch 1990). We used both methods in this study.

We applied a canonical discriminant function analysis (DFA) on the acoustic parameters of individuals. These parameters were averages for all the bouts of each individual. The individual measures were used to test whether the individuals could be correctly classified by species. Subsets of acoustic characters were analyzed to determine whether frequency aspects and temporal features classified the species' averages and individual measures equally

TABLE 2.   General description of perch-coos for 66 individuals of 16 species of *Streptopelia*. N = number of individuals recorded; N_r = reduced sample size for measurements of EX for *turtur, lugens,* and *chinensis* and of E1 for *senegalensis*; n = number of bouts analyzed (range 1 to 5 per individual); BL = average bout length; NOEL = average number of elements per coo; structure = categorical description of element structures present. *S. risoria* is the domesticated form of *S. roseogrisea*.

Species	N	N_r	n	BL	NOEL	Structure
S. turtur	5	2	21	4.0	3.4	Trill
S. lugens	4	3	4	5.0	3.7	Noise
S. hypopyrrha	1	1	3	5.7	2.0	Trill
S. orientalis	5	5	16	4.8	4.0	Noise
S. bitorquata	1	1	2	15.5	3.0	Trill
S. decaocto	5	5	25	6.4	3.0	Bow
S. risoria	5	5	21	5.4	2.0	Bow and trill
S. reichenowi	1	1	5	7.4	2.0	Bow and trill[a]
S. decipiens	5	5	17	9.4	3.0	Bow[b]
S. semitorquata	5	5	18	7.0	6.0	Bow
S. capicola	5	5	10	13.6	3.0	Bow and trill
S. vinacea	5	5	20	18.2	3.0	Bow
S. tranquebarica	5	5	22	8.3	3.8	Noise
S. picturata	4	4	8	4.6	2.0	Noise
S. chinensis	5	2	21	3.3	3.4	Bow and trill[c]
S. senegalensis	5	2	16	12.2	6.2	Bow

[a] Coo characteristics show a switch in the bout.
[b] Bout starts with a cry.
[c] Coos produced independently (see text for further explanation).

well. The parameter set used for the DFA consisted of continuous variables that could be measured in all species. Measurements concerning the coo as a whole were incorporated: COLE, INT, SOPE, PEFR, MAFR, and MIFR together with additional measurements on the first and last element of the coo: E1, PF1, EX and PFX. The measurements of other elements were not incorporated because interspecific comparison of an element such as E3 makes no sense if one species usually utters three elements, whereas the other usually utters six elements. Measurements of the first and last elements were incorporated because start and end of the coo are unambiguous across species. We further explored the data set using a principal components analysis (PCA) of the species' averages to reduce the set of 10 measurements into uncorrelated multivariate components. We used ANOVA and post-hoc comparisons to test whether the species from Goodwin's (1983) putative taxonomic groups (turtle-doves, ringed doves, *S. picturata*, and *S. chinensis / S. senegalensis*) differed from one another in these components.

Subsequently, we used cluster analyses for detailed comparison of interspecific acoustic similarity with the similarity-based taxonomic classification of Goodwin (1983). A hierarchical cluster analysis was performed using an average linkage method (UPGMA), based on a dissimilarity matrix, for which we used Euclidean distances (Romesburg 1984). The degree of similarity between perch-coos is represented by the proximity of the horizontal branches in the dendrogram, with the most similar coos closest to one another. The method produces a dendrogram with hierarchical nonoverlapping groups. The magnitude of the distortion of the original similarity relationships by the clustering procedure is reflected in the cophenetic correlation coefficient (Sokal and Rohlf 1962). The parameter set used for cluster analysis consisted of the continuous variables used in the DFA and PCA supplemented by the number of elements in a coo (a multivariate discrete variable) and the binary-coded categorical variables noise, bow, and trill. All parameters were Z-transformed to make them contribute equally to the similarity comparison. Cluster analyses were performed with the total set of 16 species, with the four groups (using group averages generated via species' averages), with only the turtle-dove subset of four species, and with only the ringed dove subset of nine species. All analyses were performed using SPSS / PC+ software.

RESULTS

We gathered recordings for all 16 species (Table 2). The total set of recordings analyzed consisted of 229 bouts from 66 individuals. For 11 of the 16 species, data were obtained for five different individuals. The number of recorded bouts per individual ranged from one to five. Some species were less common in captivity, which led to a lower number of recorded individuals. We recorded only two individuals of *S. roseogrisea* but collected data on five individuals of *S. risoria*, which is the domesticated form

TABLE 3. Temporal and frequency measurements of complete perch-coos ($\bar{x} \pm$ SD). COLE = coo length; INT = interval to start of next coo; SOPE = sound percentage (summed duration of elements divided by COLE); PEFR = peak frequency; MAFR = maximum frequency; MIFR = minimum frequency. See Table 2 for sample sizes. *S. risoria* is the domesticated form of *S. roseogrisea*.

Species	COLE (ms)	INT (ms)	SOPE (%)	PEFR (Hz)	MAFR (Hz)	MIFR (Hz)
S. turtur	2,399 ± 478	643 ± 10	70.8 ± 6.3	579 ± 28.5	767 ± 30.8	334 ± 46.3
S. lugens	3,438 ± 561	616 ± 15	67.8 ± 5.6	463 ± 80.1	638 ± 67.5	227 ± 84.7
S. hypopyrrha	1,986	743	77.4	547	872	283
S. orientalis	2,088 ± 197	334 ± 6	68.1 ± 5.3	462 ± 17.3	681 ± 77.1	241 ± 12.3
S. bitorquata	1,945	861	44.1	494	655	345
S. decaocto	1,202 ± 58	419 ± 14	70.1 ± 3.7	554 ± 32.0	807 ± 32.2	374 ± 32.8
S. risoria	1,616 ± 179	879 ± 18	82.6 ± 5.5	596 ± 24.5	822 ± 17.5	387 ± 42.5
S. reichenowi	373	172	81.5	543	785	306
S. decipiens	660 ± 122	562 ± 9	76.9 ± 5.9	467 ± 31.0	663 ± 46.4	276 ± 49.2
S. semitorquata	1,449 ± 49	358 ± 2	52.6 ± 4.6	489 ± 22.9	694 ± 72.4	315 ± 34.6
S. capicola	884 ± 74	356 ± 2	62.6 ± 3.0	902 ± 62.5	1,142 ± 84.0	602 ± 65.7
S. vinacea	433 ± 31	280 ± 5	75.9 ± 3.3	795 ± 54.0	1,037 ± 56.6	552 ± 26.0
S. tranquebarica	637 ± 116	126 ± 2	75.8 ± 3.8	521 ± 24.2	694 ± 31.0	357 ± 31.3
S. picturata	1,155 ± 409	591 ± 15	80.4 ± 6.4	367 ± 48.3	507 ± 63.3	207 ± 10.0
S. chinensis	1,141 ± 262	2,168 ± 1,700	70.2 ± 9.8	715 ± 53.1	955 ± 48.2	446 ± 47.6
S. senegalensis	1,153 ± 92	1,438 ± 590	65.3 ± 7.5	621 ± 19.0	868 ± 46.7	341 ± 42.5

of this species. Because the vocal distinctions between *S. roseogrisea* and *S. risoria* were insignificant, we used the set of *S. risoria* recordings for further analyses. For three species we obtained data for one individual only. Because the data for the other species indicated a smaller degree of intraspecific compared with interspecific variation, we included these data to provide a complete overview of all species. Nevertheless, inferences concerning these species should be considered tentative.

Description of coo characteristics.—The general perch-coo characteristics of the 16 *Streptopelia* species are summarized in Table 2. Four species produced two different element types within their coo: *S. risoria*, *S. reichenowi*, *S. capicola*, and *S. chinensis*; all produced bow and trill type elements. Peculiarities in bout structure were found for *S. reichenowi* and *S. decipiens*. *Streptopelia reichenowi* produced predominantly two-element coos but switched to one-element coos at the end of the bout; *S. decipiens* started each perch-coo bout with a cry from its species-specific repertoire (also used in other contexts). Both species produced consecutive elements that occasionally were connected by a low-fre-

TABLE 4. Temporal measurements of perch-coos of 16 species of *Streptopelia*. Durations of elements are coded as E1 to E7, and durations of pauses are coded as P1 to P6 (values are $\bar{x} \pm$ SD in ms). See Table 2 for sample sizes. *S. risoria* is the domesticated form of *S. roseogrisea*.

Species	E1	P1	E2	P2	E3	P3
S. turtur	674 ± 182	320 ± 60	352 ± 126	314 ± 178	505 ± 28	217 ± 143
S. lugens	779 ± 62	352 ± 33	627 ± 55	481 ± 121	592 ± 104	430 ± 12
S. hypopyrrha	688	437	849	—	—	—
S. orientalis	248 ± 160	180 ± 59	392 ± 140	257 ± 88	333 ± 14	237 ± 102
S. bitorquata	216	379	477	702	165	—
S. decaocto	248 ± 25	79 ± 19	403 ± 27	286 ± 47	192 ± 59	—
S. risoria	215 ± 67	276 ± 88	1,123 ± 171	—	—	—
S. reichenowi	71	63	233	—	—	—
S. decipiens	143 ± 31	98 ± 13	148 ± 40	53 ± 35	226 ± 79	—
S. semitorquata	113 ± 43	66 ± 31	150 ± 44	176 ± 124	94 ± 20	88 ± 26
S. capicola	97 ± 19	272 ± 42	399 ± 49	65 ± 32	57 ± 13	—
S. vinacea	137 ± 19	63 ± 4	101 ± 15	30 ± 7	91 ± 20	—
S. tranquebarica	159 ± 25	66 ± 10	122 ± 25	47 ± 25	80 ± 88	45 ± 1
S. picturata	142 ± 41	252 ± 105	768 ± 266	—	—	—
S. chinensis	73 ± 13	152 ± 72	186 ± 22	139 ± 35	485 ± 72	263 ± 53
S. senegalensis	92 ± 5	48 ± 49	109 ± 28	181 ± 36	151 ± 68	73 ± 18

quency sound. We based their temporal and frequency measurements on the separate elements to keep the measurements compatible with other bouts of the same or other conspecifics. An overview of the species-typical perch-coos is presented in Figure 2, and detailed measurements of temporal and spectral structure of the coos are listed in Table 3. Measurements of the duration of individual elements are listed in Table 4, and peak frequencies for individual elements are in Table 5. For all measurements, we calculated the individual averages first, which were then used to calculate averages and standard deviations for each species

Discriminant and principal components analyses.—The DFA using the individual averages of the 10 measurements led to a 100% correct classification of the individuals into species. The first of the five discriminant functions (DF1) accounted for 64.8% of the variation, and the second (DF2) accounted for 20.4% of the variation. Classification based solely on the five frequency parameters led to 64.3% correct assignment, whereas classification based on the five temporal features led to 94.6% correct assignment. Some individuals showed variation in the number of elements. In particular, some *S. senegalensis* and *S. chinensis* lacked the first or last element, respectively. This led to missing values, reducing the sample size to 56 individuals.

The results of the PCA on the 10 measurements are summarized in Table 6. Four components with eigenvalues >1 were extracted from the data set. After varimax rotation to maximize the correlation among parameters,

the first principal component (PC1) accounted for 53.3% of the variance, representing mostly the five frequency measures. The temporal features were represented in three uncorrelated components; PC2 was determined mostly by the duration measurements (COLE, E1, and to a lesser degree EX), PC3 mostly by the duration of elements relative to the duration of the pauses between them (SOPE and EX), and PC4 mostly by intervals between coos (INT). PC2, PC3, and PC4 accounted for an additional 17.3, 14.2, and 10.2% of the variance. The 16 species are depicted in two bivariate plots that show their respective values for PC1 and PC2 (Fig. 3), and PC3 and PC4 (Fig. 4). We used ANOVA to test whether the taxonomic groups differed in any of the four components. The groups differed for PC2 ($P = 0.0014$) and PC4 ($P = 0.0011$), and both were significant after Bonferroni correction. The turtle-dove group differed significantly ($P < 0.05$) from the ringed dove and the *S. chinensis/S. senegalensis* groups for PC2 (Tukey's post-hoc comparisons). The *chinensis/senegalensis* group differed significantly ($P < 0.05$) from the turtle-dove and ringed dove groups for PC4. The *S. picturata* group consists of only one species, which makes statistical testing impossible; however, *S. picturata* was well outside the range of all other species for PC1.

Cluster analysis.—The cluster procedure led to the dendrogram depicted in Figure 5A. Some of the species that are closely related according to Goodwin (1983) are clustered as nearest neighbors (*S. capicola* and *S. vinacea*).

TABLE 4.   Extended.

E4	P4	E5	P5	E6	P6	E7
395 ± 41	—	—	—	—	—	—
469 ± 30	—	—	—	—	—	—
—	—	—	—	—	—	—
441 ± 83	—	—	—	—	—	—
—	—	—	—	—	—	—
—	—	—	—	—	—	—
—	—	—	—	—	—	—
—	—	—	—	—	—	—
105 ± 25	267 ± 130	155 ± 58	91 ± 26	144 ± 49	—	—
—	—	—	—	—	—	—
141 ± 19	—	—	—	—	—	—
—	—	—	—	—	—	—
188 ± 25	—	—	—	—	—	—
151 ± 56	39 ± 24	149 ± 26	73 ± 13	112 ± 21	79 ± 30	101 ± 25

TABLE 5. Frequency measurements of perch-coos of 16 species of *Streptopelia*. Peak frequencies of elements are coded as PF1 to PF7 ($\bar{x} \pm$ SD in Hz). See Table 2 for sample sizes. *S. risoria* is the domesticated form of *S. roseogrisea*.

Species	PF1	PF2	PF3	PF4	PF5	PF6	PF7
S. turtur	542 ± 12.8	576 ± 21.8	582 ± 26.1	560 ± 38.0	—	—	—
S. lugens	431 ± 38.2	424 ± 39.2	464 ± 80.1	500 ± 107.6	—	—	—
S. hypopyrrha	547	540	—	—	—	—	—
S. orientalis	480 ± 30.5	478 ± 22.2	421 ± 59.5	451 ± 21.5	—	—	—
S. bitorquata	494	489	494 ± 7.7	—	—	—	—
S. decaocto	579 ± 39.5	541 ± 29.6	530 ± 38.4	—	—	—	—
S. risoria	607 ± 30.2	591 ± 16.5	—	—	—	—	—
S. reichenowi	585	543	—	—	—	—	—
S. decipiens	482 ± 56.7	460 ± 39.7	468 ± 43.5	—	—	—	—
S. semitorquata	489 ± 17.2	500 ± 31.3	477 ± 22.7	482 ± 32.5	472 ± 54.6	472 ± 72.0	—
S. capicola	911 ± 56.1	881 ± 70.0	814 ± 107.5	—	—	—	—
S. vinacea	819 ± 62.5	808 ± 57.7	775 ± 41.3	—	—	—	—
S. tranquebarica	525 ± 24.6	522 ± 24.4	512 ± 32.9	515 ± 28.5	—	—	—
S. picturata	266 ± 28.8	368 ± 48.3	—	—	—	—	—
S. chinensis	638 ± 78.5	719 ± 58.2	689 ± 48.9	678 ± 36.5	—	—	—
S. senegalensis	522 ± 46.1	456 ± 89.7	577 ± 61.0	615 ± 32.9	632 ± 19.5	635 ± 23.6	595 ± 47.2

However, most of the suggested intragroup relationships, and even the intergroup segregation, are absent in the dendrogram based on acoustic similarities. The dendrogram of group averages shows ringed doves and the *S. chilensis* / *S. senegalensis* group as nearest neighbors, which are subsequently more similar to turtle-doves than to *S. picturata* (Fig. 5B). Cluster analyses based on subsets of parameters (either frequency or temporal features) led to identical linkage patterns. The within-group similarities for turtle-doves and ringed doves led to the dendrograms in Figures 5C and D. Cophenetic correlation coefficients were calculated for all four dendrograms. This is an index for how accurately the original data in the dissimilarity matrix is represented by the dendrogram. A co-

efficient of 0.8 or higher is considered to indicate a useful tree, resembling the real dissimilarities (Romesburg 1984). The coefficients for the dendrograms of all 16 species, of the four groups, of the four turtle-dove species, and of the nine ringed dove species were 0.60, 0.74, 0.93, and 0.94, respectively.

DISCUSSION

The 16 species of doves in the genus *Streptopelia*, some of which are very similar in plumage pattern, all produce distinctive species-specific perch-coos. All individuals were correctly classified into species in a DFA, which means that intraspecific variation was limited relative to interspecific variation for the total

TABLE 6. Factor loadings of the 10 acoustic parameters on the four principal components after varimax rotation to maximize the correlation among the parameters. Eigenvalues and amount of variance explained by the respective components are given at bottom of table.

| Acoustic parameter	PC1	PC2	PC3	PC4
Highest frequency	0.968	−0.104	0.015	0.113
Lowest frequency	0.929	−0.245	−0.148	0.003
Overall peak frequency	0.977	−0.153	−0.066	0.097
Peak frequency of element 1	0.972	−0.126	−0.068	−0.121
Peak frequency of element 9	0.985	−0.100	−0.032	0.090
Total coo length	−0.267	0.929	−0.142	0.110
Duration of element 1	−0.097	0.936	0.147	−0.095
Duration of element 9	−0.263	0.467	0.726	0.141
Coo interval	0.093	0.009	−0.031	0.989
Sound percentage	0.016	−0.155	0.946	−0.112
Eigenvalue	5.328	1.728	1.421	1.024
% Variance explained	53.3	17.3	14.2	10.2
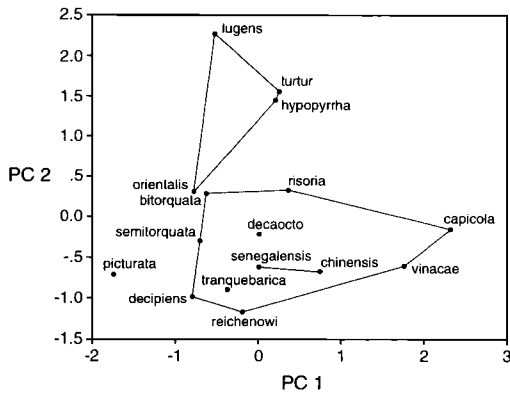
FIG. 3. Plot of the 16 species of *Streptopelia* doves in two-dimensional space defined by two principal components. PC1 is determined mostly by the five frequency measurements, and PC2 mostly by duration measurements (COLE, E1 and to a lesser degree EX). See Table 6 for factor loadings. Polygons connect and enclose all species within a taxonomic group.

set of acoustic parameters. The clustering of species using the acoustic data set showed little congruence with the taxonomic clustering of Goodwin (1983), which is based on morphological characteristics and geographic distribution. This indicates that evolutionary differentiation in plumage pattern does not necessarily coincide with differentiation in acoustic characteristics. However, our analysis does not con-
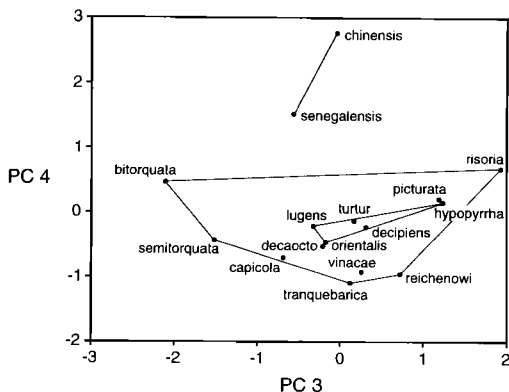
FIG. 4. Plot of the 16 *Streptopelia* in two-dimensional space defined by two principal components. PC3 is determined mostly by the duration of elements relative to the duration of the pauses between them (SOPE and EX) and PC4 by intervals between coos (INT). See Table 6 for factor loadings. Polygons connect and enclose all species within a taxonomic group.
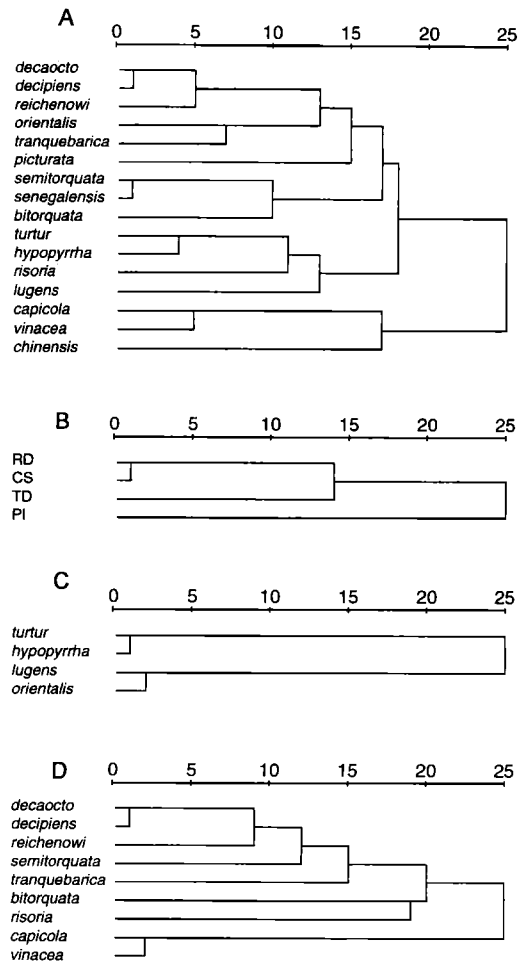
FIG. 5. Dendrograms created by hierarchical cluster analyses of the four *Streptopelia* groups using the UPGMA average-linkage method, based on Euclidian distances. Shown are (A) all 16 species; (B) group averages; (C) turtle-dove group; and (D) ringed dove group. RD = ringed dove group, CS = *S. chinensis/S. senegalensis* group, TD = turtle-dove group, and PI = *S. picturata*.

tradict the subdivision into four taxonomic groups. Two of the four groups (turtle-doves and *chinensis/senegalensis*) differed significantly from the other groups in one of the components of the PCA (PC2 and PC4, respectively). The cluster analysis with the turtle-dove subset of four species (Fig. 5C), and with the ringed dove subset of nine species (Fig. 5D), led to dendrograms with high cophenetic correlation coefficients, which indicates that they adequately reflect similarities among species. This

makes them suitable for future evaluation of evolutionary transitions using a phylogeny based on an independent data set. Such an analysis may shed light on intriguing situations such as in the turtle-dove group. Here, *S. turtur* and *S. orientalis* are closely matched in appearance, as are *S. hypopyrrha* and *S. lugens.* Nevertheless, acoustically, *S. turtur* is much more similar to *S. hypopyrrha,* and *S. orientalis* is much more similar to *S. lugens.*

Vocal differentiation among *Streptopelia* doves concerns temporal features in particular. The success with which we correctly assigned individuals into species was dramatically reduced, only 64.3% correct, when we used the set of frequency parameters only. If we used the set of temporal features only, the analysis still correctly classified most (94.6%) of the species. The PCA led to one component mostly representing frequency measures and three uncorrelated components mostly representing temporal measurements. The bivariate plots of the four principal components clearly showed the parameters for which the groups differed, and they indicated that each group can be characterized by distinctive temporal aspects. The DFA and PCA results may be due to anatomical restrictions in producing variation in frequency range or frequency modulation patterns (Warner 1972, Ballintijn et al. 1995). The relatively simple syringeal morphology of doves may be better suited to varying the rate and pattern of airflow (Gaunt 1988, ten Cate and Ballintijn 1996). The neural basis for such variation in vocal control might be less conservative than syringeal morphology. The acoustic parameters that best discriminate among the *Streptopelia* doves are in line with a study of quail (*Coturnix*) vocalizations in which temporal parameters also yielded the best discrimination between species (Collins and Goldsmith 1998). McCracken and Sheldon (1997) concluded from their comparative study of heron vocalizations that the number of syllables, syllable structure, and fundamental frequency were the most phylogenetically informative parameters, whereas frequency measurements concerning higher ranges were more subject to habitat-dependent convergence.

The smaller species (*S. vinacea* and *S. capicola*) used higher frequencies, and the larger *S. picturata* used relatively low ones (Tables 3 and 5). This agrees with other studies on the relationship between body size and vocalization frequency (Wallschläger 1980, Ryan and Brenowitz 1985, Tubaro and Mahler 1998). On the other hand, *S. tranquebarica,* which is the smallest species (see Table 1), used a surprisingly low frequency range. However, the range of frequencies used by all 16 species was relatively small, especially compared with songbirds for which frequency-dependent attenuation may cause differential selection pressures in different habitats (see Morton 1975, Hunter and Krebs 1979, Wiley and Richards 1982, Badyaev and Leaf 1997). Whether the variation in temporal and frequency measurements of *Streptopelia* vocalizations is meaningful to the doves themselves awaits investigations based on playback experiments in a natural context (see Slabbekoorn and ten Cate 1996, 1997, 1999).

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