BEHAVIOR AND TAXONOMIC STATUS OF GRAYSON'S DOVE[1]

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ABSTRACT.—Grayson's Dove (*Zenaida graysoni*) is extinct in the wild but is still found in aviaries. It has been treated variously as a full species or as a subspecies of the Mourning Dove (*Z. macroura*). The two taxa differ in shape, color, and color pattern of the rectrices and can be readily distinguished by characteristics of museum skins. They also differ in vocalizations and visual displays. Previous studies described differences in serology. The two taxa interbreed only rarely in captivity. It is proposed that *Z. graysoni* be recognized as a full species, closely related to *Z. macroura*. *Received 8 November 1982, accepted 8 July 1983.*

THE Socorro or Grayson's Dove (*Zenaida graysoni*) is probably extinct in the wild (Jehl and Parkes 1982). It was endemic to Socorro Island, the largest member of the Revillagigedo Archipelago, 320 km southwest of the tip of the Baja California peninsula, and has been treated variously as a full species (Friedmann et al. 1950, Blake 1953, Peterson and Chalif 1973, Ridgway 1916) or a geographic race of the Mourning Dove (*Z. macroura*) (Goodwin 1967). Short (*in* Mayr and Short 1970) considers it closely related to and possibly conspecific with the Eared Dove (*Z. auriculata*) and Mourning Dove. We describe herein the vocalizations and displays of captive Grayson's Doves and compare them with those of wild Mourning Doves. We also discuss some external characters in the two species and comment on the taxonomic status of *Z. graysoni* and its relationship to *Z. auriculata*.

METHODS AND MATERIALS

We studied the behavior of 5 *Z. graysoni* in indoor cages (3 males, 2 females) and 14 in outdoor aviaries. Free-living *Z. macroura* were studied in Los Angeles, Lompoc, Sonoma, and San Francisco, California. Vocalizations were taped on Nagra E and Nagra 4.2 tape recorders and analyzed on the Kay Electric Sound Spectrograph (Sonagraph) Machine (Model 7029A) with a 300 Hz bandwidth filter. Measurements of frequency in kHz were made from wide-band sound spectrograms. The Kay Electric amplitude display attachment (Model 6076C) was used to analyze amplitude modulations within some of the vocalizations.

We measured various characters from study skins after the methods outlined by Baldwin et al. (1931). The characters, followed by their abbreviations in parentheses, are: wing length (WL), length of rectrix 1 (TL1), length of rectrix 2 (TL2), length of rectrix 7 (TL7), difference between first- and second-longest rectrices (TL1-2), width of rectrix seven at widest point (TW), length of longest undertail covert (CL), distance from tip of longest undertail covert to tip of longest rectrix (CT-1), chord of exposed culmen (CULEX), bill length from edge of nostril to tip of culmen (CULN), culmen width from base of exposed culmen (CULW), and tarsus length (TRL).

The following ratios were calculated from the above measurements: WL/TL1, WL/CULN, WL/TRL, TL1/CULN, TL1/TRL, TL1/CL, TL2/CL, TL1/TW, TL1/TL2, CULN/TRL, CULN/CULW, TL1/TL7, TL2/TL7, TL7/CL.

Analyses were performed on the San Francisco State University Data Center's CYBER 174 computer using the Statistical Package for the Social Sciences (SPSS) (Nie et al. 1975).

All mensural characters were log transformed and subjected to a direct discriminant function analysis. All SPSS default criteria were utilized. Worn or damaged specimens were omitted from appropriate analyses so that sample sizes differed depending upon variables utilized.

Materials representing seven subspecies of *Z. auriculata* were pooled in our analyses, as we were pri-

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[1] The Grayson's Dove is also known as the Socorro Dove (see Jehl, J. R., Jr., and K. C. Parkes, 1983. "Replacements" of landbird species on Socorro Island, Mexico. Auk 100: 551-559).

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TABLE 1. Descriptive statistics on duration and other features of advertising coos and their component syllables. Syllables are labelled as in Fig. 2C, D.

	Z. graysoni				*Z. macroura*				Significance level
	n	$\bar{x}$	SD	Range	*n*	$\bar{x}$	SD	Range	
Syllables[a]									
A	10	1.06	0.10	0.98-1.13	10	1.12	0.10	1.05-1.20	0.165
B	10	0.67	0.10	0.60-0.74	10	0.67	0.08	0.62-0.73	0.836
C	10	0.30	0.07	0.25-0.34	10	0.41	0.13	0.32-0.50	0.026
D	10	0.87	0.03	0.85-0.89	10	0.42	0.09	0.35-0.48	0.000
E	10	0.97	0.02	0.96-0.99	—	—	—	—	—
Intersyllable intervals[a]									
A-B	10	0.24	0.01	0.22-0.25	10	0.25	0.06	0.20-0.29	0.603
B-C	10	0.37	0.05	0.33-0.40	10	0.29	0.08	0.24-0.35	0.024
C-D	10	0.17	0.03	0.15-0.20	10	0.30	0.08	0.24-0.36	0.001
D-E	10	0.59	0.06	0.55-0.63	—	—	—	—	—
Total duration[b]	10	5.24	0.25	5.06-5.42	10	3.46	0.30	3.25-3.67	0.000
Frequency[b]									
High	10	600	32.3	577-623	9	723	31.7	699-747	0.000
Low	10	356	30.2	335-378	9	438	0	—	0.000

[a] Duration in seconds.
[b] Frequency in Hz.

marily interested in the relationship of *Z. graysoni* to *Z. macroura*. The subspecies of *Z. macroura* were not pooled, because two subspecies, *Z. m. macroura* and *Z. m. clarionensis*, exhibited morphological characters reminiscent of *Z. graysoni*. We felt it necessary to distinguish between characters indicating species distinctness versus characters typical of birds adapted for island living.

Due to small sample sizes in some taxa, sexes were pooled in all taxa. Because most groups show some amount of sexual dimorphism, all measurements were then subjected to a one-way analysis of variance to determine whether or not this would obscure the results. There was greater variation between than within taxa tested ($P \leq 0.001$) for all variables. Results of discriminant analysis performed only on males were comparable to those only for females and for both sexes grouped. For these reasons we feel justified in lumping the sexes for all mensural analyses herein reported. Specimens examined are listed in the Appendix.

RESULTS

VOCALIZATIONS

Gifford (1927) did not find any significant differences between calls of *Z. graysoni* and *Z. macroura*. Goodwin (1967) interpreted Gifford's statement as meaning that the calls of the two taxa do not differ. This is contrary to our experience, as the following analyses will show.

The vocal repertoire of *Zenaida* doves consists of about six distinct utterances. These vocalizations appear to be discrete rather than graded. The first of these calls treated herein, the advertising coo (= perch coo of some other investigators), is functionally equivalent to advertising song in passerines. Jackson and Baskett (1964) noted that unmated males gave this call much more frequently than mated males. These calls are also given during aggressive encounters. The second call, the nest coo, is usually given by the male from the nest or the site where the nest is most likely to be built. The third call, the greeting call, is usually given by the male on the approach of his mate after a period of separation. The fourth call, the nest defence call, may be given by both sexes while trying to drive away an intruder from the nest. The fifth call, the alarm call, is given by either sex during fearful situations. The last call, the "growl," appears to be given mostly by females while calling their mates to the nest. All the above calls were sometimes given in some other contexts, as discussed below.

Advertising coo.—This vocalization in *Zenaida* doves is homologous to the bow-coo of other columbiforms. Goodwin (1967) describes the advertising coo of *Z. macroura* as a disyllabic coo followed by two or three louder coos, or "Coo-oo, OO, OO, OO!" We noted that some

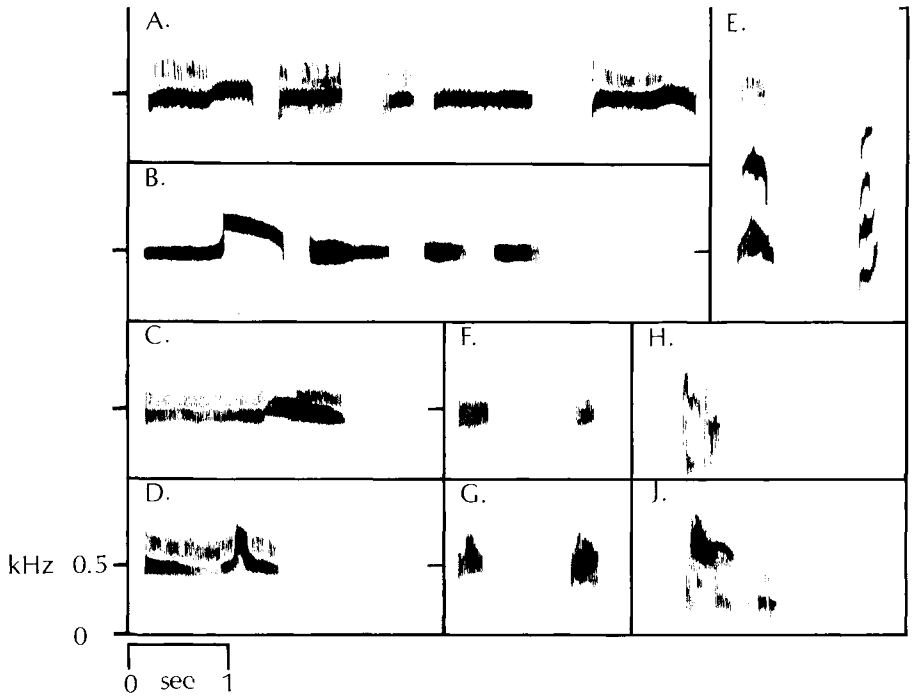

Fig. 1. Ink tracings of some dove vocalizations. A. Advertising coo of Grayson's Dove. B. Advertising coo of Mourning Dove. C. Nest coo of Grayson's Dove. D. Nest coo of Mourning Dove. E. Nest-defence call of Grayson's Dove. F. Greeting call of Grayson's Dove. G. Greeting call of Mourning Dove. H. Alarm call of Grayson's Dove. J. Alarm call of Mourning Dove.

individuals of this species would add a fourth coo to the dissyllabic introduction. The advertising coo of Z. *graysoni* begins with a disyllabic coo, is followed by three single coos, and ends with another disyllabic coo, or "Coo-oo, OO,OO,OO, Coo-oo!" This vocalization is longer in duration than that of Z. *macroura* (5.24 s vs. 3.46 s, Table 1).

The duration of individual syllables and the intervals between them provide rhythms, which may function in species recognition. There are no differences in the durations of syllables A and B in the two taxa. Syllable C, however, is slightly longer in the Mourning Dove (Table 1, two-tailed t, $P \leq 0.026$). Syllable D is longer in Grayson's Dove. Syllable E is rarely heard in Z. *macroura* so that a comparison is not possible.

There are no differences in the intervals of silence between syllables A and B in the two taxa. The interval between syllables B and C, however, is slightly longer in Z. *graysoni* (Table 1). Conversely, the interval between elements C and D is longer in Z. *macroura* ($P \leq 0.001$). Both highest and lowest frequencies of the advertising call are higher in the Mourning Dove (Table 1).

There are also differences in frequency and amplitude modulation in calls of the two species. Syllable A in the Mourning Dove's call rises noticeably in frequency but does not change appreciably in amplitude (Figs. 1, 2). Syllable A in the Grayson's call changes only slightly in frequency but rises noticeably in amplitude about two-thirds of the way into the call. Elements B, C, and D in the Mourning Dove's call begin at a high amplitude and descend to a lower amplitude. Amplitude change in elements B and D are less noticeable in the call of Grayson's Dove. Element E in the Grayson's call begins with a small rise in amplitude, descends slightly, then rises again. Disyllabic elements (element A) in the Mourning Dove's calls are due to frequency modulation. Disyllabic elements in the Grayson's Dove's call (elements A and E) are due mostly to amplitude

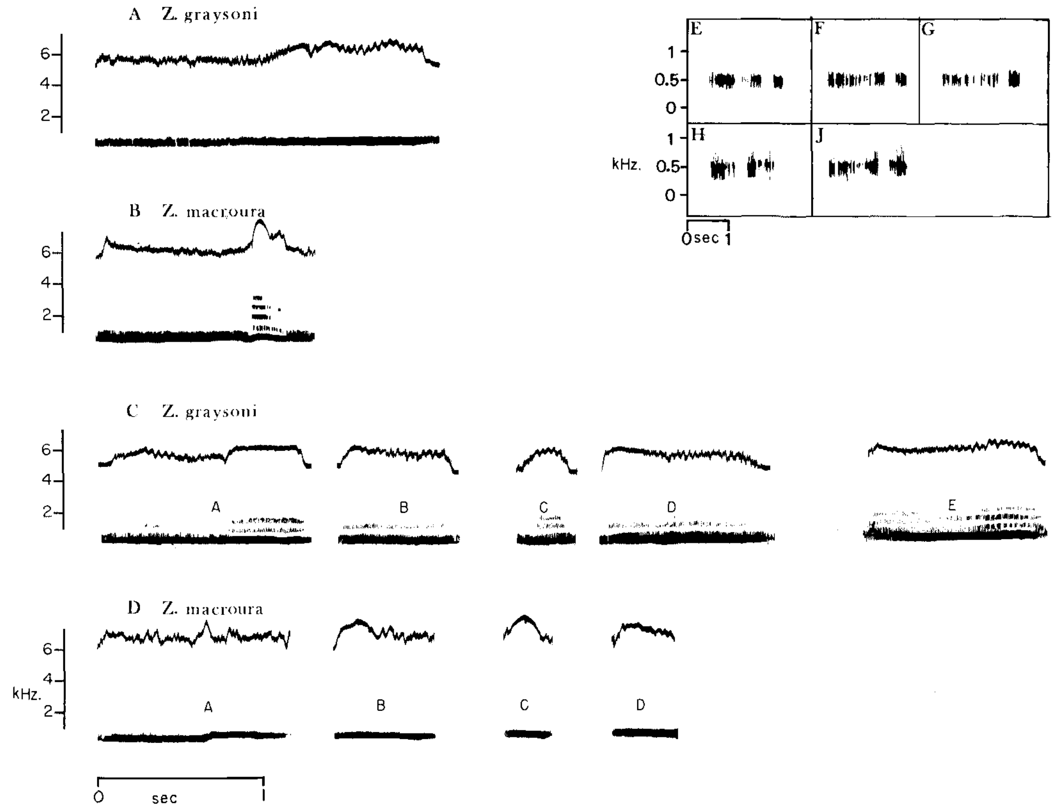

Fig. 2. Ink tracings of some dove vocalizations, including displays of amplitude modulations. A. Nest coo of Grayson's Dove. B. Nest coo of Mourning Dove. Note difference in amplitude modulation between this and the homologous call in Grayson's Dove. C. Advertising coo of Grayson's Dove. D. Advertising coo of Mourning Dove. E to G in insert are calls of female Grayson's Doves while sitting on the nest. H to J were recorded while both members of a pair were foraging together. It was not clear which sex produced the calls.

modulation. There are apparent differences in harmonic complexity between calls of the two taxa (Fig. 2). These may not be real but may reflect recording distances. Advertising coos of Mourning Doves were made in the field, whereas all other recordings were from captives in the laboratory. In sum, advertising calls of the two taxa differ in duration, rhythm, frequency and tonal characteristics.

Nest coo.—Goodwin (1967) describes the nest-coo of the Mourning Dove as a fairly loud "Coo-oo!" The nest coo of the Grayson's Dove is longer in duration than that of the Mourning Dove [1.92 ± 0.10 s ($n = 10$) vs. 1.12 ± 0.03 s ($n = 10$)]. Amplitude rises in the last third of the Grayson's Dove's call but not as dramatically as in that of the Mourning Dove (Fig. 2). Frequency modulation, notably in the last third of the call, is more dramatic in the Mourning Dove (Fig. 1). The Mourning Dove's call is delivered at a higher frequency than that of Grayson's Dove: mean of highest frequency in the nest-coo of the Mourning Dove is 734 ± 33 Hz ($n = 10$) versus 562 ± 0 ($n = 10$) in that of the Grayson's Dove. Lowest frequency in the nest-coo of the Mourning Dove is 403 ± 10 Hz ($n = 10$) versus 372 ± 10 Hz ($n = 10$) in that of the Grayson's Dove.

Greeting call.—The greeting call of *Z. macroura* sounds like a soft "ork." We recorded three "ork" calls, which lasted 0.26, 0.26, and 0.28 s. We recorded six "ork" calls from a *Z. graysoni*, which ranged from 0.15 to 0.56 s ($\bar{x} = 0.28$ s). The fundamental frequency of the Mourning Dove's "ork" ranges from 375 to 750 Hz ($\bar{x} = 562$ Hz). The fundamental frequency of the Grayson's Dove's call ranges from 312 to 625 Hz ($\bar{x} = 468$ Hz) (Fig. 1). The Mourning

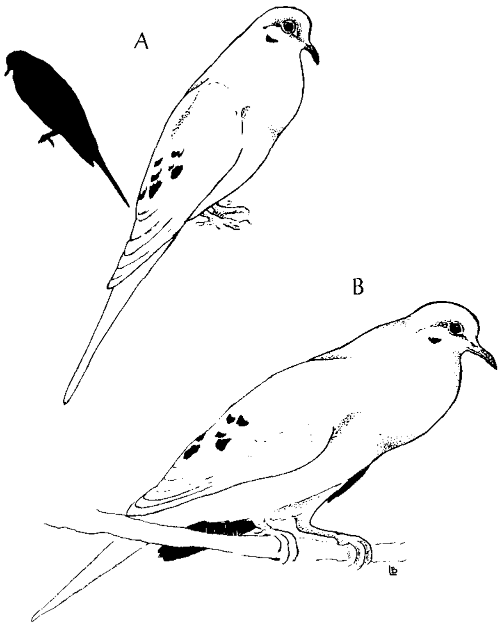

Fig. 3. A. Two advertising-coo postures of Mourning Dove. B. Advertising-coo posture of Grayson's Dove. Drawings were traced from photographs.

Dove's calls are thus delivered at a frequency higher than those of the Grayson's Dove. This same call may be performed by both sexes in both species after copulation (Craig 1911, Whitman 1919, this study), in which case the bill is held wide open. Craig (1911) noted that this is the only call performed with the bill open.

Nest defence.—A Grayson's Dove of either sex disturbed on the nest would beat the investigator's hand with a wing. These "attacks" were accompanied by two kinds of "Rooo" sounds (Fig. 1), one with a fundamental frequency at about 500 Hz and a second with a fundamental frequency at about 312 Hz. Both call types are harmonically rich. We could not elicit similar displays from female Mourning Doves.

Alarm call.—By chasing single females of Grayson's and Mourning doves off the nest, we were able to record single alarm calls of each species as they were leaving (Fig. 1). Under these circumstances the calls sounded like "Rooo-oo!" The call of the Mourning Dove lasted about 0.78 s and that of the Grayson's Dove 0.32 s. The "Rooo" portion ranges from 500 to 750 Hz in the calls of both species. The "oo" portion that follows ranges from about 125 to 312 Hz in the Mourning Dove's calls.

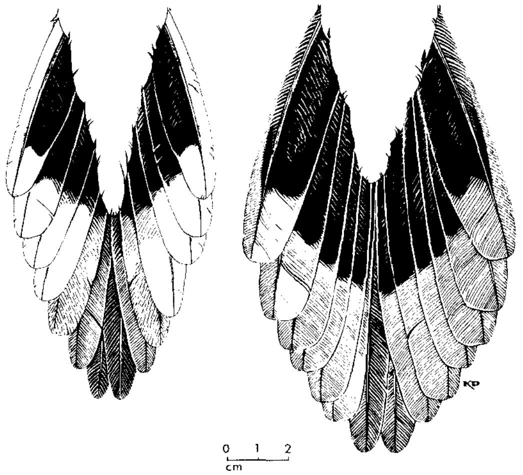

Fig. 4. Tails of Mourning Dove (left) and Grayson's Dove (right).

Female calls.—This call in Grayson's Dove sounded phonetically like "oohr-oor" (Fig. 2: F, G), or "ohr-ohr-ohr" (Fig. 2: E, H). These calls appear to consist of modified greeting calls (compare with Fig. 1: F). Five calls ranged in duration from 1.37 s to 1.68 s ($\bar{x} = 1.59$ s). Highest frequency of five calls ranged from 625 to 750 Hz ($\bar{x} = 650$ Hz). Lowest frequency of five calls ranged from 312 to 375 Hz ($\bar{x} = 343$ Hz).

These calls were given periodically by an incubating female. Sometimes her calls were followed by the male approaching and nest exchange. On one occasion it appeared that both members of a pair uttered this call as they were foraging together and wing-flicking rapidly. Calls H and J (Fig. 2) appeared to be from the male during such a foraging bout, although we were never sure.

This call is similar in structure and function and may be "homologous" to the "growl" described for White-crowned Pigeons (*Columba leucocephala*) (Wiley and Wiley 1979).

VISUAL DISPLAYS

Advertising and courtship.—The postures assumed when birds give the advertising coo or during courtship are similar. With the exception of the White-winged Dove (*Zenaida asiatica*), members of the genus *Zenaida* do not have a bowing display during courtship (Goodwin 1967). Males of both Grayson's and Mourning doves chase ("drive") females, then stop and

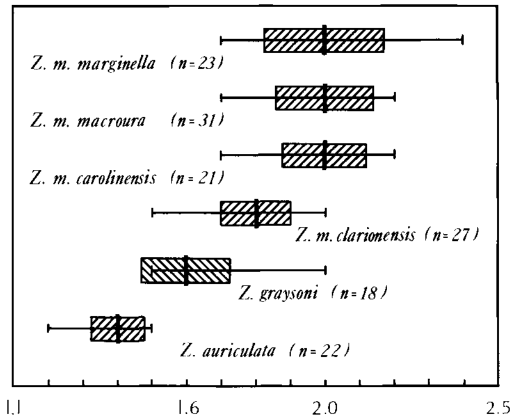

Fig. 5. Index of tail graduation expressed as ratio of rectrix one to seven in six taxa of *Zenaida* doves. Horizontal line represents the range, vertical line the arithmetic mean, with one standard deviation on each side of the mean represented by cross-hatched bars.

utter the advertising coo with the neck swollen and head held erect but at an angle slightly below the vertical (Fig. 3). Our visual impression, borne out by photographs, is that *Z. grayson*i holds its head a little lower than *Z. macroura* when performing this display. The bill in *Z. macroura* is also pointed down more than that in *Z. grayson*i during this display. The tail in *Z. grayson*i is held more horizontally than in *Z. macroura*. The wings may be slightly spread and drooped in both taxa during cooing.

There are differences also in the driving portion of this display in the two taxa. At the beginning of the drive, a male Grayson's Dove gives a series of hops. This soon passes into running as he chases the fleeing female. The male may have his wings extended for balance as he chases her. The male Mourning Dove also begins the drive with a series of hops. This passes into a short run, which develops into exaggerated, loud, clapping flight as he pursues her on the ground. The difference in behavior between the two doves may be a result of differences in hind-limb anatomy. *Zenaida grayson*i is longer-legged (see below) and is well adapted for running on the ground; *Z. macroura* is shorter-legged and is apparently not adapted for running locomotion, and thus it flies at the end of a drive.

Nest showing display.—This display is usually conducted at the nest site or potential nest site. It is usually performed by the male and functions to call the female to him or to the nest or nest site. Crouched on the chosen site, the male Mourning Dove nest-coos with wings twitching rapidly up and down. The head is lowered with each coo, and the tail may be raised to a 45° angle. The tail is spread just enough to show the white tips as the male utters the first note, then is closed until the next call (Craig 1911). Tail spreading is sometimes absent in this display (Whitman 1919). At highest intensity this display in *Z. grayson*i is performed with tail fanned open. The tail is spread even more as the male utters the first coo note; then it is closed slightly. The tail is not shut completely between coos as in *Z. macroura*; otherwise, the display is similar to that of *Z. macroura*. At lower intensities, tail movements are similar to those described for the Mourning Dove (Craig 1911), or the tail is not opened at all.

Jackson and Baskett (1964) quantified the frequency at which this display is given in Mourning Doves. They found that males displayed most while selecting a nest site or during nest building, after which nest calling may continue but at a greatly decreased frequency.

MORPHOLOGICAL DIFFERENCES

We follow Aldrich and Duvall (1958) in recognizing only four subspecies of *Z. macroura* for the United States and Mexico. A long-winged, dark population, *Z. m. carolinensis*, breeds in the eastern United States and southern Ontario. A long-winged, pale population, *Z. m. marginella*, breeds in the western United States, southwestern Canada, and parts of Mexico. The nominate, *Z. m. macroura*, is short-winged and dark and breeds in the West Indies and Florida Keys. Finally, a dark, large-footed, long-billed form, *Z. m. clarionensis*, is endemic to Clarion Island of the Revillagigedo Archipelago. Mourning Doves are known to migrate to, but not breed on, the Tres Marias Islands (Aldrich and Duvall 1958, Grant and Mc T. Cowan 1964), so we follow these authors in not recognizing the validity of the trinomial *Z. m. tresmariae*.

Color and tail shape.—Terms used to describe colors are taken from Ridgway (1916). *Zenaida grayson*i is a much darker bird throughout than *Z. macroura*. *Zenaida m. clarionensis* approaches *Z. grayson*i in some characters but is undoubtedly a Mourning Dove. The forehead of *Z. grayson*i tends to be pecan brown passing into vinaceous russet, whereas the forehead of *Z. macroura* is fawn colored. Foreheads in *Z. m. clarionensis* tend to be similar to those in *Z. graysoni* but not consistently. A male *Z. m. clarionensis* in the collection of the Los Angeles County Museum (♂ 19079) had a fawn forehead like mainland Mourning Doves. Back color of *Z. m. clarionensis* also approaches that of *Z. graysoni* in darkness.

Underparts of *Z. graysoni* tend to be bright mikado brown or deep orange cinnamon, whereas the underparts of the *Z. macroura* races are vinaceous fawn. Undertail coverts of *Z. graysoni* are brown like the belly, whereas undertail coverts in *Z. macroura* are fawnish-white. The distal portions of rectrices 4 through 7 are gray in *Z. graysoni* but white in *Z. macroura.* The outer vane of rectrix 7 is white in *Z. macroura* but black in *Z. graysoni* in all specimens examined (Fig. 4).

Rectrices 2 through 7 tend to be squarer at the tips in *Z. graysoni* than in *Z. macroura* (Fig. 4). If the ratio of rectrix 1 to rectrix 7 is used as an index of tail graduation, *Z. graysoni* tails are less graduated and approach those of *Z. auriculata* (Fig. 5). *Zenaida m. clarionensis* is intermediate between *Z. graysoni* and the other Mourning Dove taxa (Fig. 5). The difference in tail graduation between *Z. graysoni* and *Z. m. clarionenesis,* however, is significant ($\bar{x} = 1.6 \pm 0.13$ SD versus $\bar{x} = 1.8 \pm 0.10$ SD; *t*-test, $P \leq 0.005$).

Bill.—Bills of *Z. macroura* are black with some red near the gape. Bills of *Z. graysoni* are black from the tip to about the distal point of the cere, where they are red until the gape of the bill. The amount of red in *Z. graysoni* bills is variable, some individuals having black bills as in *Z. macroura.* The amount of red may vary with reproductive stages and/or age, however.

Weight.—Four adult *Z. graysoni* males weighed 215, 200, 185, and 165 g ($\bar{x} = 191$ g); two females weighed 205 and 180 g ($\bar{x} = 192$ g). Data on *Z. macroura carolinensis* are from Clench and Leberman (1978): 9 weights from 3 wild males trapped repeatedly over 5 months averaged 135.4 g ± 5.03 SD, 7 weights from 3 females trapped over 3 months averaged 133.1 ± 7.9. Thus, *Z. graysoni* is about 43% heavier than the eastern subspecies of *Z. macroura.*

Mensural characters.—Mensural and proportional (ratio) data for 12 morphological characters are summarized in Table 2 and the *t*-test results in Table 3. The two mainland forms, *Z. m. carolinensis* and *Z. m. marginella,* are similar in 16 characters and different in 10 others ($P \leq 0.05$ for each difference). The nominate subspecies differs from *Z. m. marginella* in 14 characters and from *Z. m. carolinensis* in 14 characters. The nominate subspecies is similar to *Z. m. marginella* in 12 characters and to *Z. m. carolinensis* in 13 characters (Table 3). The fact that they are similar in several culmen, tarsus, wing, and tail characters indicates that these three taxa are similarly proportioned (Table 3).

Z. m. clarionensis differs significantly from *Z. m. marginella* in 24 characters, from *Z. m. carolinensis* in 20 characters, and from *Z. m. macroura* in 16 characters. *Z. m. clarionensis* is undoubtedly the most distinct in color, size, and proportions of the Mourning Doves treated. As evidenced by wing/tarsus, tail/culmen, and tail/tarsus ratios, *Z. m. clarionensis* and *Z. m. macroura* are similar to *Z. graysoni* in being proportionately longer-billed and longer-legged than the mainland forms (Tables 2, 3). This was pointed out earlier by Aldrich and Duvall (1958).

Direct discriminant function analysis on the 12 log-transformed mensural characters (Table 4) was performed to compare and contrast the taxa treated herein. Because *Z. auriculata* is often regarded as a superspecies with *Z. macroura,* we include seven subspecies of *Z. auriculata* in this analysis.

The first three discriminant functions explained 97% of the variation: 57% was explained by the first, 30% by the second, and 10% by the third. The first two functions are sufficient to separate all three species completely with no overlap (Fig. 6). Whereas the univariate analyses indicate that *Z. m. clarionensis* is intermediate between mainland forms and *Z. graysoni,* the former clusters with the other subspecies of *Z. macroura* in multivariate space. The largest contributions to discrimination among species on discriminant axis I were provided by the TL1 and TRL measurements (Table 4). The largest contributions to discriminant axis II were CT-1, TL1 and WL measurements. *Z. auriculata* clearly separates from all races of *Z. macroura,* supporting treatment of the two as two distinct species.

IMMUNOLOGICAL STUDIES

Out of 8 antigens studied by Irwin and Miller (1961), *Z. graysoni* shared 6 with *Z. macroura*

TABLE 2. Descriptive statistics ($\bar{x}$ ± SD, *n*) for morphological characters of various taxa of *Zenaida*. Sexes are pooled in all taxa. Character abbreviations are described in Methods. Taxon abbreviations are as follows: Z.a. = *Zenaida auriculata* (races pooled), Z.g. = *Z. graysoni*, Z.m. = *Z. macroura* (races pooled), Z.cl. = *Z. macroura clarionensis*, Z.mac. = *Z. m. macroura*, Z.car. = *Z. m. carolinensis*, Z.mar. = *Z. m. marginella*.

Character	Z.a.	Z.g.	Z.m.	Z.cl.	Z.mac.	Z.car.	Z.mar.
WL	147 ± 6.2 (23)	153 ± 5.7 (22)	141 ± 6.5 (128)	138 ± 4.4 (32)	136 ± 5.6 (33)	143 ± 6.4 (21)	145 ± 5.2 (43)
TL1	93 ± 6.2 (23)	129 ± 9.7 (21)	124 ± 13.1 (117)	114 ± 7.8 (25)	117 ± 9.4 (31)	128 ± 10.5 (21)	134 ± 11.7 (41)
TL2	90 ± 5.5 (23)	124 ± 10.1 (21)	112 ± 10.1 (117)	104 ± 8.6 (25)	107 ± 7.4 (31)	114 ± 8.3 (21)	119 ± 9.3 (41)
TL7	68 ± 4.0 (22)	83 ± 6.7 (19)	64 ± 5.6 (119)	64 ± 3.5 (31)	60 ± 5.6 (31)	67 ± 6.5 (23)	67 ± 5.6 (36)
T1-2	2 ± 2.2 (23)	6 ± 3.5 (21)	12 ± 5.0 (118)	10 ± 3.0 (25)	10 ± 4.2 (32)	14 ± 5.3 (21)	15 ± 5.0 (41)
TW	15 ± 1.4 (23)	17 ± 1.4 (21)	14 ± 1.6 (117)	13 ± 1.1 (25)	14 ± 1.2 (32)	14 ± 1.6 (21)	15 ± 1.9 (40)
CL	60 ± 5.6 (23)	64 ± 7.9 (22)	61 ± 6.0 (127)	59 ± 3.5 (32)	59 ± 5.1 (32)	61 ± 6.3 (21)	65 ± 6.2 (43)
CT-1	32 ± 4.3 (23)	65 ± 6.4 (21)	62 ± 9.6 (118)	55 ± 5.6 (25)	57 ± 6.5 (32)	65 ± 7.7 (21)	68 ± 9.9 (41)
CULEX	14.6 ± 0.89 (22)	16.3 ± 0.80 (22)	13.8 ± 1.34 (127)	15.6 ± 0.77 (32)	12.9 ± 0.67 (33)	13.2 ± 0.81 (20)	13.4 ± 1.02 (43)
CULN	10.2 ± 0.57 (22)	11.9 ± 0.52 (22)	10.2 ± 1.20 (128)	11.6 ± 0.88 (32)	9.4 ± 0.62 (33)	10.0 ± 0.46 (21)	9.8 ± 1.04 (43)
CULW	3.6 ± 0.57 (22)	4.9 ± 0.49 (22)	3.6 ± 0.67 (127)	4.2 ± 0.75 (31)	3.5 ± 0.58 (33)	3.2 ± 0.39 (21)	3.6 ± 0.57 (43)
TRL	22.8 ± 1.08 (23)	28.2 ± 0.90 (22)	21.0 ± 1.00 (128)	21.8 ± 0.95 (32)	20.6 ± 0.79 (33)	20.8 ± 0.66 (21)	20.7 ± 0.98 (43)
WL/TL1	1.6 ± 0.10 (23)	1.2 ± 0.07 (21)	1.1 ± 0.08 (117)	1.2 ± 0.06 (25)	1.2 ± 0.07 (31)	1.1 ± 0.06 (21)	1.1 ± 0.08 (41)
WL/CULN	14.5 ± 1.18 (22)	12.9 ± 0.59 (22)	14.0 ± 1.82 (128)	11.9 ± 0.99 (32)	14.6 ± 1.15 (33)	14.3 ± 0.85 (21)	15.1 ± 1.80 (43)
WL/TRL	6.4 ± 0.27 (23)	5.4 ± 0.24 (22)	6.7 ± 0.44 (128)	6.3 ± 0.33 (32)	6.6 ± 0.36 (33)	6.8 ± 0.31 (21)	7.0 ± 0.38 (43)
TL1/CULN	9.2 ± 0.90 (22)	10.8 ± 0.81 (21)	12.5 ± 2.06 (117)	9.9 ± 0.78 (25)	12.6 ± 1.4 (31)	12.9 ± 1.22 (21)	13.9 ± 1.85 (41)

Table 2. Continued.

Character	Z.a.	Z.g.	Z.m.	Z.cl.	Z.mac.	Z.car.	Z.mar.
TL1/TRL	4.1 ± 0.40 (23)	4.6 ± 0.37 (21)	6.0 ± 0.70 (117)	5.3 ± 0.41 (25)	5.7 ± 0.44 (31)	6.1 ± 0.49 (21)	6.5 ± 0.63 (41)
TL1/CL	1.6 ± 0.09 (23)	2.0 ± 0.20 (21)	2.0 ± 0.20 (117)	1.9 ± 0.09 (25)	2.0 ± 0.13 (31)	2.1 ± 0.26 (21)	2.1 ± 0.18 (41)
TL2/CL	1.5 ± 0.08 (23)	1.9 ± 0.19 (21)	1.8 ± 0.15 (119)	1.8 ± 0.09 (25)	1.8 ± 0.12 (31)	1.9 ± 0.24 (21)	1.8 ± 0.13 (41)
TL1/TW	6.1 ± 0.75 (23)	7.8 ± 0.58 (21)	9.0 ± 1.24 (116)	9.0 ± 1.05 (25)	8.4 ± 0.68 (31)	8.9 ± 1.26 (21)	9.4 ± 1.51 (40)
TL1/TL2	1.0 ± 0.02 (23)	1.0 ± 0.03 (21)	1.1 ± 0.04 (117)	1.1 ± 0.04 (25)	1.1 ± 0.04 (31)	1.1 ± 0.05 (21)	1.1 ± 0.04 (41)
CULN/TRL	0.45 ± 0.032 (22)	0.42 ± 0.024 (22)	0.50 ± 0.049 (128)	0.53 ± 0.041 (32)	0.46 ± 0.034 (33)	0.48 ± 0.030 (21)	0.47 ± 0.440 (43)
CULN/CULW	2.8 ± 0.43 (21)	2.4 ± 0.28 (22)	2.8 ± 0.50 (127)	2.9 ± 0.57 (31)	2.7 ± 0.45 (33)	3.1 ± 0.35 (21)	2.8 ± 0.52 (43)
TL1/TL7	1.4 ± 0.08 (22)	1.6 ± 0.13 (18)	1.9 ± 0.16 (115)	1.8 ± 0.10 (27)	2.0 ± 0.14 (31)	2.0 ± 0.12 (21)	2.0 ± 0.17 (23)
TL2/TL7	1.3 ± 0.06 (22)	1.5 ± 0.08 (18)	1.8 ± 0.14 (115)	1.6 ± 0.11 (27)	1.8 ± 0.13 (31)	1.8 ± 0.11 (21)	1.8 ± 0.16 (23)
TL7/CL	1.1 ± 0.05 (22)	1.3 ± 0.15 (18)	1.0 ± 0.10 (115)	1.1 ± 0.07 (27)	1.0 ± 0.09 (31)	1.1 ± 0.12 (21)	1.0 ± 0.10 (23)

TABLE 3. Results of t-test for difference among means of all variables for comparisons among all taxa of *Zenaida* measured. *** = $P < 0.005$; ** = $P < 0.05$; * = $P < 0.1$; — = $P > 0.1$. Character abbreviations are described in Methods. Taxon abbreviations are described in Table 2.

Character	Z.g. vs. Z.a.	Z.g. vs. Z.m.	Z.g. vs. Z.mar.	Z.g. vs. Z.car.	Z.g. vs. Z.cl.	Z.g. vs. Z.mac.	Z.mar. vs. Z.car.	Z.mac. vs. Z.mar.	Z.mac. vs. Z.car.	Z.mac. vs. Z.cl.	Z.mar. vs. Z.cl.	Z.car. vs. Z.cl.
WL	***	***	***	***	***	***	**	***	***	—	***	**
TL1	***	—	—	—	***	***	**	***	***	—	***	***
TL2	***	***	*	***	***	***	**	***	***	—	***	***
TL7	***	***	***	***	***	***	—	***	***	***	**	—
T1-2	***	***	***	***	***	***	—	***	***	—	***	***
TW	***	***	***	***	***	***	—	**	—	***	***	***
CL	**	**	—	—	**	***	**	***	—	—	***	—
CT-1	***	*	—	—	***	***	—	***	***	—	***	***
CULEX	***	***	***	***	***	***	—	*	—	***	***	***
CULN	***	***	***	***	—	***	—	—	***	***	***	***
CULW	***	***	***	***	***	***	**	—	*	***	***	***
TRL	***	***	***	***	***	***	—	—	—	***	***	***
WL/TL1	***	**	***	***	—	—	—	***	**	**	***	***
WL/CULN	***	***	***	***	***	***	**	*	—	***	***	***
WL/TRL	***	***	***	***	***	***	**	***	**	***	***	***
TL1/CULN	***	***	***	***	***	***	**	***	—	***	***	***
TL1/TRL	***	***	***	***	***	***	**	***	***	***	***	***
TL1/CL	***	—	—	—	*	—	—	*	*	*	***	**
TL2/CL	***	***	**	—	***	**	—	—	—	—	**	*
TL1/TW	***	***	***	***	***	***	—	***	—	**	—	—
TL1/TL2	**	***	***	***	***	***	—	**	**	—	***	**
CULN/TRL	***	***	***	***	***	***	—	—	**	***	***	***
CULN/CULW	***	***	***	***	***	***	**	—	***	—	—	*
TL1/TL7	***	***	***	***	***	***	—	*	—	***	***	***
TL2/TL7	***	***	***	***	***	***	—	—	—	***	***	***
TL7/CL	***	***	***	***	***	***	—	—	—	**	**	—

and differed in 2. *Zenaida graysoni* shared 7 antigens with *Z. auriculata* and differed in 1. Finally, *Z. auriculata* shared 5 antigens with *Z. macroura* but differed in 3.

DISCUSSION

In this study we documented differences in vocalizations, visual displays, and morphology between *Z. macroura* and *Z. graysoni*. Behavioral acts acquire added weight as taxonomic characters that distinguish species if they can be shown to be genetically coded and free of the influence of learning. Cross-fostering experiments with doves in the genus *Streptopelia* and *Zenaida* revealed that species-specific songs (coos) and displays may be produced without learning from conspecific adults (Craig 1908, Whitman 1919, Lade and Thorpe 1964). Hybrids between congenerics produced vocalizations or performed displays with characters similar to one or the other parental species, intermediate between two species, or unlike either species (Lade and Thorpe 1964, Davies 1970, Baptista and Abs 1983). Backcrossed individuals produced vocalizations similar to one of the parental forms (Lade and Thorpe 1964).

TABLE 4. Standardized canonical discriminant function coefficients for the 12 mensural variables used in the analysis of all six *Zenaida* taxa. Function 1 accounts for 57% of the variance, Function 2 for 30%, and Function 3 for 10%. Variable abbreviations described in Methods.

Variable	Function 1	Function 2	Function 3
WL	0.161	−0.584	−0.321
TL1	−1.015	−0.673	−0.462
TL2	0.299	0.444	0.116
TL7	0.515	−0.037	−0.137
TL1-2	0.017	0.037	0.226
TW	0.015	−0.088	−0.497
CL	0.005	0.304	0.266
CT-1	0.130	1.261	0.082
CULEX	0.251	−0.126	0.410
CULN	0.102	0.149	0.432
CULW	0.249	0.267	0.211
TRL	0.694	0.427	−0.223

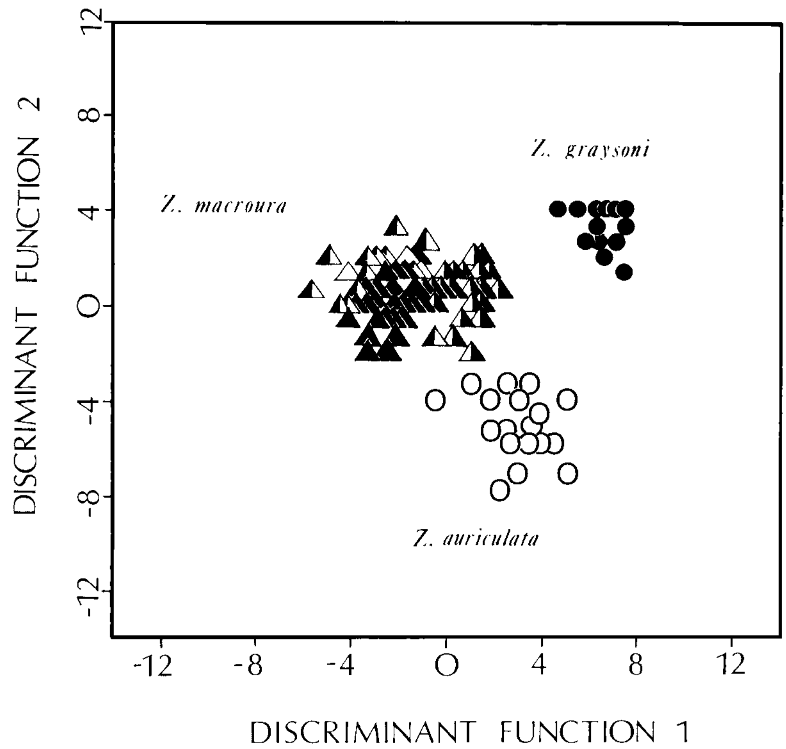

Fig. 6. Discriminant function analysis comparing six taxa of *Zenaida* doves. Clear circles are *Z. auriculata.* Black circles are *Z. graysoni.* Black triangles are *Z. m. macroura.* Clear triangles are *Z. m. carolinensis.* Triangles with the left half blackened are *Z. m. marginella.* Triangles with the right half blackened are *Z. m. clarionensis.* Some points on the graph may represent more than one individual.

Deafened Ring Doves (*Streptopelia risoria*) produced normal vocalizations, indicating a genetically coded motor output without need for audiosensory feedback (Nottebohm and Nottebohm 1971). These data argue for the heritable nature of vocalizations and displays in doves. Crosses between Mourning Dove and Ring Dove (Whitman 1919) and Grayson's Dove and Ring Dove (Baptista unpubl.) yielded data similar to those reported by Lade and Thorpe (1964) and Davies (1970). The differences in the vocalizations and displays of *Z. macroura* and *Z. graysoni* reported herein are most likely inherited. Dove vocalizations are very conservative, and no marked geographical variation within species is known to date. The differences in displays described for the two taxa of *Zenaida* argue for their treatment as two distinct species. The role of columbiform displays as ethological isolating mechanisms between species has been treated by Johnston (1961).

Z. graysoni is markedly different in color from *Z. macroura,* the former being much darker throughout. Pigeons (*Columba livia*) are known to imprint sexually on the color morph of their parents or foster-parents in cross-fostering experiments (Warriner et al. 1963, Goodwin 1967). Goodwin (1967) suggests that color differences may function as strong ethological isolating mechanisms in columbiforms if squabs imprint sexually on the colors of their parents. Sexual imprinting is well known in the Mourning Dove (Klinghammer 1967). Yellow headmarks placed on female Mourning Doves disrupted the pair-formation process (Goforth and Baskett 1965), suggesting that colors may be important in species recognition. We feel that the color differences between *Z. graysoni* and *Z. macroura* are great enough to effect sexual imprinting on color by each taxon and will prevent interbreeding between the two taxa. Although the two forms are known to interbreed in captivity, our experience indicates that hybrid pairings are not easy to produce. These data, especially, argue for maintaining *Z. graysoni* as a distinct species.

The insular races of Mourning Dove, *Z. m. macroura* and *Z. m. clarionensis*, are proportionately longer-legged and longer-billed than their mainland counterparts and in these respects resemble *Z. graysoni*. We do not regard these similarities as indicative of close relationships but rather as a manifestation of parallel evolution due to selection for certain character states on islands. Insular forms often have longer bills and legs than their relatives on mainlands (Power 1980).

Earlier, we called attention to the differences in tail shape and length between *Z. graysoni* and other *Zenaida* taxa. Tail shape and length are intraspecifically conservative in doves and have been used by a number of early authors as generic characters (review in Goodwin 1958). The graduation in tail shape in *Z. m. clarionensis* is intermediate between that in *Z. graysoni* and all other races of *Z. macroura*. Nonetheless, one has no trouble recognizing *Z. m. clarionensis* as a race of *Z. macroura* based on tail shape alone. This is borne out also by our discriminant function analysis, in which *Z. m. clarionensis* clusters closely with other races of *Z. macroura* (Fig. 6). *Z. graysoni* is readily separable from all other taxa of *Zenaida* in multivariate space. We also called attention to a study on serological differences between the three *Zenaida* species treated herein.

In sum, pairing preference and differences in displays, morphology, and serology indicate that *Z. graysoni* is a species distinct from *Z. macroura*. *Zenaida graysoni* is closely related to *Z. macroura*, however, and must have evolved from an ancestor that invaded the Revillagigedos long before the ancestral form that gave rise to *Z. m. clarionensis*.

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APPENDIX. Localities where collected, museums where housed, sexes, and sample sizes of specimens measured.

Taxon	Localities	Museum[a] (sample size, sex)
Z. graysoni	Socorro Island, Mexico	CAS(8m, 3f, 3?); LACMNH(3m, 2f); MVZ(1m, 1f); WFVB(1m)
Z. m. marginella	Alberta, Arizona, Baja California, British Columbia, California, Durango, Idaho, Jalisco, Morelos, Nevada, Oaxaca, Oregon, Wisconsin	CAS(20m, 6f); LACMNH(1m); MVZ(7m, 6f)
Z. m. carolinensis	Florida, Georgia, Guerrero, Illinois, Massachusetts, Michigan, Missouri, New Jersey, New York, Ontario, South Carolina, Wisconsin	CAS(3m, 3f); MVZ(8m, 7f)
Z. m. macroura	Cuba, Haiti, Hispaniola	CM(11m, 2f); MCZ(5m, 5f); USNM(5m, 5f)
Z. m. clarionensis	Clarion Island, Mexico	CAS(9m, 5f); LACMNH(8m, 8f); MVZ(1m, 1f); WFVB(1m, 1f)
Z. auriculata	Argentina, Chile, Colombia, Ecuador, Peru, Venezuela	LACMNH(10m, 1f); MVZ(7m, 4f); WFVB(1f)

[a] CAS = California Academy of Sciences; CM = Carnegie Museum; LACMNH = Los Angeles County Museum of Natural History; MCZ = Museum of Comparative Zoology; MVZ = Museum of Vertebrate Zoology; USNM = United States National Museum; WFVB = Western Foundation for Vertebrate Biology.