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# BULLETIN

of the Florida Museum of Natural History

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## VOCALIZATIONS OF UNICOLORED JAYS (*APHELOCOMA UNICOLOR*) AT MONTEBELLO, CHIAPAS, MEXICO

Tom Webber and Nancy G. Stotz

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Vol. 57, No. 1, pp. 1–75  
ISSN 2373-9991

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October 11, 2019

UNIVERSITY OF FLORIDA

GAINESVILLE

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ISSN: 2373-9991

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Publication Date: October 11, 2019

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Editor of the Bulletin; Florida Museum of Natural History; University of Florida; P.O. Box 117800;  
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Tom Webber<sup>1</sup> and Nancy G. Stotz<sup>2</sup>

## ABSTRACT

Unicolored Jays (*Aphelocoma unicolor*) are little-known social corvids of Mexico and Middle America. Like other birds in the family Corvidae they possess a vocabulary composed of sounds usually referred to as calls rather than songs. Here we provide the first description of this species' rich vocabulary. We studied vocalizations of color-banded Unicolored Jays in Chiapas, Mexico from January through May of 1987. There they live in cooperatively breeding groups of four to nine birds. We distinguish 697 long-range call variants from our recordings, which probably did not exhaustively sample the range of jay sounds on our study site. The sonograms of the sounds can be divided into broad categories with finely graded spectrum-like variation within them, and generally no sharp boundaries between them. Nearly any sonogram in the vocabulary can be connected structurally to any other through a range of intermediates.

The jays tended to introduce many new related variations on a call theme in a single calling session, and many of these variants were not recorded again. There is some indication that the jays favored using a few call types in particular behavior contexts, but they used the great majority of them in a range of widely varying settings. The jay groups shared only a minority of their call collections with one another, but many of the unshared calls were rarely recorded and may not have represented typical vocal differences between them. A few commonly used calls did seem to be peculiar to one or a few jay groups.

Vocalizations recorded on our study site in 1987 differ notably from those recorded there in 2006, strongly suggesting cultural turnover in the local assortment of calls. Recordings from other *A. unicolor* populations in southern Mexico show marked geographic variation on a regional scale. We suggest that the tendency of Unicolored Jays to produce series of similar and apparently new calls in spates, geographical variation in calls on scales small and large, and turnover in calls at a single locality may all reflect call learning, call improvisation, and the process of random vocal change known as culture drift. We also describe a variety of the jays' soft short-range calls, some of them strikingly similar to those in other species of *Aphelocoma*, and others, including some common ones, not previously known in this genus. Like other *Aphelocoma*, *A. unicolor* on our study site had rattle calls (one fast and one slow), and whisper song. The precise similarities between certain calls of *A. unicolor* and those of its relatives show either a startling degree of fidelity in vocal copying over thousands of generations, or a strong innate tendency to reproduce certain details of their vocabularies.

**Key words:** Corvidae; *Aphelocoma*; jays; vocalizations; calls; social behavior; cooperative breeding; Mexico.

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## INTRODUCTION

Behavior that varies from one species to another within a well-defined taxonomic group offers opportunities to understand how the behavior evolved as the group radiated. One such behavior is the characteristic collection of a species' sounds. The New World jays represent one widespread radiation that shows striking interspecific differences in vocal behavior.

The crows, jays, and their allies (family Corvidae), lack broadcast advertising song in the usual sense of the term (Spector, 1994), and instead collectively utter an astonishingly varied range of sounds commonly referred to as calls (e.g., Hardy, 1990). The distinction between songs and calls is not entirely clear (Spector, 1994), but is widely recognized and used (e.g., Hartshorne, 1992; Kroodsmma, 2005:37–38). Compared to typical oscine advertising song, the sounds referred to as calls are generally shorter, often noisy or unmusical sounding, and tend not to be delivered in trains that have a consistently repeated internal sequence, such as the advertising songs of thrushes, titmice, or wrens. Jays and crows tend not to broadcast their sounds continuously and spontaneously from a song perch, cycling through a repertoire of sound types, and instead when calling often seem to be engaging the attention of particular recipients, whether during territory boundary defense, remaining in long-range contact with flock members, or mobbing a predator. These non-song sounds have not been a primary object of study among passerine vocalizations (Marler, 2004; Benedict and Krakauer, 2013). Here we provide the first description of the sounds of Unicolored Jays (*Aphelocoma unicolor*), a little-known member of a New World genus that has otherwise been the subject of intensive study.

The New World jays (here not including *Perisoreus*) are a monophyletic group (Zusi, 1987; Ericson et al., 2005; Bonaccorso and Peterson, 2007) comprising seven genera and about 25 species distributed from southern Alaska to the southern cone of South America. They occupy a variety of habitats including cloud forest, pine-oak forest, cerrado, and chaparral. At least 10 species are

cooperative breeders (dos Anjos et al., 2009).

The genus *Aphelocoma* is currently considered to consist of seven species (AOS, 1997), though recognition of more species-level distinctions seems likely (McCormack et al., 2011, Venkatraman et al., 2018). *Aphelocoma* jays occur from northern Washington State to eastern Honduras, in habitats ranging from desert scrub to chaparral, mid-elevation pine-oak-juniper forest, and wet montane forest. Florida Scrub-Jays (*A. coerulescens*; Woolfenden and Fitzpatrick, 1996), some western scrub-jays (*A. woodhouseii*; Burt and Peterson, 1993), Mexican Jays (*A. wollweberi*; McCormack and Brown, 2008), and Unicolored Jays (Webber and Brown, 1994) exhibit variations on the theme of cooperative breeding. Florida Scrub-Jays and Mexican Jays have been studied in detail for decades.

Unicolored Jays range from Hidalgo, Mexico, to eastern Honduras, in humid mid-elevation montane habitats composed mainly of pines and oaks (Pitelka, 1951). At our study site in southeastern Chiapas, Mexico in 1987 (Fig. 1), the jays lived in groups of from four to nine birds one year old and older. We were able to distinguish three adult age classes among them. Each group had a female breeder and one or more non-breeding females, plus a dominant male and one or more subordinate males. The adult composition of the groups remained unchanged throughout our stay, except that Group 3 occasionally had an adult female visitor from 31 January through 28 February, and four banded adults of Group 5 vanished at about the same time in May. Subordinate males competed with the dominant males for opportunities to mate with the female breeder. Each group had only one nest at a time, built primarily by the breeding pair with some contributions by other group members. Only the female breeder incubated and brooded young. All group members helped to feed the female breeder on the nest, and most group members helped to feed nestlings and fledglings. We found the earliest active nest on 19 January. Nest activity peaked in March and April, and jay attendance at the last nest of the season ended on 28 May. All adult members of each group helped to

defend the boundaries of their all-purpose territory (Webber and Brown, 1994).

Here we present a complete inventory of the range of variation in the loud long-range calls we recorded from this population in 1987, an essay at classifying them, and a detailed description of the way in which the jays used them. We also provide a short account of the population's shorter-range vocalizations, and a brief comparison of its sounds with those of other *Aphelocoma*.

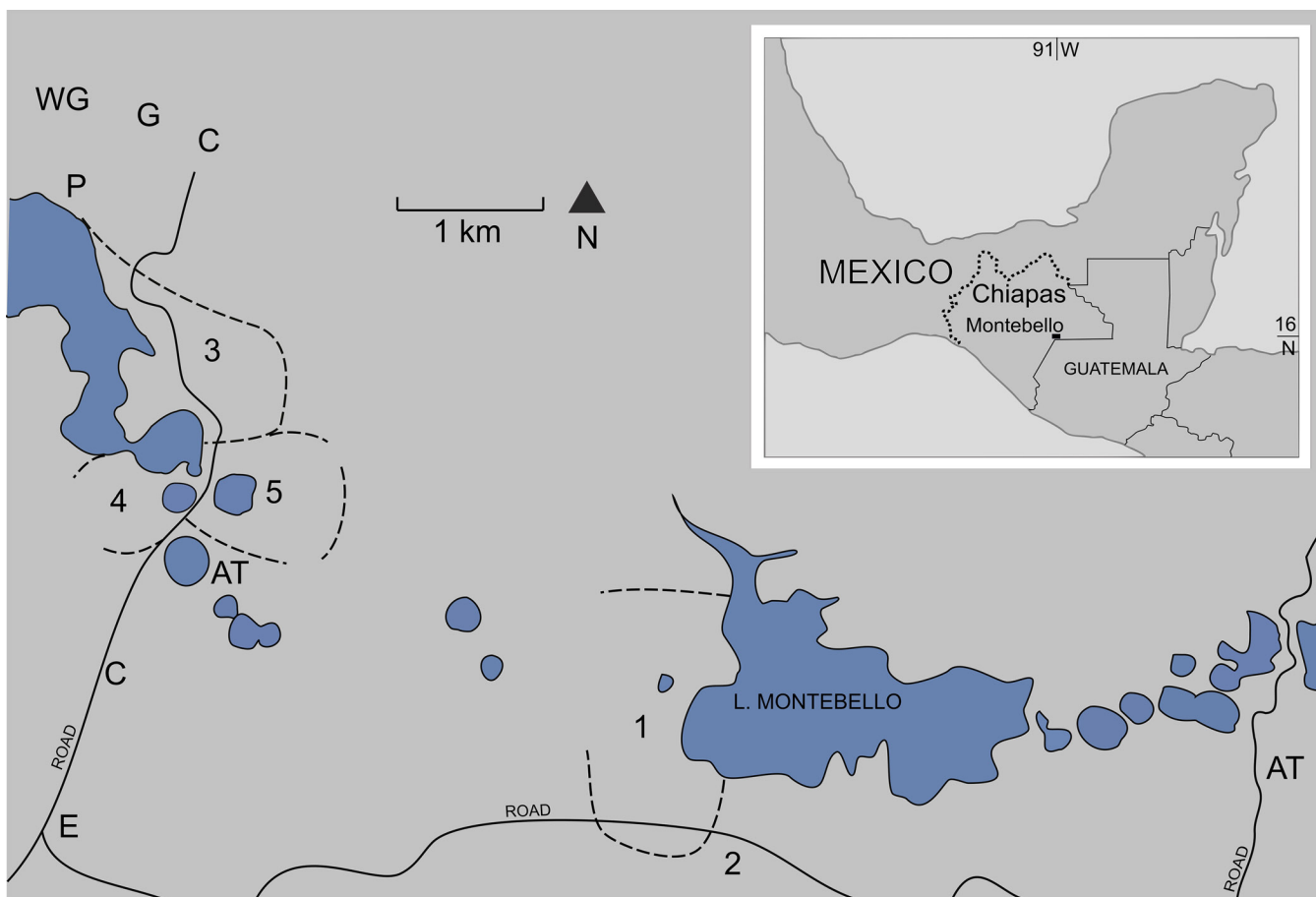
### GENERAL METHODS

We studied Unicolored Jays at Lagunas de Montebello National Park in Chiapas, Mexico, from 10 January through 1 June 1987; the total time of observation was about 1,500 person-hours. The jay

habitat there is mainly pine-oak forest at an elevation of about 1,500 m (Webber and Brown, 1994; Fig. 1).

We color-banded most of the adults in four groups (Groups 1, 3, 4, and 5; Fig. 1). We also observed birds of nine other groups at the locations shown in Figure 1.

We made audio recordings with Sony WMD6 and Marantz C 105 cassette recorders and an Ambico V-0620 electrostatic microphone. We recorded the jays of the 13 groups in 76 sessions from 14 January through 23 May (Table 1), often during our regular nest watches from 07:00-12:00 and 15:00-17:00 local time, but on an opportunistic schedule. We added spoken notes on the birds' behavior as we recorded them. Digital copies of



**Figure 1.** The Unicolored Jay study site at Lagunas de Montebello, Chiapas, Mexico, Jan-May 1987. Dotted lines show the territory boundaries of our banded jay groups 1, 3, 4, and 5. Letters and one number indicate the places where we most often observed jays in unbanded groups. From upper left to lower right these are WG = West of Grutas, G = Grutas, C = Casita, P = Paso del Soldado, AT = Agua Tinta, CE = Cementerio, E = Entrada, 2 = Group 2, and CL = Cinco Lagos.

**Table 1.** Dates and durations of recording sessions per Unicolored Jay group, Lagunas de Montebello, Chiapas, Mexico, January–May 1987. See Figure 1 for the locations of the jay groups.

Jay group	Number of sessions	Total recording time (min)	Range of recording time (min)	Range of dates
1	17	148	2.1–24.8	14 Jan–23 May
2	1	6.4		19 Jan
3	22	193	0.67–26.3	30 Jan–24 May
4	13	120	0.67–41.2	9 Feb–26 May
5	3	24.0	3.9–11.5	17 Feb–16 May
Casita	21	85.3	0.2–15.5	5 Feb–30 May
Agua Tinta	2	9.8	1.8, 8.0	9 Feb, 21 Mar
Cementerio	1	6.0		20 Mar
Entrada	1	4.0		6 Feb
Paso del Soldado	1	3.0		9 Feb
Grutas	2	2.9	1.6, 1.3	24 Mar, 16 May
Cinco Lagos	1	3.75		27 Apr
West of Grutas	1	5.0		16 May

these recordings are in the audio archives of the Division of Birds, Florida Museum of Natural History. We also present for comparison examples of *Aphelocoma* calls recorded by others at Montebello in 2006 and several other localities.

We used Raven (Cornell Laboratory of Ornithology, Ithaca, NY) to digitize the recordings at 44.1 kHz and 16 bits. We also used Raven to compare and classify the sounds of the jays (Blackman window, window size 580 samples, 3 dB filter bandwidth 125 Hz, time grid overlap 70%, DFT size 1024 samples). We distinguished sonograms of the

calls from one another according to differences in degree and kind commonly used by many authors to separate units of bird sounds, including number, direction, and extent of inflections in the traces of the sonograms, as well as length, frequency range, and frequency emphasis. The distinctions we made are similar in degree to those recognized in, for instance, the sounds of Budgerigars (*Melopsittacus undulatus*, Psittacidae; Farabaugh and Dooling, 1996), American Crows (*Corvus brachyrhynchos*, Corvidae; Brown and Farabaugh, 1997:fig. 7.8), House Wrens (*Troglodytes aedon*, Troglodyti-

dae; Rendall and Kaluthota, 2013), Clay-colored Thrushes (*Turdus grayi*, Turdidae; Vargas-Castro et al., 2012), Corn Buntings (*Miliaria calandris*, Emberizidae; Latruffe et al., 2000:fig. 2), and Red Crossbills (*Loxia curvirostra*, Fringillidae; Hynes and Miller, 2014).

Most important, these degrees of difference are also on the same scale as those that Mexican Jays use to distinguish members of one flock from another (Hopp et al., 2001; Fig. 27 row C at right).

As we scrolled through and identified the calls in our recordings we made a paper print of each new call type we encountered. We used this accumulating catalog as our standard for direct visual comparison and classification of each clear sonogram in the recordings. We conducted this classification twice, checking the second pass against the first and reconciling the few differences between the two. We used only our audio recordings summarized in Table 1 for counting calls and describing the contexts in which they occurred, and used only sonograms of the calls, not the way they sounded to us. We have voluminous written notes on the behavior of the jays, including many remarks on their vocalizations, but we did not use these in compiling the call data in this paper because of the difficulty of recognizing individual sounds by ear.

Here, a “call” is the smallest named category of Unicolored Jay sound, such as the ones we designate as 537, 218, and 410, in Figure 2 row A. For variety we sometimes use the terms *call*, *sonogram*, *variant*, and *sound* interchangeably. A “rendition” of a call is a particular instance in which a jay gave that type of call. Sometimes the jays delivered a rapid-fire burst of a single call type, with uniform intervals between the calls of less than 0.25 sec. We considered each such burst to be one utterance and counted it as a single rendition. Our recordings yielded about 6,500 renditions recorded and scanned clearly enough for identification. We use the term “vocabulary” to refer to the entire collection of sounds the jays made, a term we prefer when discussing corvid sounds to the word “repertoire,” which is commonly used for typical passerine advertising *song*. By this term we do not imply any language-like properties for the jays’ vocalizations.

We made the sonograms in Figures 2–24, 26, and 27 using Praat (Boersma and Weenink, 2017) with its default settings. In RESULTS we describe other methods specific to particular parts of the data.

## RESULTS

### FORM AND VARIETY OF LONG-RANGE CALLS

We distinguished 697 variants among the long-range calls we recorded at Montebello in 1987 (Figs. 2–20). To each of these calls we assigned a unique identifying number, shown just below each sonogram. We assigned these numbers consecutively as we encountered each call type for the first time while we scrolled through the recordings from earliest to latest, so the numbers in the sonogram figures are not in order when the calls are grouped together by their similarity.

The letters and numbers above each call type in Figures 2–20 show how many times we recorded it in each jay group. Letters and numbers preceding the colon indicate the names of the jay groups as abbreviated in Figure 1. Two jay-group names separated by a slash (e.g., 4/5), indicate that we recorded the call while birds of both groups were calling, and could not tell from which particular group the calls came. A single number following a colon indicates the total number of renditions counted from that jay group, and that we recorded all during a single session (cf. Table 1). When two numbers separated by a comma follow the colon, the first number indicates the number of sessions in which we recorded the call type, and the second indicates the total number of renditions of the call type in all sessions for that jay group. For instance, we recorded call type 527 (fifth from the left in row A, Fig. 2), once from Group 4, once from Groups 4 and 5 calling simultaneously, and from the Casita group (C) a total of 10 times in two sessions.

The sonograms of many calls contain two major traces that we call *bands*, one lower in pitch overall (e.g., arrows, call 537 at the left end of row A, Fig. 2) and often rising and falling (e.g., Fig. 14). We occasionally refer to the upper part of a band as the *head* and the lower part as the *tail*. We introduce some other terms for features of the



sonograms in the captions of the figures where they first appear.

In Figure 2 through Figure 20 row A, we have placed each sonogram next to its most similar neighbor or neighbors, as explained more fully in the captions of the figures. Variation within some parts of the resulting spectrum follows a trend, such as the general progressive change in frequency inflection in the segment from row A of Figure 2 through row B of Figure 4 (see the captions of those figures for a detailed description). Other segments of the spectrum show variety but no clear trend in form, for instance the calls in row C of Figure 7.

Many of the jay sounds grade finely into one another, and calls that clearly show the two-banded framework can be linked by intermediates to calls that appear radically different. For example, in Figure 18, two-banded calls such as 426 (row A) exhibit a series of graded variations that approach the structure of multibanded calls such as 129 (rows B and C).

We present examples of certain call types reproduced with great fidelity from one rendition to another, even in different jay groups and in different recording sessions (Fig. 20 rows B and C; Fig. 21 rows A and B).

In addition to the two widespread major bands, certain small details appear that are precisely similar in calls that are otherwise quite different and therefore far apart on the spectrum. We call attention to a few of these particulate similarities with blue arrows in the sonogram figures. Examples include a distinctive curvature at the base of the lower band (e.g., call 536, Fig. 2 row A)

We refer to certain segments of the overall vocabulary spectrum as *call groups*, giving each group the name of one of the calls within it. In Figures 2–20, we identify these call groups by a colored line beneath the members of each group, with labels in italics showing where each group begins and ends, and where in some cases they continue from one figure to another. When we identify more than one call group in a single figure, the lines designating one call group are in a color different from that of the other group. For instance, Figure 9 shows part of call group 458, underlined in blue,

and part of call group 150, underlined in red.

We have had to arrange the calls in a series that runs as a single line through the figures, but their relationships to one another would be better represented by a branching pattern. For instance, the calls beginning at the left end of Figure 4 row C do not much resemble those immediately preceding them in row B, giving the impression of a break in the continuity of the spectrum. If we had room to show the calls in row C branching off from a point in Figure 2 row A, the transition would appear to be much smoother. Call 533, for instance, could serve as a link between the two series as they diverge in structure (see the figure captions for descriptions of the progressive changes in the calls' components as they diverge). We call attention to certain of these virtual branching points in Figures 2–20 with the notation "cf.," and the name of the call or calls to which they connect; we have not labeled all such points. When viewing the vocabulary this way, it is possible to connect nearly any long-range call to any other through a series of more-or-less close intermediates (Fig. 25).

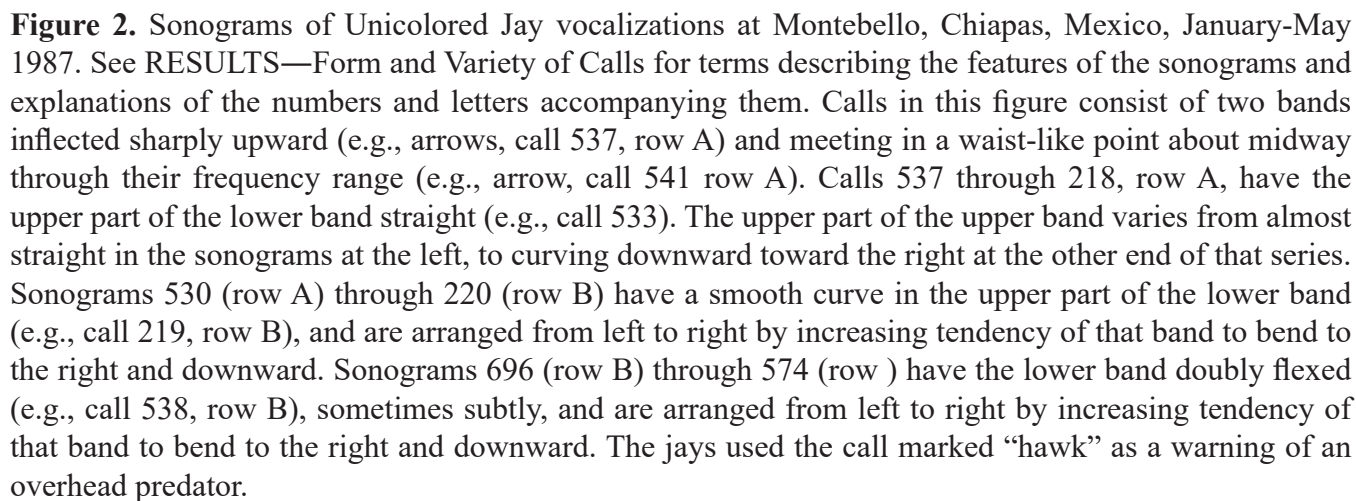
We describe the preceding features in more detail in the sonogram-figure captions (Figs. 2–20).

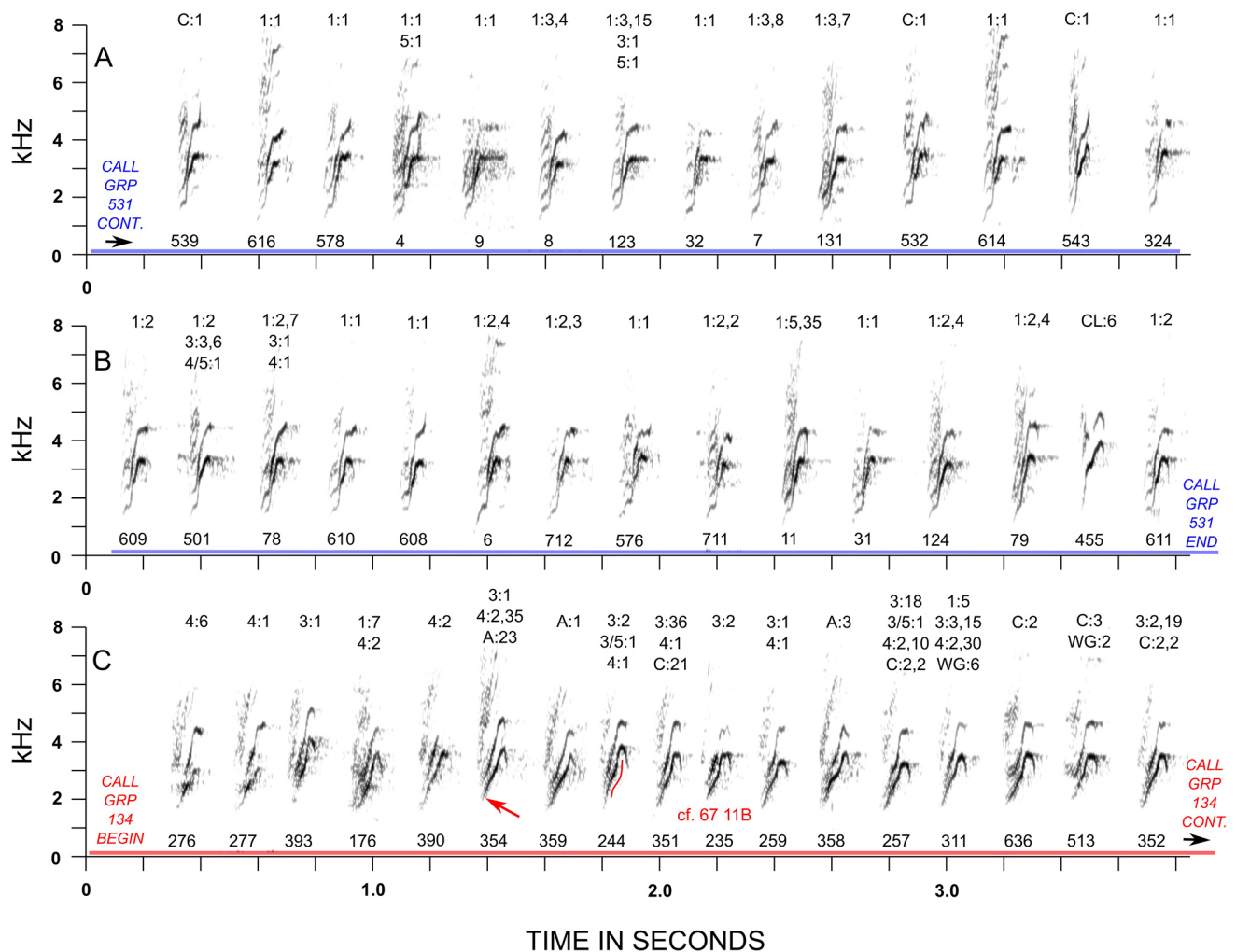
#### COMPLETENESS OF THE VOCABULARY SAMPLE

We probably did not completely sample the variety of calls among our four most-recorded jay groups in 1987. In each of those four groups we had recorded examples of each call group known from that jay group by the sixth recording session, but the number of new individual call types still seems to have been increasing marginally at the end of observations, at least in the Casita group (Fig. 28).

#### CALLS COMMON AND UNCOMMON

Among the call types we recorded from only one jay group each (see RESULTS—Distribution of Calls Among Jay Groups), the great majority appear in five or fewer renditions, and the greatest number appear in only one (Fig. 32A). These rare call types may have been literally one-time improvisations (see the DISCUSSION), indicating little about the true distinctiveness of each jay group's *commonly* used vocabulary. They might also have appeared more abundantly and spread more widely through





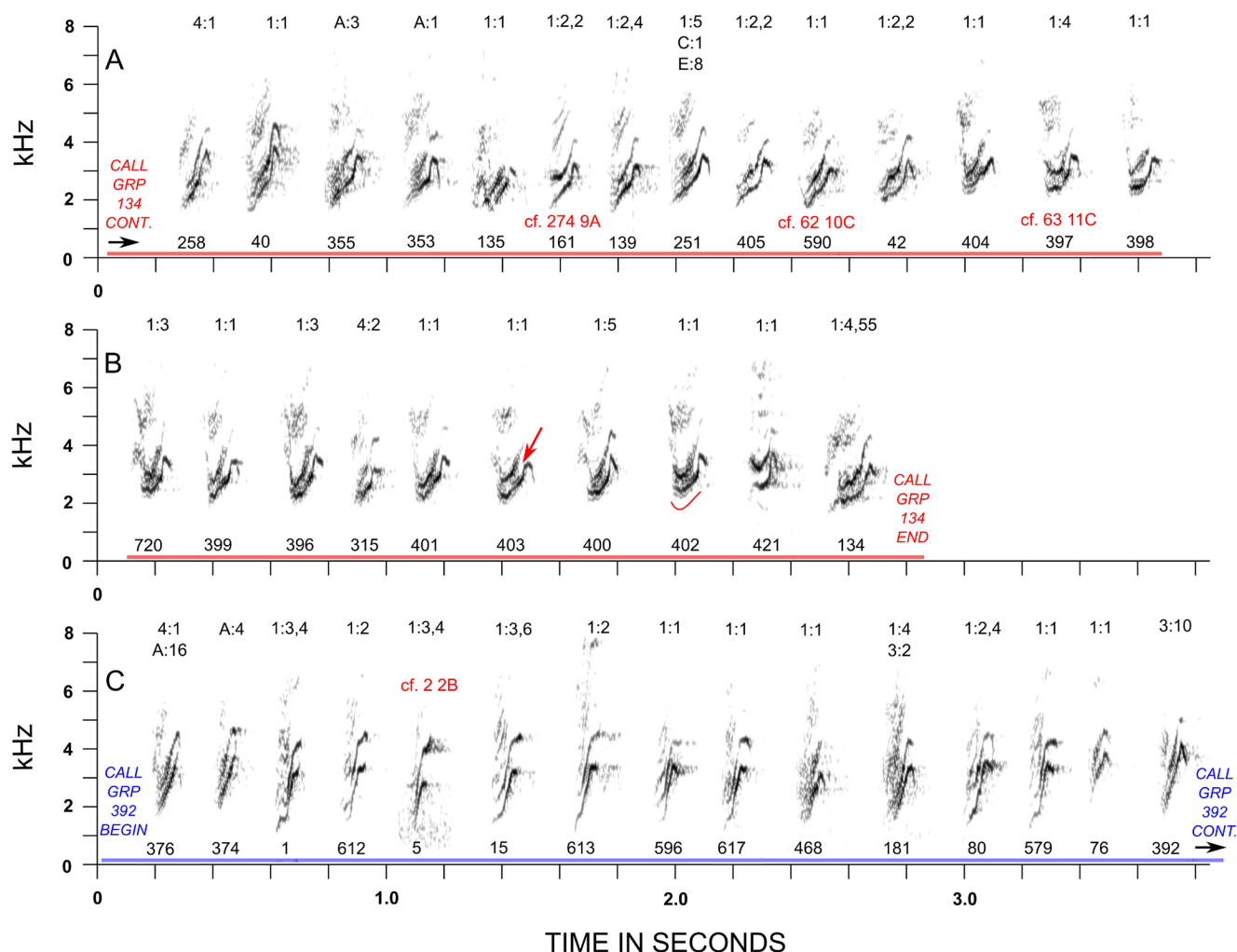
**Figure 3.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Form and Variety of Calls for terms describing the features of the sonograms and explanations of the numbers and letters accompanying them. Sonograms 539-611 (rows A and B) continue the series of calls with narrow waists from Figure 2, and the tendency for the top of the lower band to bend downward and to the right as they are arranged from left to right. 276-352 (row C) have, like those preceding them in both figures, two bands with sharp upward inflection, but the bands do not join at a waist-like point, and the lower tips of the traces do not end in a flourish to the left. The lower bands typically are doubly flexed (e.g., call 244) much as in the calls immediately preceding them.

the jay groups if we had simply recorded a larger sample, as suggested by the wide distribution of the abundant calls 172 (Fig. 13 row A), 337, 85B, 327, and 336 (Fig. 14).

Rare calls and common calls occurred in most call groups (see the numbers above the individual sonograms in Figs. 2–20). For example,

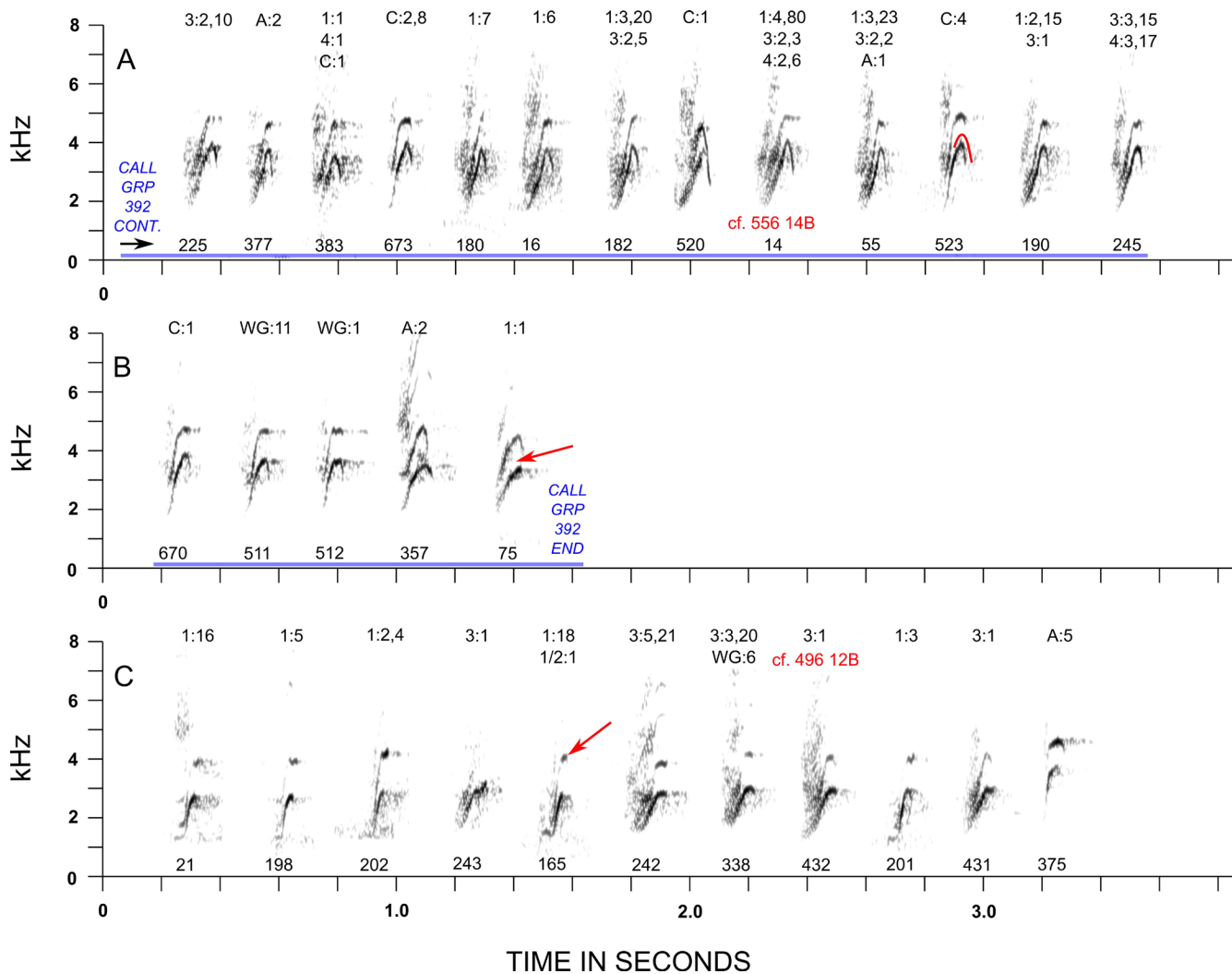
in call group 531, call 219 (Fig. 2 row B) occurred in 48 renditions among at least four jay groups and nine recording sessions, while calls 410 (Fig. 2 row A), 504 (Fig. 2 row B), and 529 (Fig. 2 row C) each occurred in only one rendition.

[Text resumes on page 35]

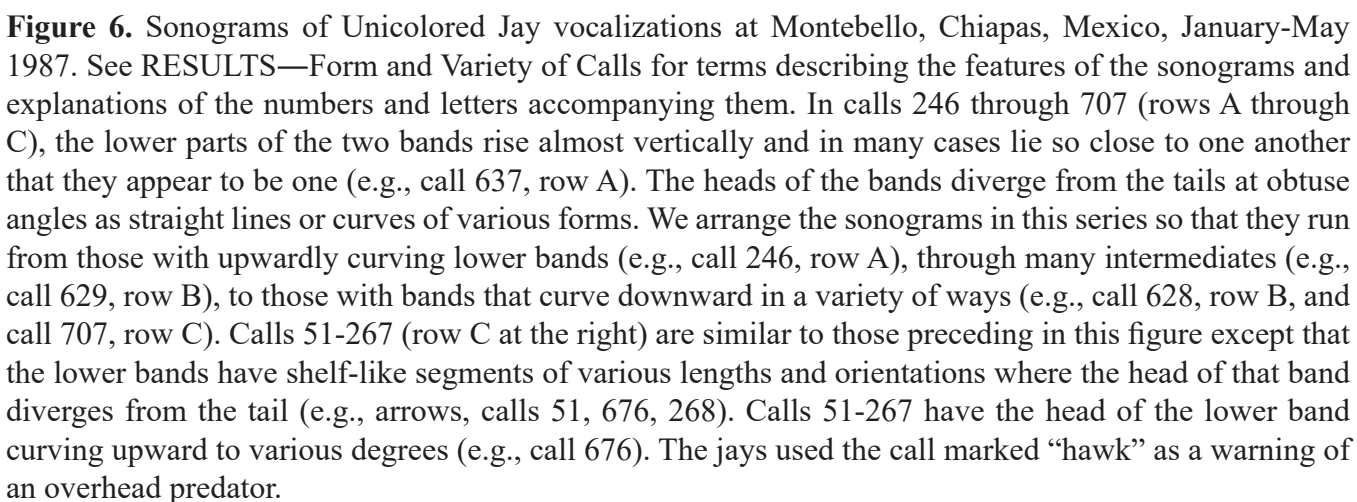


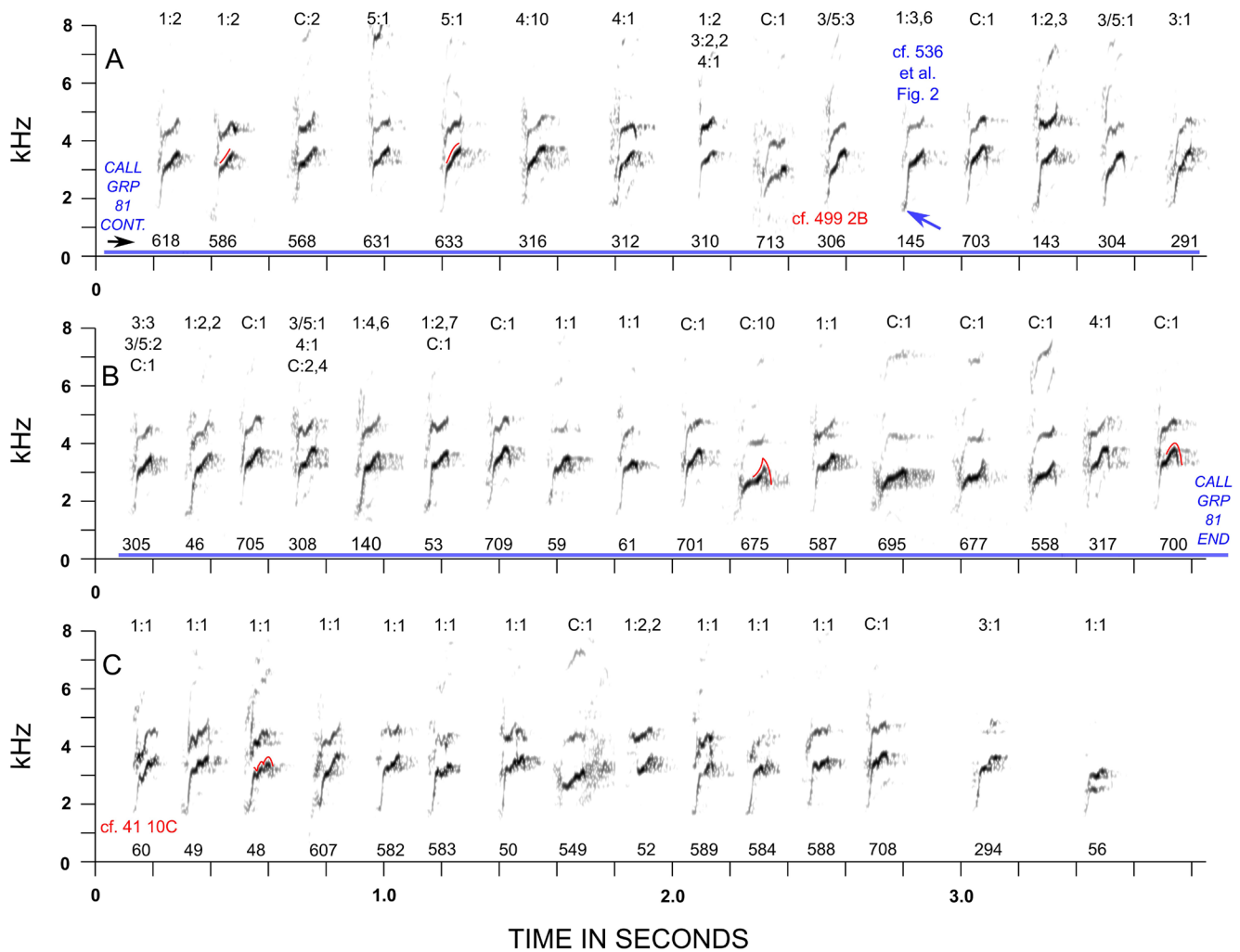
**Figure 4.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Form and Variety of Calls for terms describing the features of the sonograms and explanations of the numbers and letters accompanying them. Calls 258-134 (rows A and B), continue the series of waistless calls from Figure 3, and as they are arranged from left to right show a tendency for the space between the bands to enlarge (e.g., call 403, row B), and for the tails of the bands to curve to the left and upward (e.g., call 402, row B). Calls 376-392 (row C), resemble those in Figure 2 and the last row of Figure 3, but they have no waist and the bands are essentially straight, not doubly flexed. They can be arranged in a series as shown with the top of the lower band straight at the left of the series and flexed downward in various ways at the right of the series.



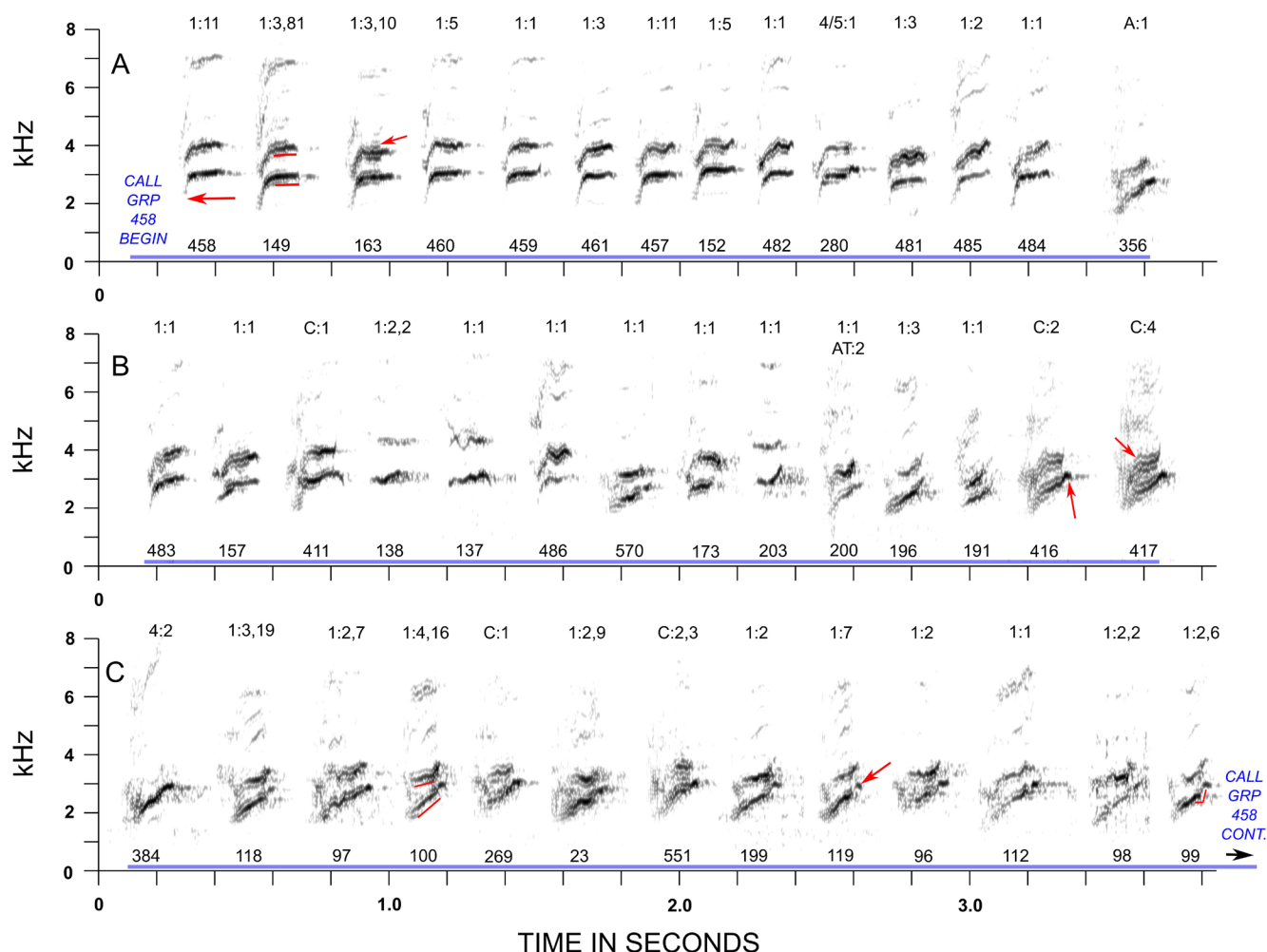


**Figure 5.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Form and Variety of Calls for terms describing the features of the sonograms and explanations of the numbers and letters accompanying them. Calls 225-75 (rows A and B) continue the trend established in the last row of Figure 4. The calls can be arranged as shown to exhibit a general trend from left to right in which the space between bands increases (e.g., call 75, row B), the overall curvature of one or both bands increases (e.g., call 523, row A), and the overall frequency of the bands rises less sharply. Calls 21-375 (row C) have the lower band simple and pronounced, with a marked gap between the peak frequency (e.g., arrow, call 165) and the rest of the sound.

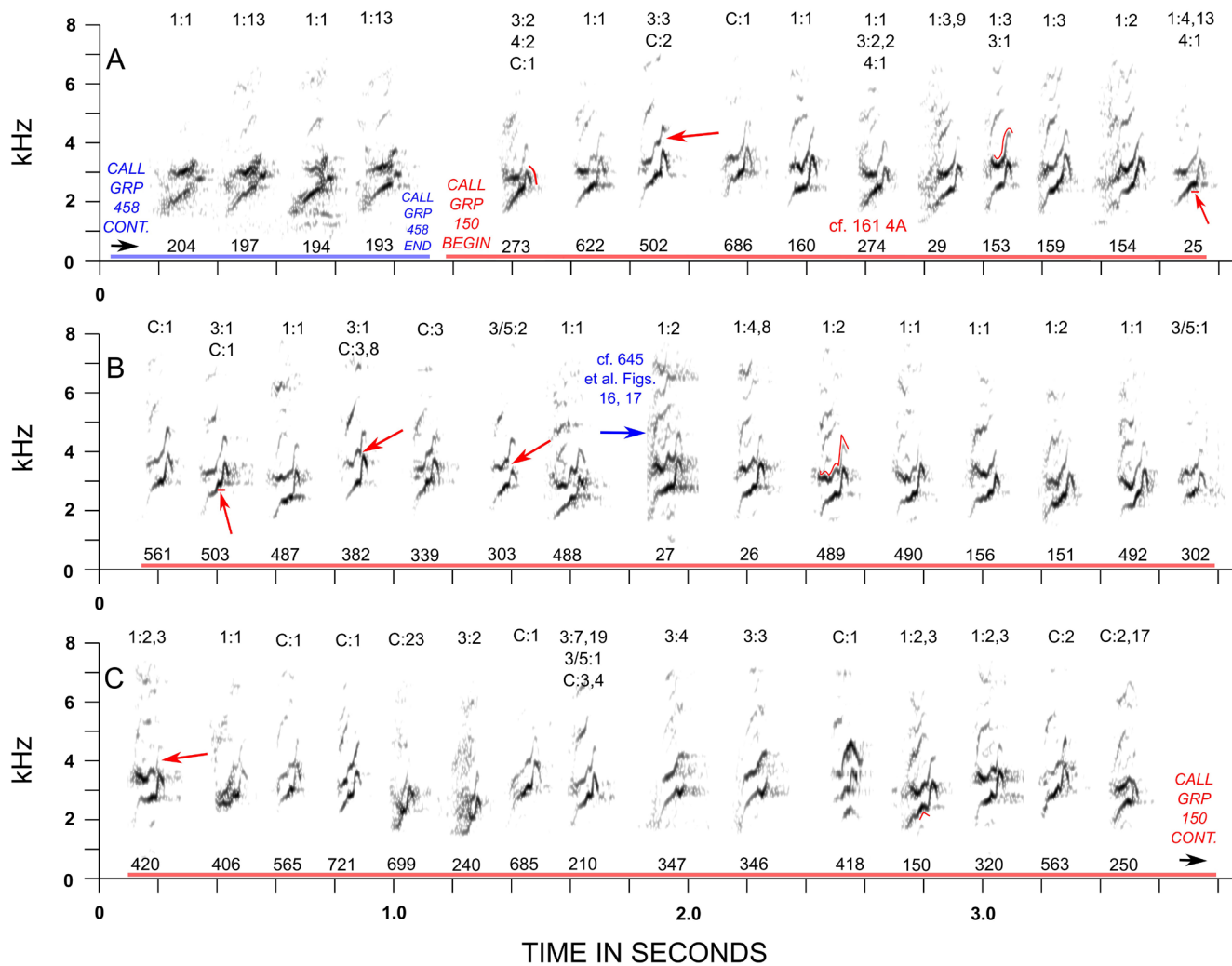




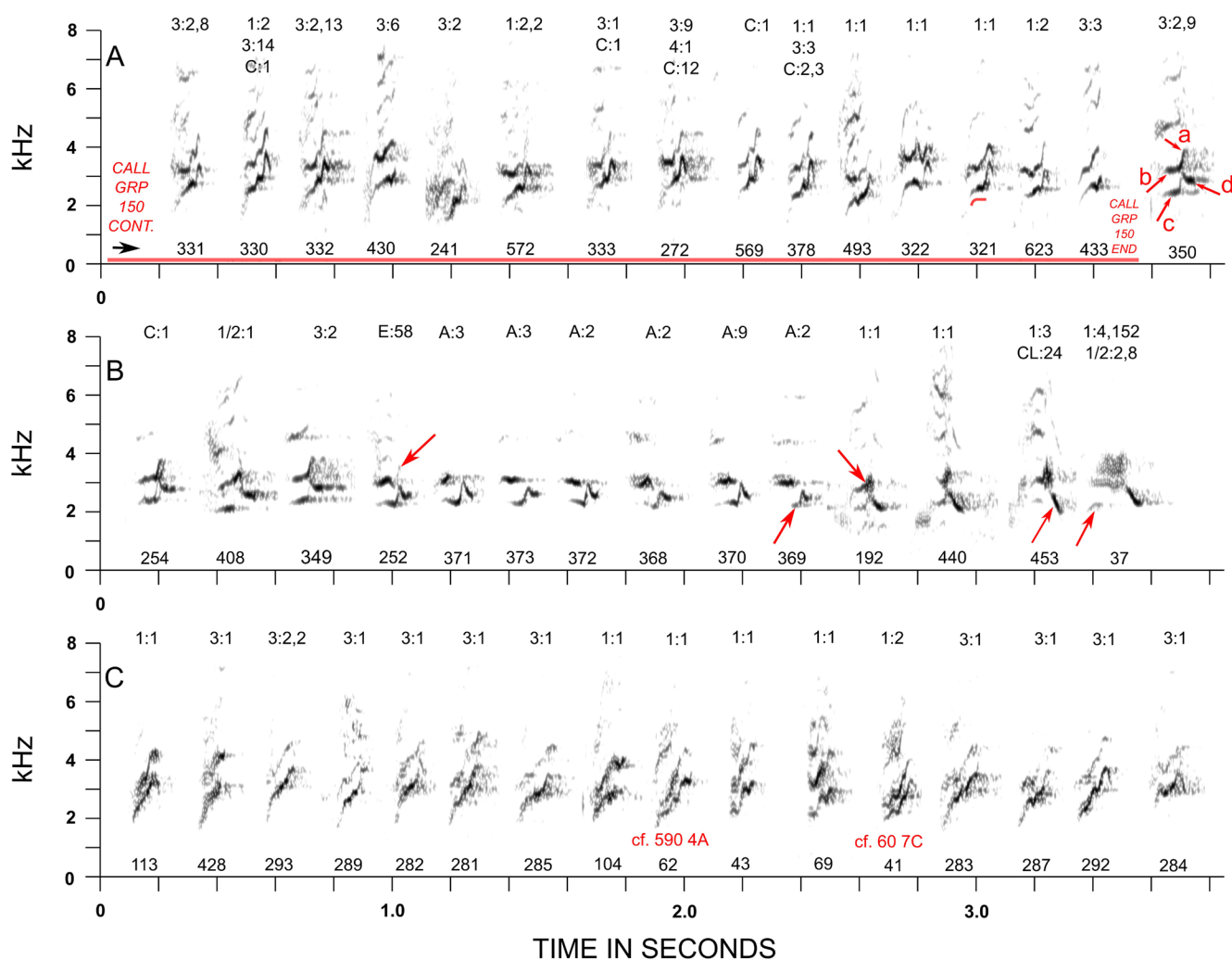
**Figure 7.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Form and Variety of Calls for terms describing the features of the sonograms and explanations of the numbers and letters accompanying them. Calls 618-700 (rows A and B) continue the trend established in the last part of Figure 6 (calls 51-267, row C), with the heads of the lower bands curving upward subtly among those on the left (e.g., call 586, row A), through those curving gently downward (e.g., call 633, row A), to those with these bands flexed strongly downward to the right (e.g., calls 675 and 700, row B). The sonograms in row C are generally similar to the others in Figures 6 and 7, but the heads of the bands show markedly greater fluctuation in frequency (e.g., call 48).



**Figure 8.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Form and Variety of Calls for terms describing the features of the sonograms and explanations of the numbers and letters accompanying them. Here begins a series of sonograms similar to those in Figures 6 and 7, but with the tails faint (e.g., arrow, call 458, row A) or absent, and most with a distinctive penumbra or halo of sound energy parallel to the darker traces of the heads (e.g., arrows, call 163, row A, and 417, row B). As we have arranged them here, the overall tendency from left to right is for the tails to go from faint to absent, for the orientation of the bands to vary from roughly horizontal (e.g., call 149, row A) to upwardly inflected (e.g., call 100, row C), and for the penumbra to lose its distinctive banded appearance. Several calls at the right end of the series have a kink or angle in the upper part of the lower band (e.g., call 99, row C), with a bar extending to the right at its peak (e.g., arrow, call 119, row C).

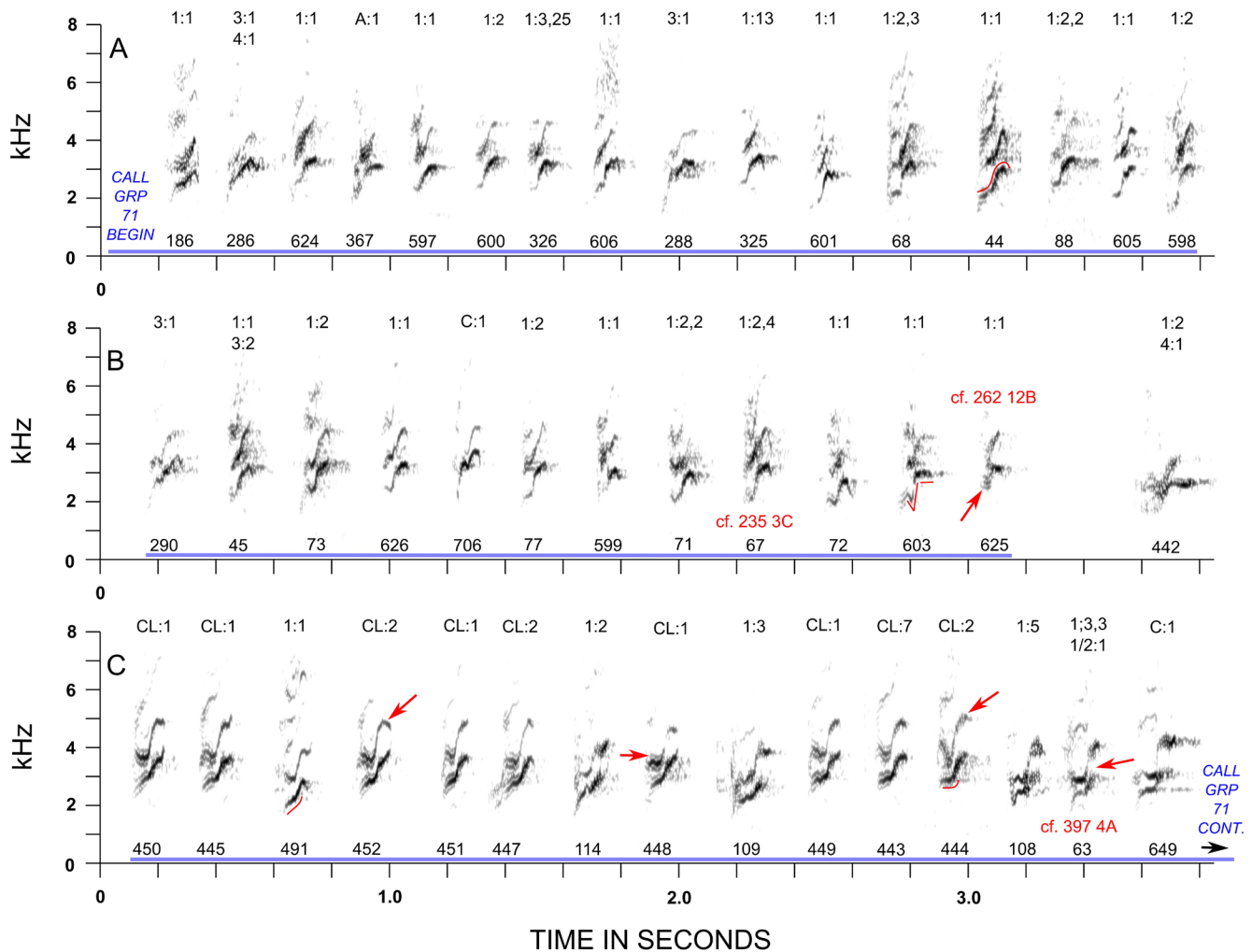


**Figure 9.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Form and Variety of Calls for terms describing the features of the sonograms and explanations of the numbers and letters accompanying them. The sonograms at the left in row A share the same basic features as those at the right in row C of Figure 8. The sonograms to the right of 193 have a down-swept stroke instead of the bar at the top of the lower band (e.g., call 273, row A), and most have more sharply defined bands. In calls 502 (row A) through 420 (row C), the lower band shows a short horizontal shelf (e.g., arrows, calls 25, row A, and 503, row B). Among these calls, there is an overall trend from left to right for the upper band to become more complexly inflected (e.g., 153, row A vs. 489, row B). There is also variety in the degree to which the bands are separated from one another (e.g., arrows, 382 vs. 303, row B), and in the extent or darkness of the upper band (e.g., arrows, 502, row A, vs. 420, row C). In call 420, the combination of indistinctness in the upper band and the close approach of the upper and lower gives the overall sonogram trace an atypical box-like structure, which however can clearly be seen to be constructed of the same basic elements as the other calls in this figure. Calls 406 through 250 (row C) have instead of a horizontal shelf an upward-pointing notch (e.g., call 150, row C); these calls also show a range of variation in separation between the bands, and the extent of the upper band.

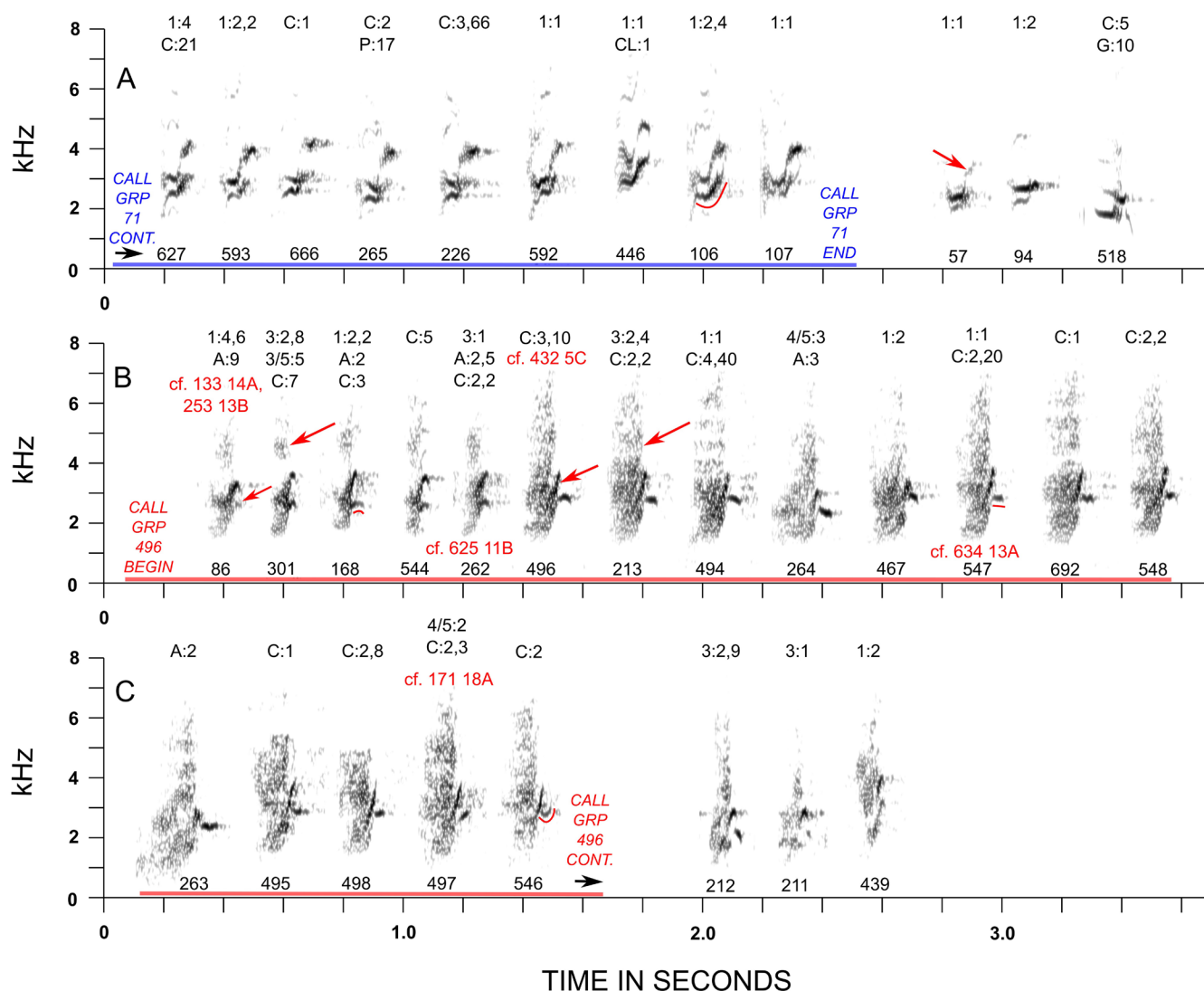


**Figure 10.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Form and Variety of Calls for terms describing the features of the sonograms and explanations of the numbers and letters accompanying them. The sonograms to the left in row A are similar to those of row C in Figure 9. Those toward the right in row A show a tendency for the base of the lower band to be oriented horizontally overall (e.g., call 321). Call 350, row A, serves as a link between the calls in that row and those in row B. As the sequence continues to the right through row B, the head of the upper band (call 350, arrow a) drops out, the lower part of the upper band (350 b) is roughly horizontal, and is eventually replaced by a peaked blob of diffuse texture (arrow, call 192). The lower part of the lower band (350 c) becomes smaller, fainter, and disconnected from the rest of the sonogram (e.g., arrows, calls 369, 37) while the upper part of the lower band (350 d) becomes heavier and inflected downward more strongly (e.g., arrow, call 453). Thus calls as dissimilar as 331 (row A) and 37 (row B) can be seen to be the results of successive multiple modifications to a few basic elements. The calls in row C recall those in the row C of Figure 4, but the bands are not as sharply defined and show more modulation in frequency.



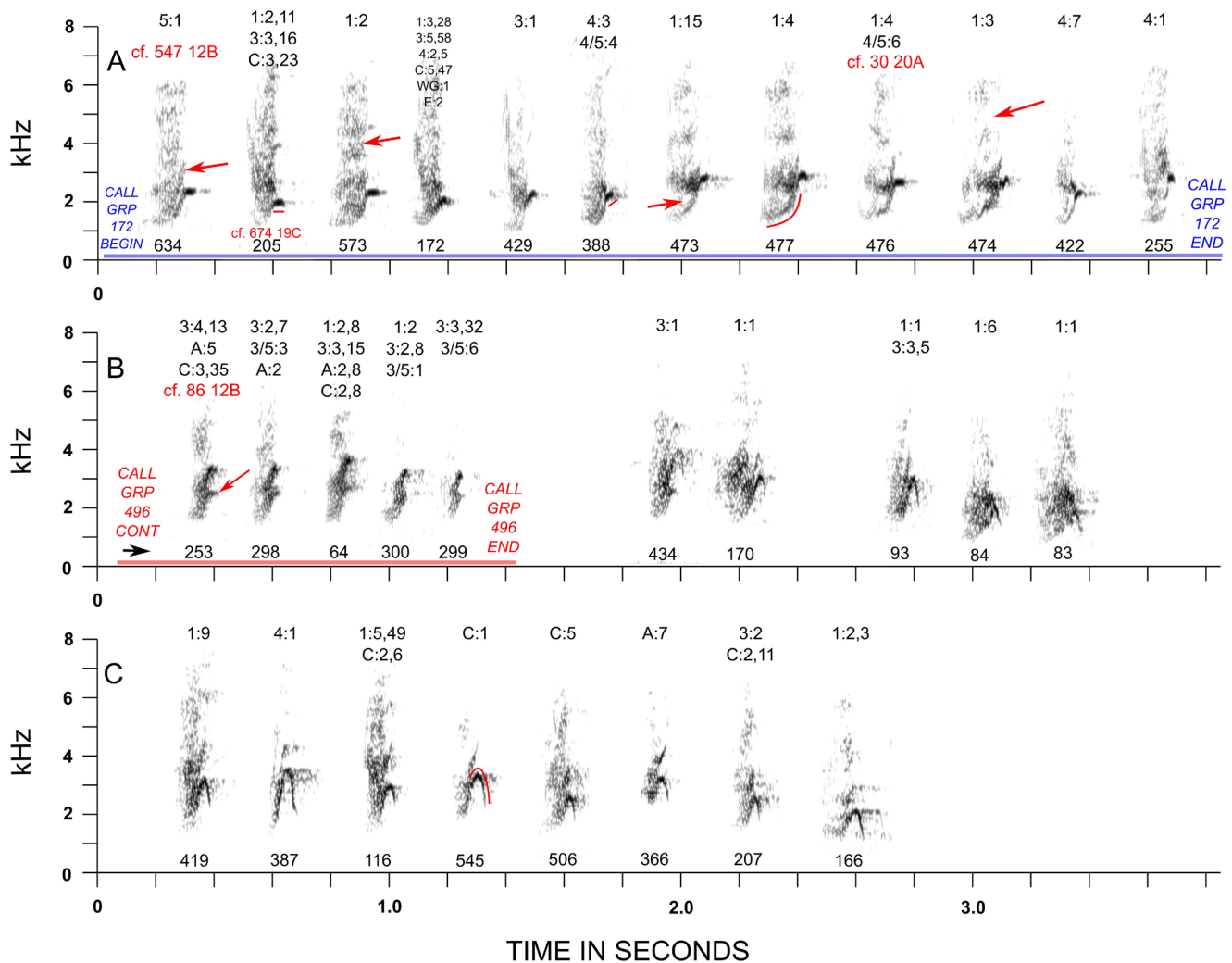


**Figure 11.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Form and Variety of Calls for terms describing the features of the sonograms and explanations of the numbers and letters accompanying them. These calls are similar to those in row C of Figure 10. As the series progresses to the right, the lower bands develop a characteristic smooth sigmoid curve (e.g., call 44, row A). Calls 603 and 625 of row B stand out but still show affinities to those preceding them. Both of these calls retain the indistinct head of the upper band seen in call 72, while 603 also retains the characteristic frequency modulation in the tail of the lower band. In both, the terminal part of the lower band is horizontal rather than curved downward, while in 625 the tail of the lower band is replaced by a series of faint bars (arrow) resembling those in the sonograms of row C, and forming a link with those calls. Call 442 does not fit neatly into this series, but we place it here (row B) for lack of closer affinity with any other group of calls. The sonograms in row C exhibit halo-like traces (e.g., arrow, call 448) similar to those of call 625, row B (and those in Fig. 8). From left to right in row C there is a tendency for the base of the lower band to incline toward the horizontal (e.g., call 491 vs. call 444), for the upper part of the lower band to be de-emphasized (e.g., arrow, call 63), and for the tip of the upper band to take on a club-like form with an open lattice-like texture (e.g., arrows, call 452 vs. 444).

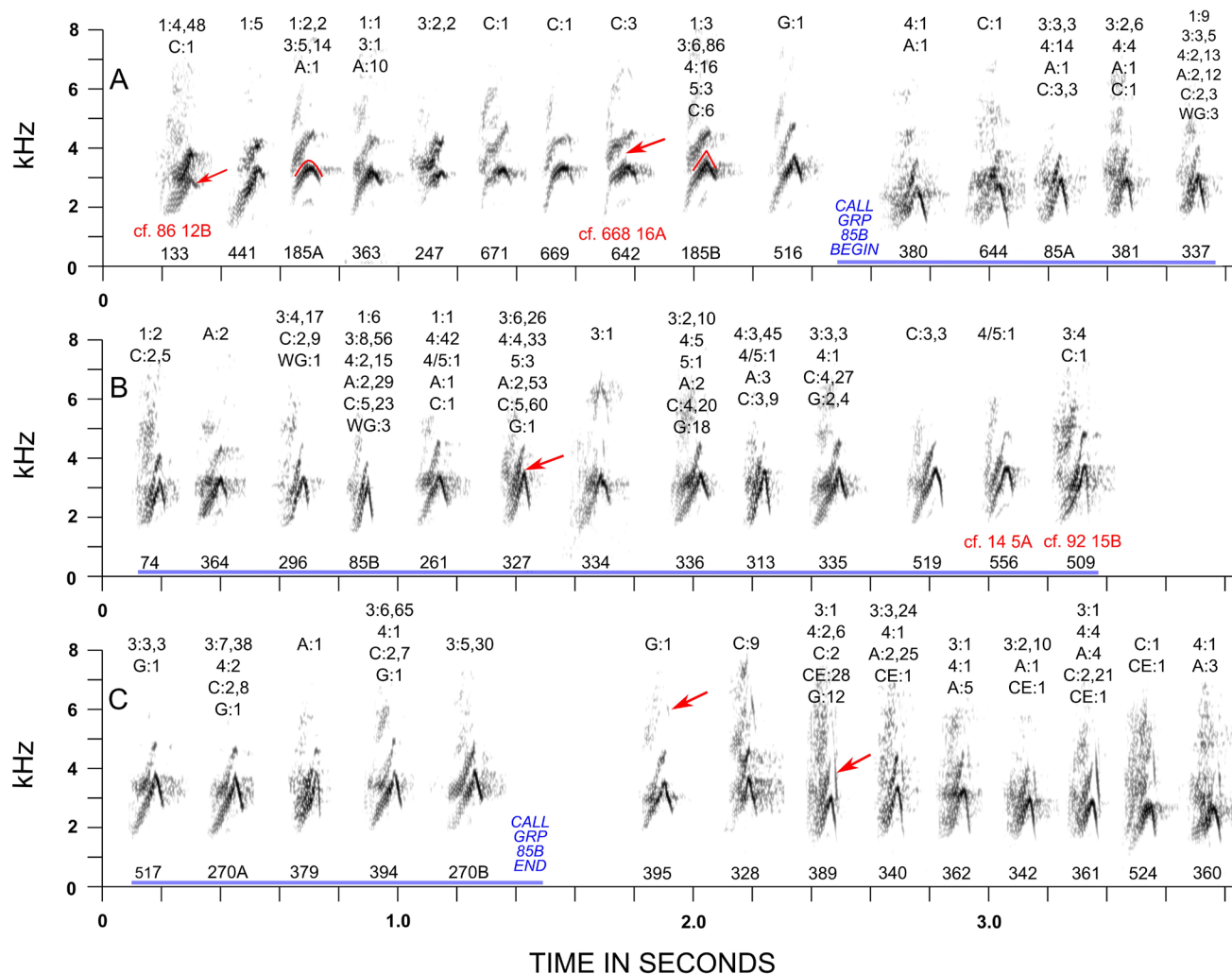


**Figure 12.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Form and Variety of Calls for terms describing the features of the sonograms and explanations of the numbers and letters accompanying them. The calls in row A continue the series begun in row C of Figure 11, with a tendency for the sonograms at the right to have the tail of the lower band extending upward, giving the band a J shape (e.g., call 106). Sonogram 57 stands out but still shows affinities with calls preceding it, including the orientation of the lower parts of the two bands and a faint upward extension of the lower band (arrow). Call 94 has no upward extension of the upper band, but still shows the two main traces visible in call 57. Call 518 is yet further distinguished from the rest of the calls in this row; we place it here for lack of closer affinity with any other group of sonograms. In comparison to the dark and sharply rendered forms of many calls in previous figures (e.g., Fig. 2), the sonograms at the left in row B have broad traces and a hazy texture. They and the calls following them, through 546 in row C, show an overall tendency for the blur of unorganized higher-frequency sound above the main call to increase in length and volume (e.g., arrows, call 301 vs. 213); for the upper band to become more distinct and taper to a point (e.g., arrow, call 496); and for the head of the lower band to vary from a barely visible stub (arrow, call 86), through a downward curve (e.g., call 168), then a straight nearly horizontal line (e.g., call 547), and then an upward curve (e.g., call 546). Calls 212 through 439 in row C do not fit neatly into this series, but we place them here for lack of closer affinity with any other group of calls.

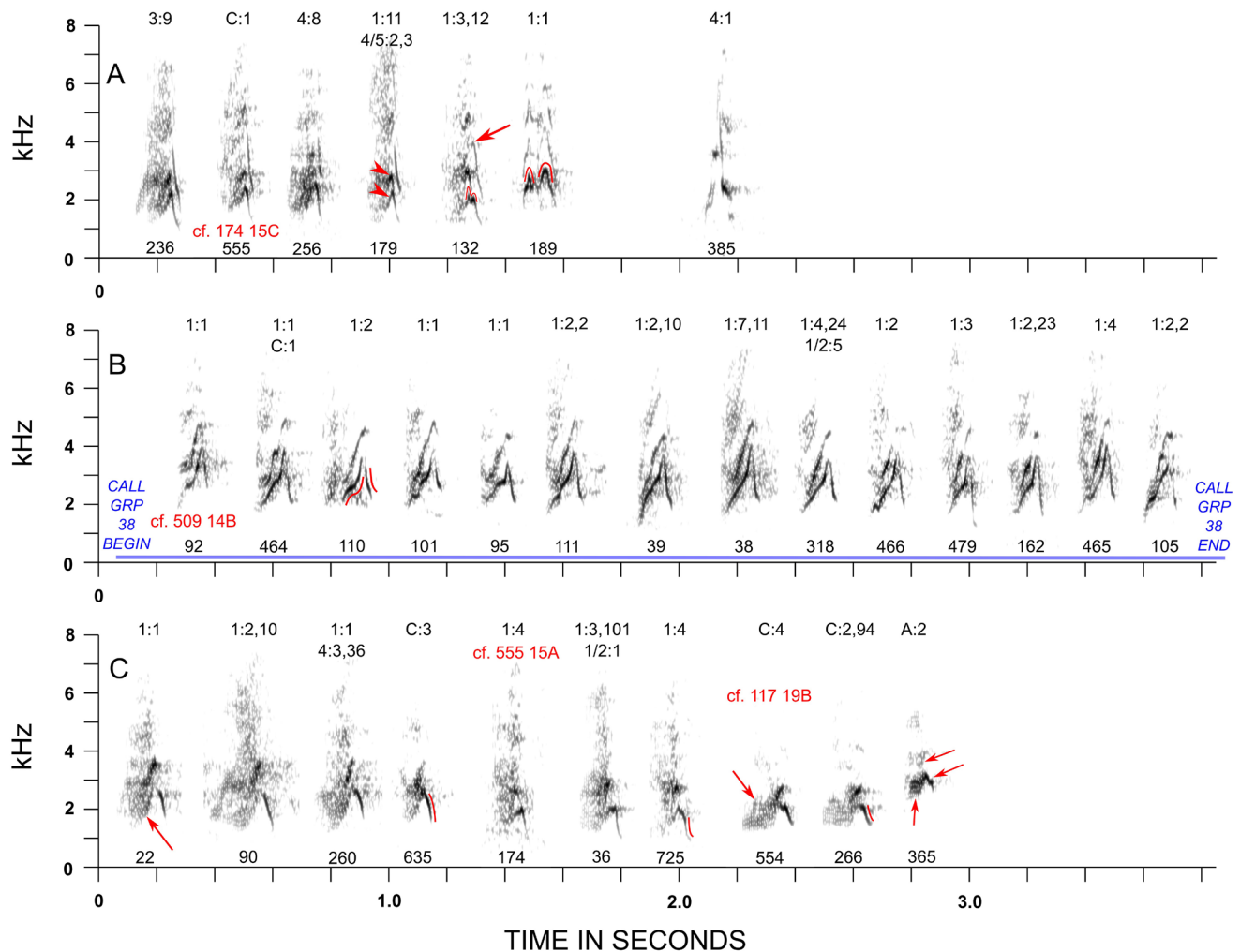




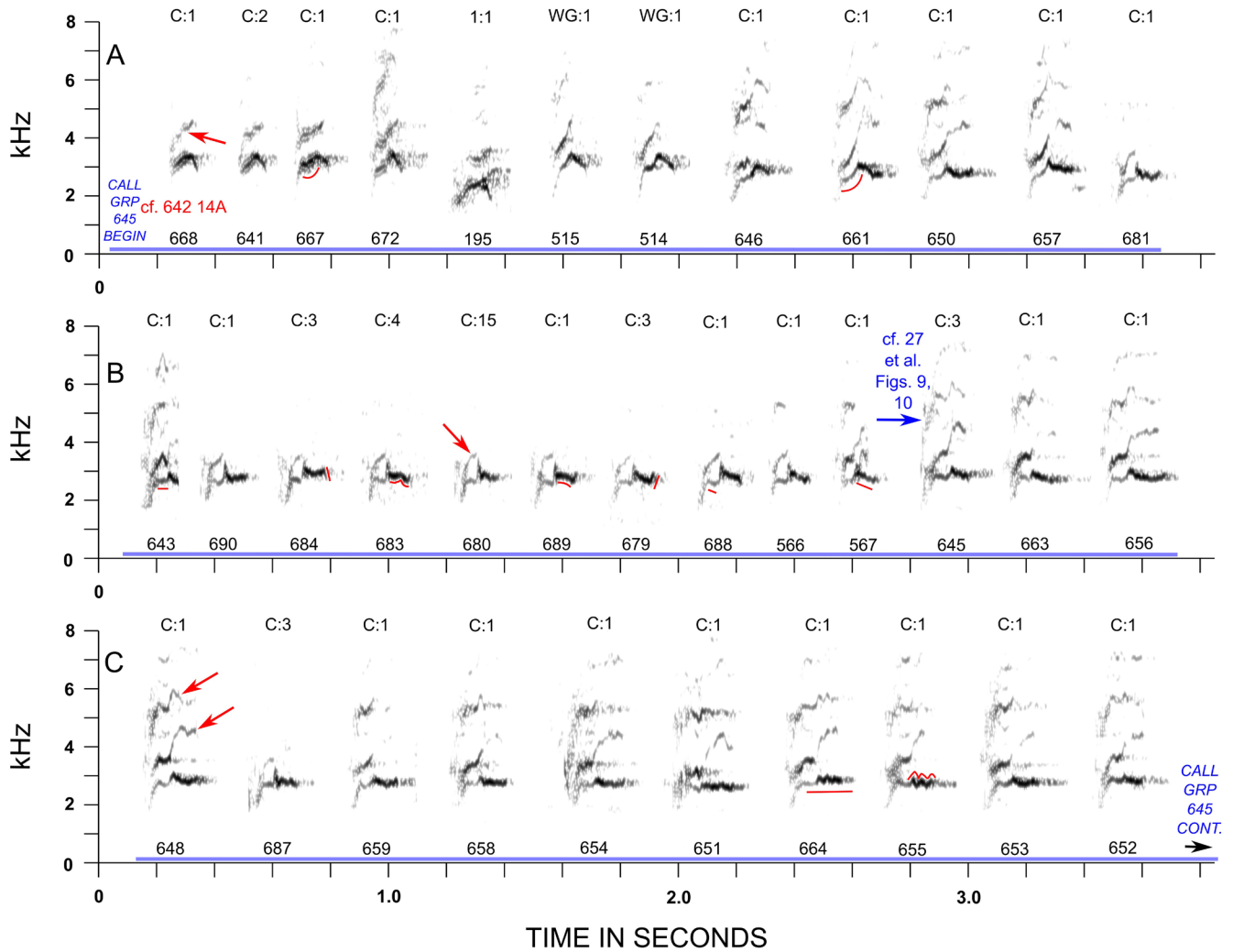
**Figure 13.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Form and Variety of Calls for terms describing the features of the sonograms and explanations of the numbers and letters accompanying them. At the far left of row A, note the similarity of call 634, including its faint upper band (arrow), to call 213 in row B, Figure 12, from which the series of calls in row A can be considered to branch. From left to right the calls in row A show an overall trend toward reduction in the mass of unorganized higher-frequency sound (e.g., arrows, call 573 vs. 474), for the top of the lower band to range from horizontal toward more upwardly inflected (e.g., call 205 vs. 388), and for a space to open up between the tails of the upper and lower bands (e.g., arrow, call 473). All the calls also show a characteristic long, smooth upward sweep of the lower band (e.g., call 477). At the far left of row B, note the similarity of call 253 to call 86 in row B, Figure 12, from which call 253 through 299 can be considered to branch. From left to right in this row, the trend is toward reduction in the rightward extension of the lower band (arrow, call 253), and simplification of the entire sonogram. The remaining calls in row B are a miscellany of sounds that do not fit readily into any of the broad categories of calls illustrated in these figures. The calls in row C are distinctive in having the lower band rising and falling in a long smooth curve (e.g., call 545) rather than in the form of a sharp inverted chevron, such as in most of those in the second row of Figure 14.



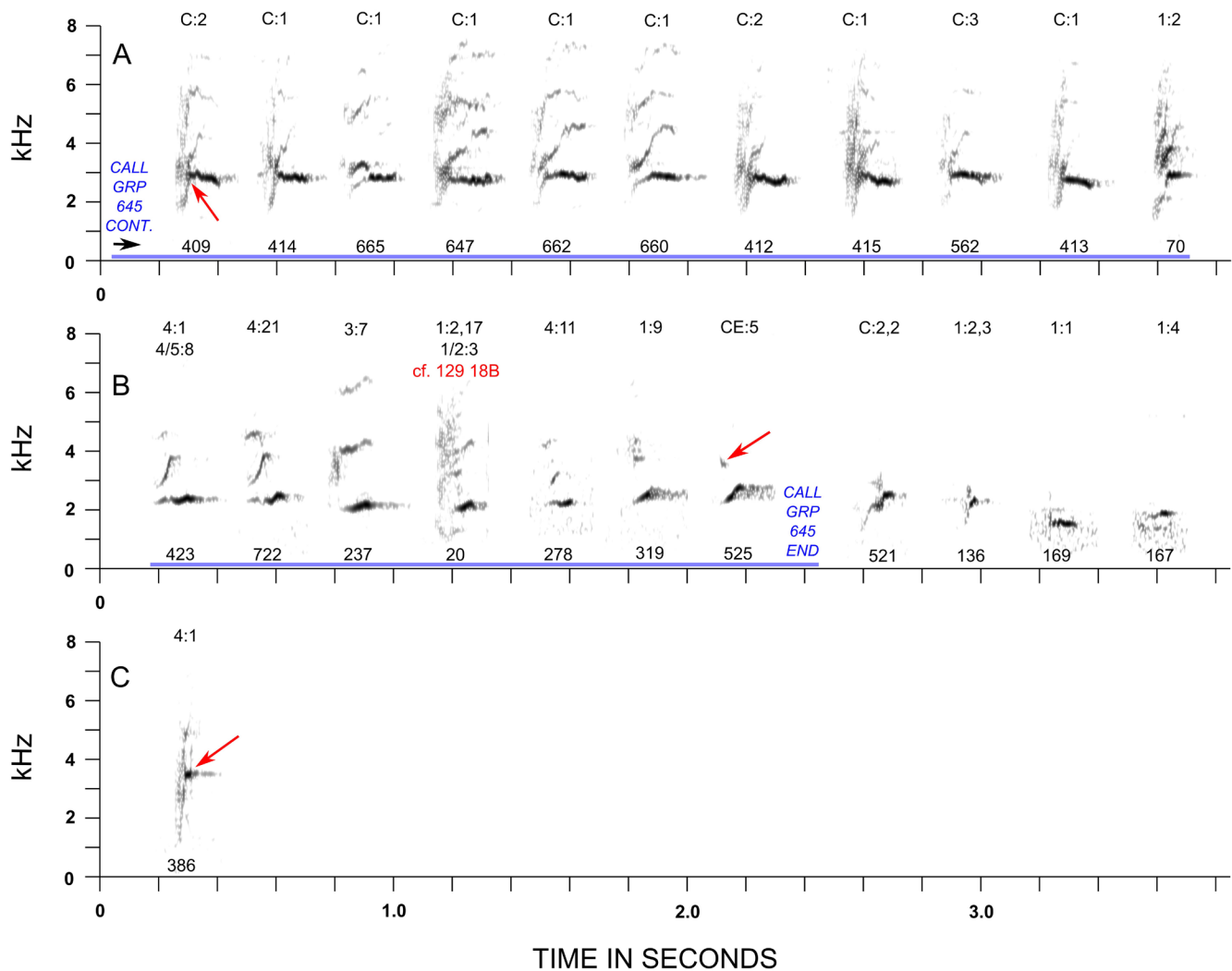
**Figure 14.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Form and Variety of Calls for terms describing the features of the sonograms and explanations of the numbers and letters accompanying them. Note the similarity of call 133 in row A to call 86 in row B of Figure 12, from which the series of calls through 516 in row A can be considered to branch. Sonograms 133 through 516 share with call 86 their broad traces and hazy texture, unlike, for instance, the sharp and dark traces of the sonograms in Figure 2. As this series progresses toward the right the calls show a general tendency for the two bands to separate from one another and for the head of the lower band (e.g., arrow, call 133) to lengthen, in some cases in a smooth downward curve (e.g., call 185A) or in others to form an angle (e.g., call 185B). Call 516 is a link to the series of calls from 380, row A, through 270B, row C, which resemble it in having the upper band and the tail of the lower with the same blurry texture; the head of the lower tends to be more sharply defined and descends sharply from its peak (e.g., arrow, call 327). Calls 380 through 270B are distinguished from one another by differences in the relative lengths of, and the acuity of the angle between, the rising and falling parts of the lower band; small differences in the curvature of the bands, and in the height of the lower band's peak. The peak for call 380 is 2.75 kHz, for call 261, 3.4 kHz, and for call 270B, 4.0 kHz. Calls 389-360, row C (and to a lesser extent, calls 395 and 328), are similar to 380-270B but have an additional sharply descending terminal tone (e.g., arrows, calls 395, 389).



**Figure 15.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Form and Variety of Calls for terms describing the features of the sonograms and explanations of the numbers and letters accompanying them. Calls 236 through 189, row A, have the sharply down-swept high-frequency tones (e.g., arrow, call 132) of calls 389-360 in row C of Figure 14. Short arrows (call 179) indicate peaks in both upper and lower bands, and red lines trace the double inflections of the lower bands in calls 132 and 189. Call 385 is much simplified in comparison to the others in row A. The calls in row B are similar in overall form to calls 380-270 in rows A through C of Figure 14, but differ in having the bands broadly flexed (e.g., call 110) and generally more sharply defined. Calls 22 through 266 of row C make up another series of calls similar to 380-270B of Figure 14, but with the lower parts of both bands generally ill defined (e.g., arrows, calls 22 and 554), and most with distinctive curves in the descending limb of the the lower band (e.g., arrows, calls 635, 725, 266). Call 365 is allied tenuously to the rest to the calls in this series by virtue of traces of three elements it has in common with them (arrows).

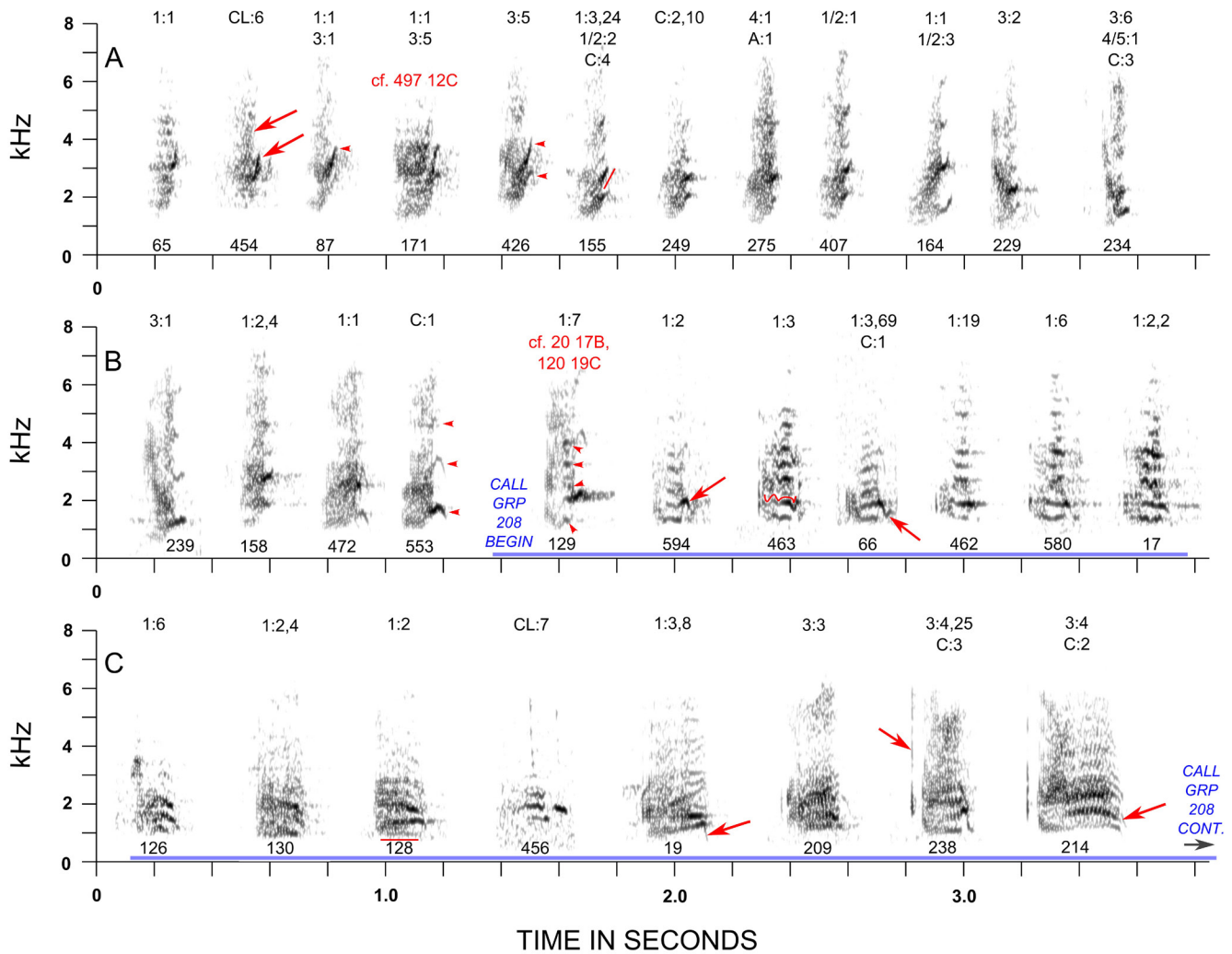


**Figure 16.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Form and Variety of Calls for terms describing the features of the sonograms and explanations of the numbers and letters accompanying them. Note the similarity between call 668 at the left of row A, and call 642 in row A of Figure 14, from which the long transforming series of calls in this and Figure 17 can be considered to branch. As the series proceeds to the right from call 667 in row A, the upward curve in the lower band (e.g., calls 667, 661) is replaced by segments with a major horizontal component (e.g., call 643, row B) or downwardly inflected component (e.g., call 688, row B). In this same series the head of the lower band proceeds generally from downwardly inflected (e.g., call 567, row B) to horizontal (e.g., call 664, row C). These calls exhibit variety in modulation of the lower bands (e.g., calls 684, 683, 689, 679 in row B; 655 in row C), and in the complex elaboration of the upper bands (e.g., arrows, call 680 in row B vs. call 648 in row C) that does not seem to form any overall trend.

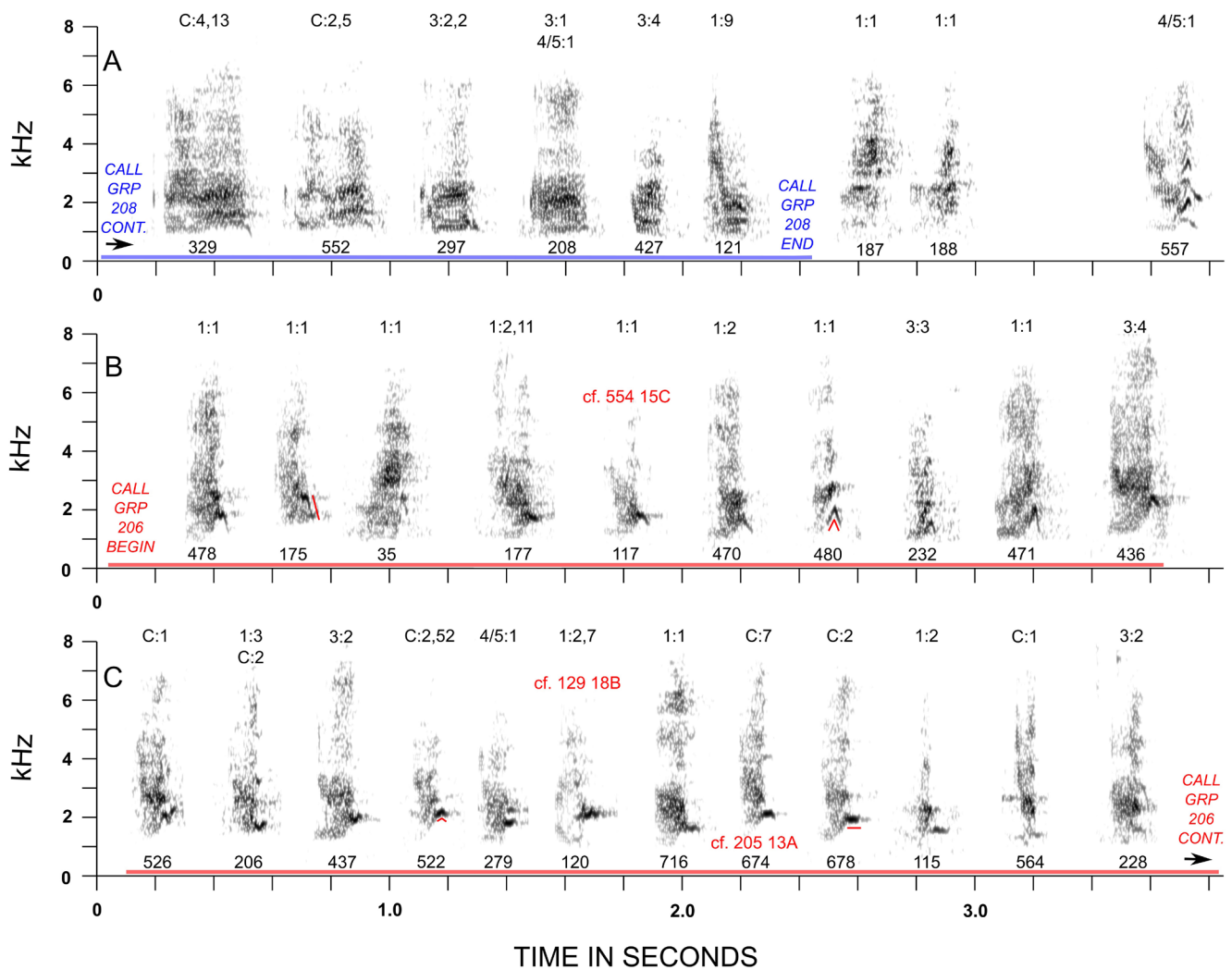


**Figure 17.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Form and Variety of Calls for terms describing the features of the sonograms and explanations of the numbers and letters accompanying them. Calls 409 (row A) through 167 (row B) continue the series begun in Figure 16, but lack the curving or angled segment at the junction of the tail and head of the lower band (e.g., arrow, call 409; compare to calls 661, 643, and 688 in rows A and B of Fig. 16). From left to right the sequence in rows A and B shows a gradual and overall reduction in the upper bands (e.g., arrow, call 525, row B) and simplification of the lower band, to a point at which the calls at the far right in row B only faintly resemble those at the beginning of row A. Call 386, row C, does not fit well into the series but does resemble call 70 (far right, row A) in its short duration and the extreme brevity of the darkest trace in the lower band (arrow).

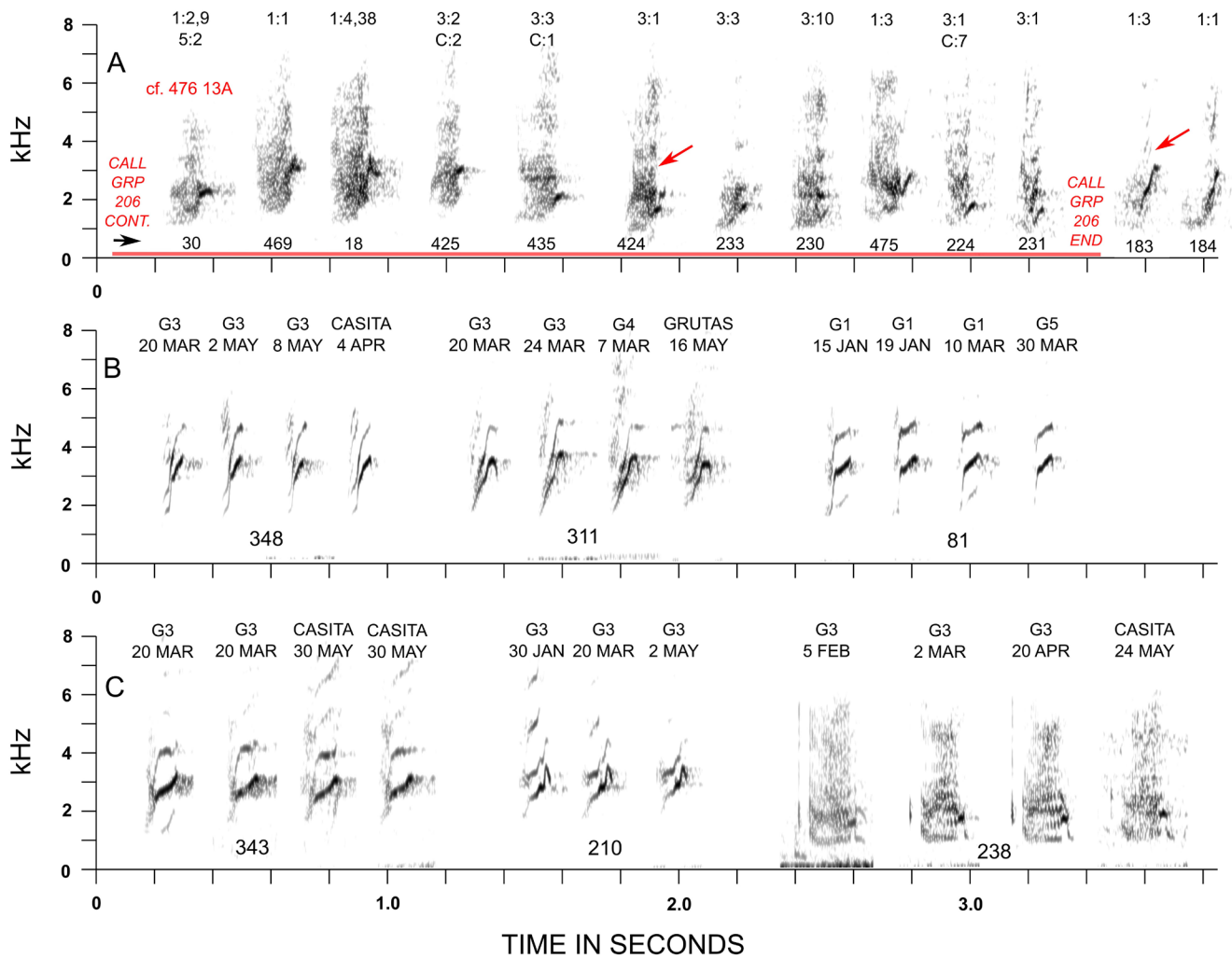




**Figure 18.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Form and Variety of Calls for terms describing the features of the sonograms and explanations of the numbers and letters accompanying them. Note the similarity of call 171 in row A to call 496 and its neighbors in row B of Figure 12, from which the transforming series of calls in the present figure can be considered to branch. The calls at the left of row A have single bands rising sharply out of a mass of unorganized sound (e.g., arrows, call 454). The overall trend from left to right throughout this figure is for the duration of the calls to increase; the unorganized sound to resolve into bands, which increase in number (e.g., short arrows, calls 87 and 426, row A, calls 553 and 129, row B); the bands to change from upwardly inflected (e.g., call 155, row A) to near horizontal (e.g., call 128, row C); and for the bands to show rapid changes in frequency (e.g., call 463, row B). Some at the right end of the series show an audible click at the beginning (e.g., arrow, call 238, row C). At various points in the series some of the finely drawn bands have a flourish that can be inflected downward (e.g., arrows, calls 594, row B; calls 19, 214, row C, this last one subtle), or downward and then upward (arrow, call 66, row B). Thus a series of intermediate graded stages connect strongly dissimilar calls at the end points.

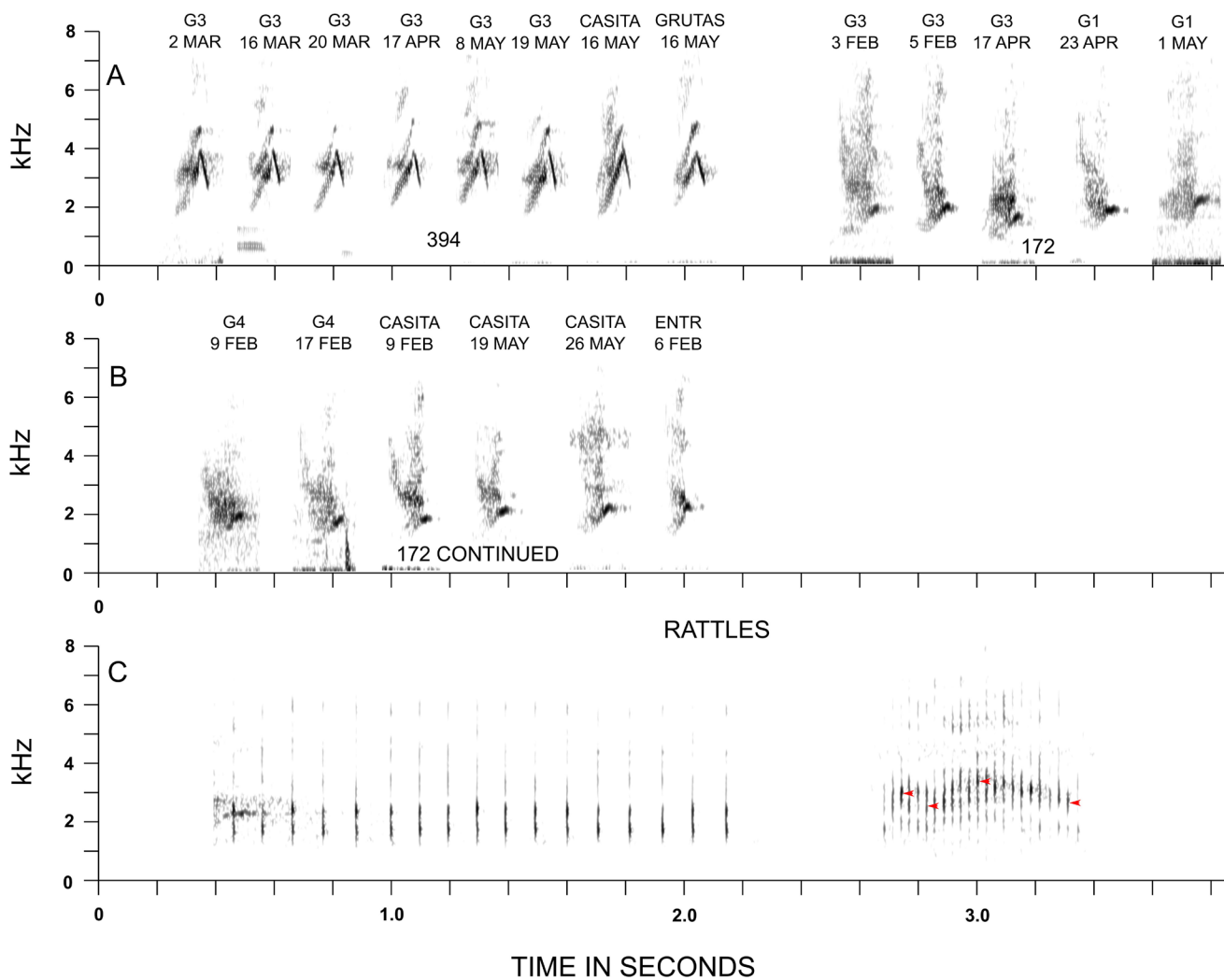


**Figure 19.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Form and Variety of Calls for terms describing the features of the sonograms and explanations of the numbers and letters accompanying them. In row A, calls similar to those in row C of Figure 18 grade into calls of shorter duration with bands less sharply defined, but retaining their horizontal orientation. The multiple bands of call 557 are similar to those of certain others in Figures 18 and 19, but this call does not fit readily into that sequence, and we place it here for lack of closer affinity to any other group of calls. The calls in rows B and C resemble those at the left in row A of of Figure 18, but the terminal flourish arising from the noisy mass lies at a lower frequency (generally 1.1 kHz to 2.5 kHz), and is not oriented upward. In row B this feature is oriented downward (e.g., call 175) or has the form of a chevron (e.g., call 480). These connect by a graded series to calls in row C, with the flourish horizontal (e.g., call 678) or nearly so (e.g., call 522).

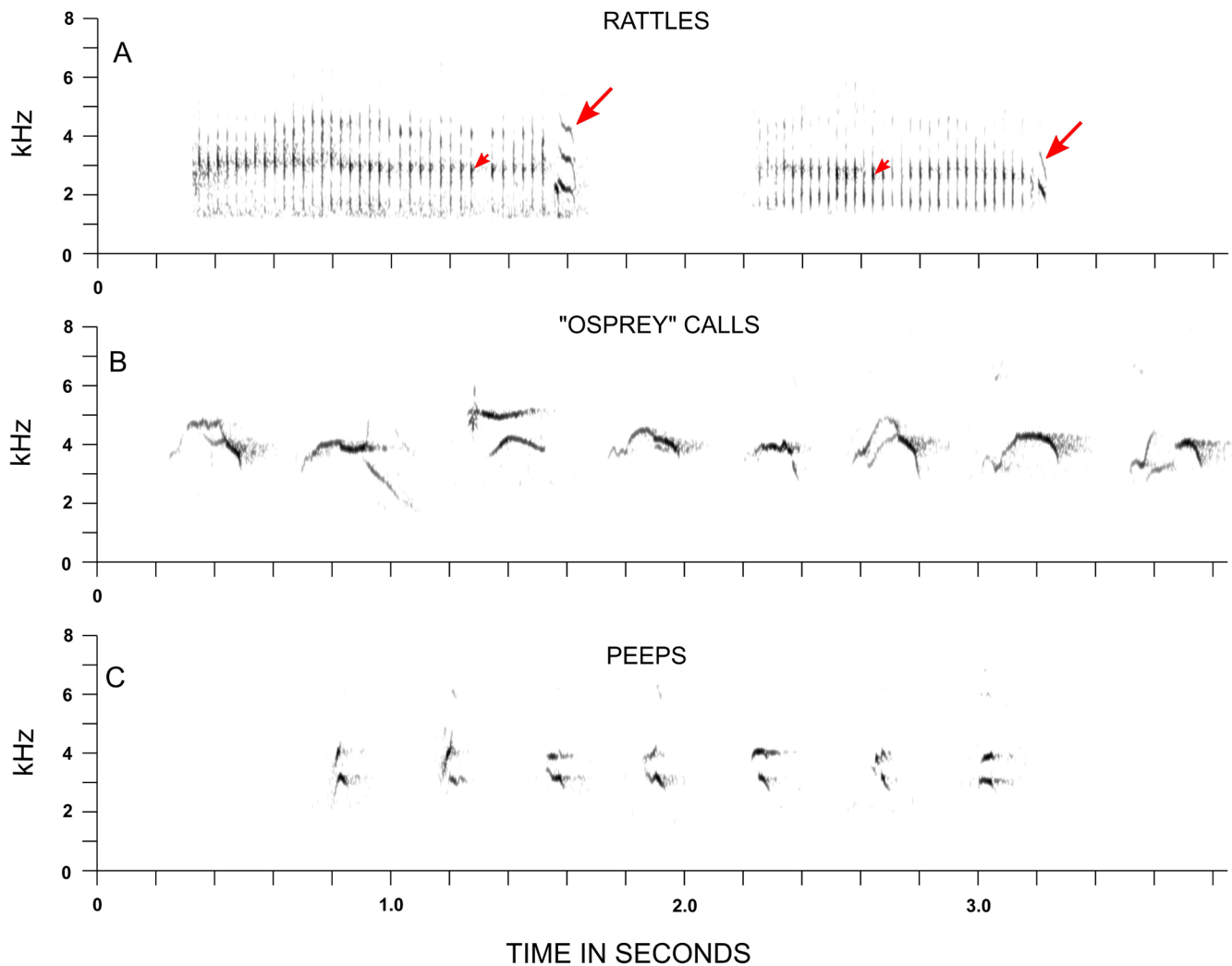


**Figure 20.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Form and Variety of Calls for terms describing the features of the sonograms and explanations of the numbers and letters accompanying them. The calls in row A continue the series begun in row C of Figure 19, with the terminal flourish of call 30 nearly horizontal, and those in the calls to the right upwardly inflected overall. There is also a general tendency for the calls toward the right to be shorter, with the unorganized sound greatly reduced (e.g., arrows, call 424 vs. 183). Note the similarity of call 30 to call 476 in row A of Figure 13, from which the series of calls in this row can also be considered to branch. Rows B and C show examples of consistency from one rendition to another in certain calls of Unicolored Jays at Montebello from January to May 1987. Notations above each sonogram show the jay group in and the date when we recorded it. In each category denoted by the name of a call, such as 343 (left, row B), we judged the individual renditions shown to be closer to one another than to any other variants we scanned, and included them in the counts of that call type.

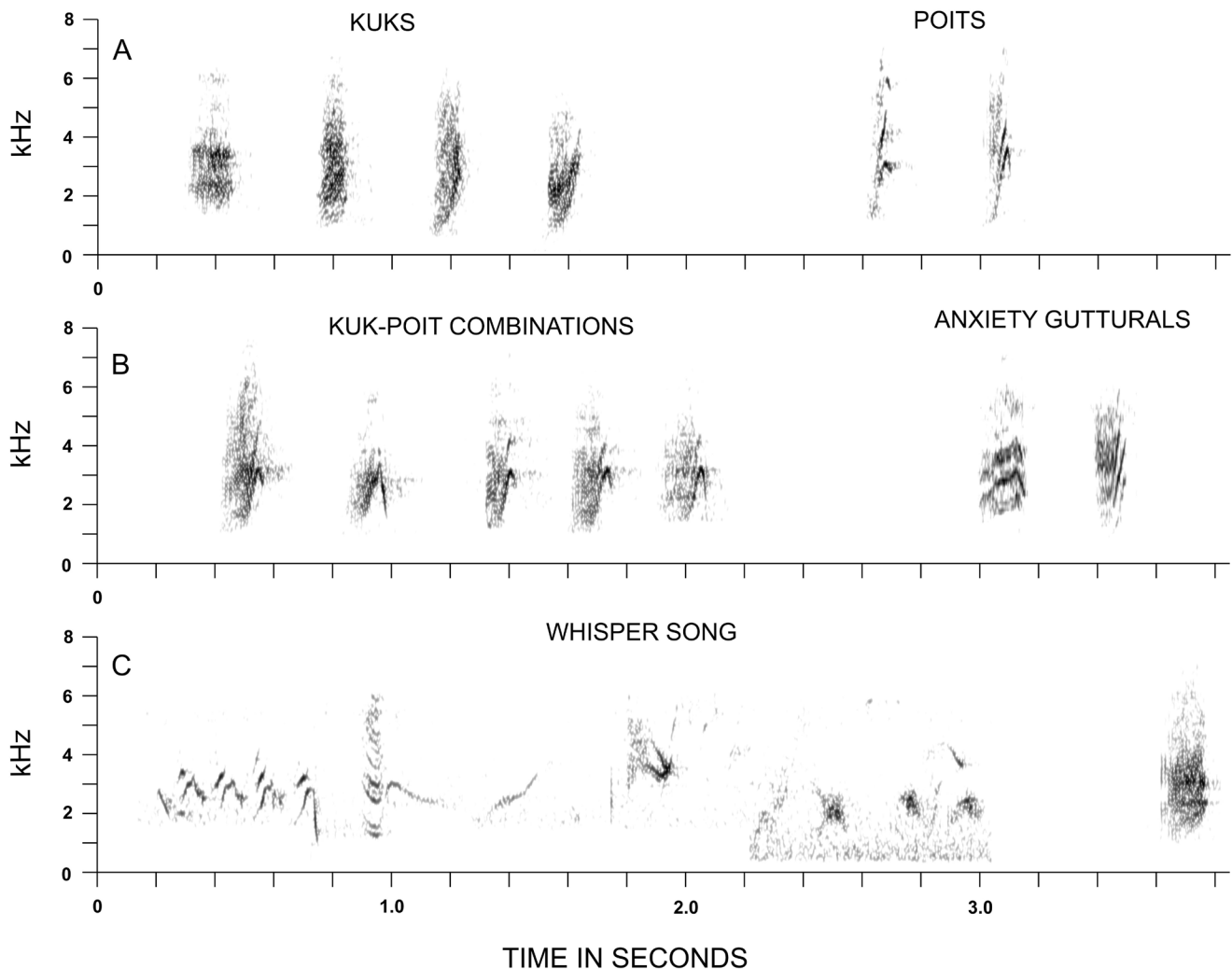




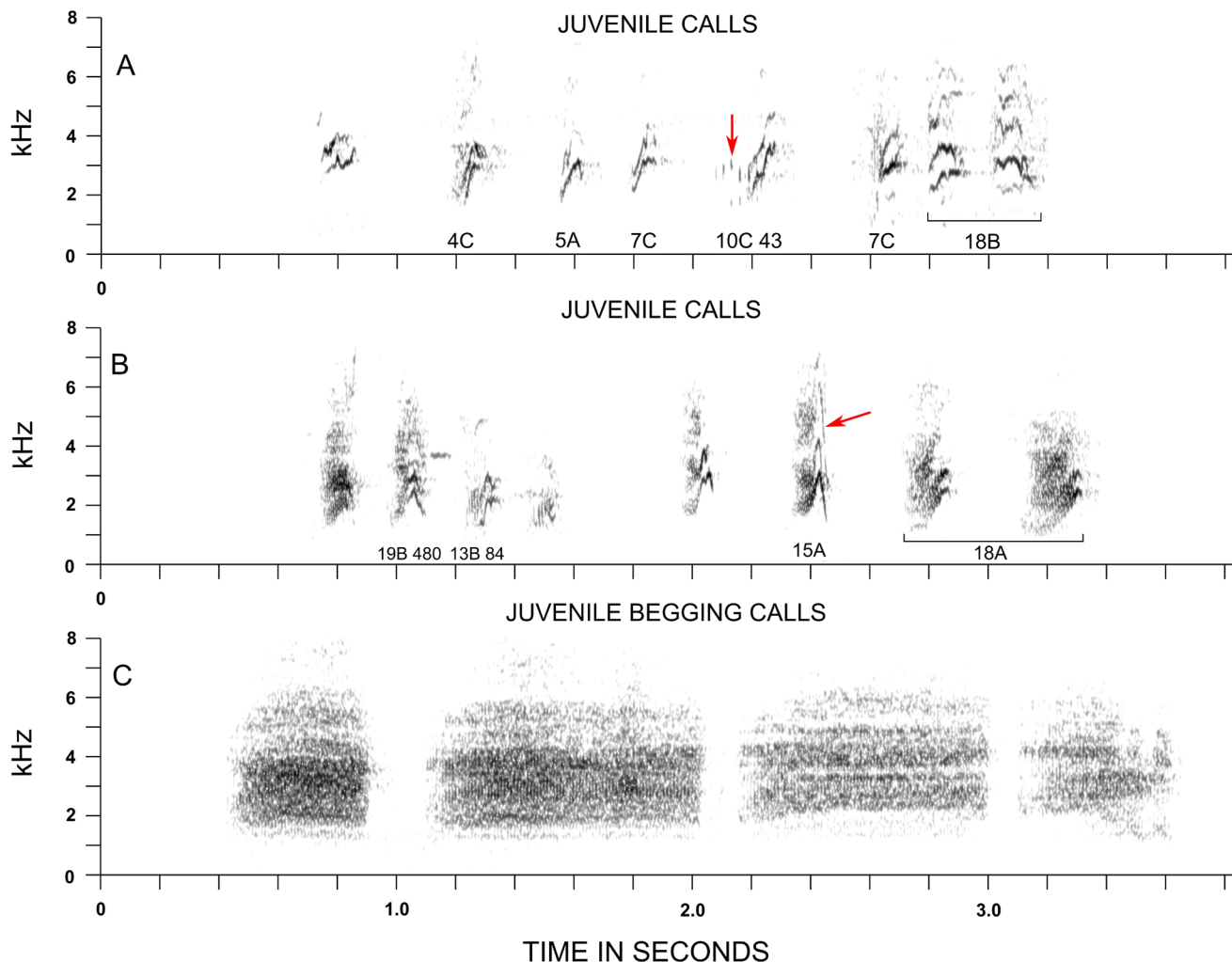
**Figure 21.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. Rows A and B continue examples of consistency in call types. The renditions of call 172 show some variation around the central feature we consider diagnostic for this call: the moderately upward inflection of the terminal flourish. Compare this feature with those of the calls most similar to 172 in Figure 13 row A. Row C, calls of volume lower than those of Figure 2 through row B of Figure 21. We do not show an exhaustive inventory of the variation we recorded in such relatively short-range calls. Row C shows rattle calls, one slow and one fast. Note how the dominant frequency (arrows) in one rattle drifts up and down.



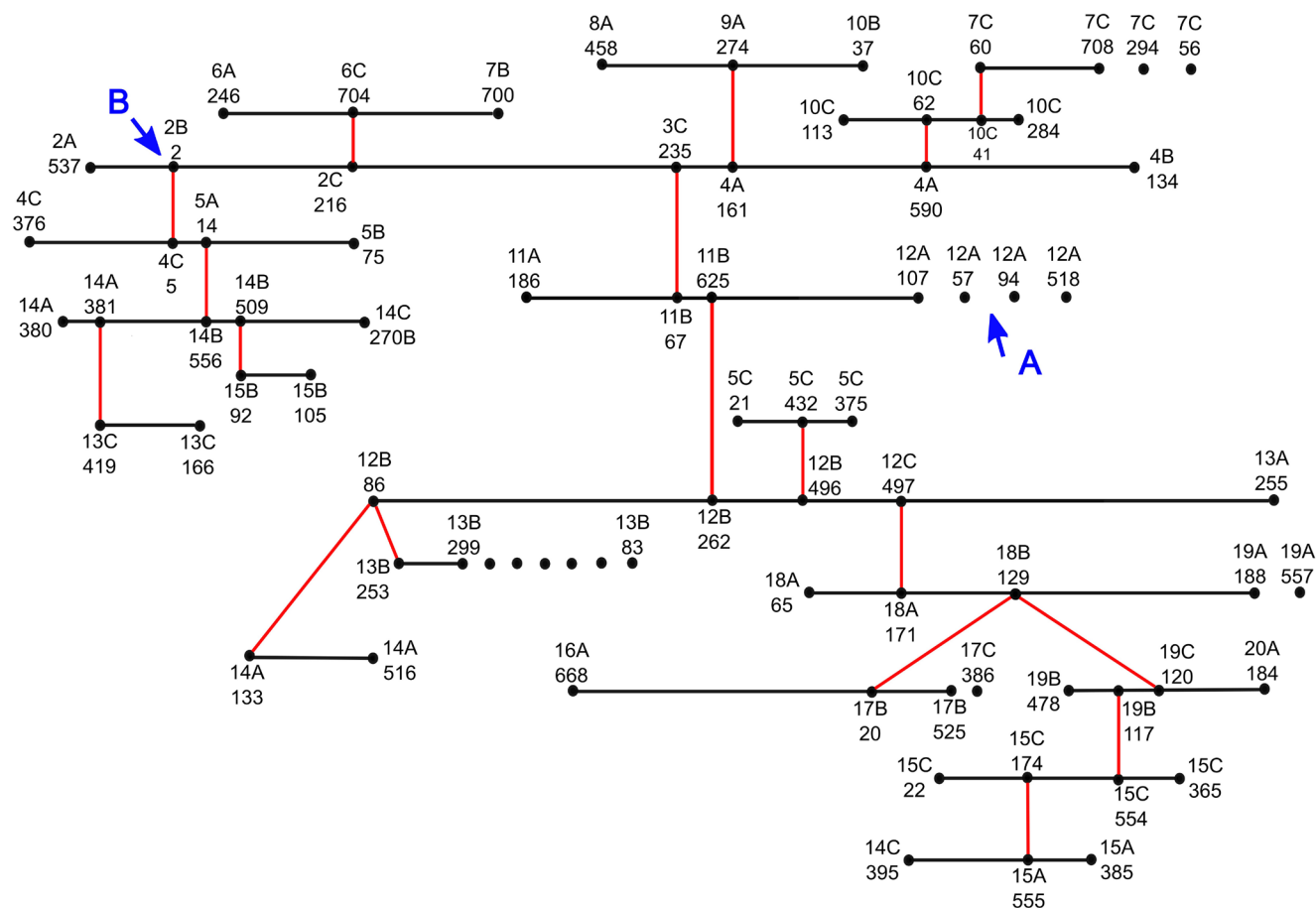
**Figure 22.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. Calls of volume lower than those of Figure 2 through row B of Figure 21. We do not show an exhaustive inventory of the variation we recorded in such relatively short-range calls. Row A, two fast rattles of different lengths, with slightly different versions of the optional squeaky flourish at the end (arrows). Note that the dominant frequency (short arrows) remains fairly steady, unlike the fast rattle in row C of Figure 21. Row B, a variety of Osprey calls, given only on or near the nest. Row C, a variety of peeps, given in contexts similar to those of Osprey calls. Unlike the whisper-song sounds in Figure 23 row C, the series of Osprey calls and peeps here are not continuous sonogram transcripts of single uninterrupted performances by a single bird; they consist of individual calls from several recording sessions placed together, and the intervals between the sounds are reduced.



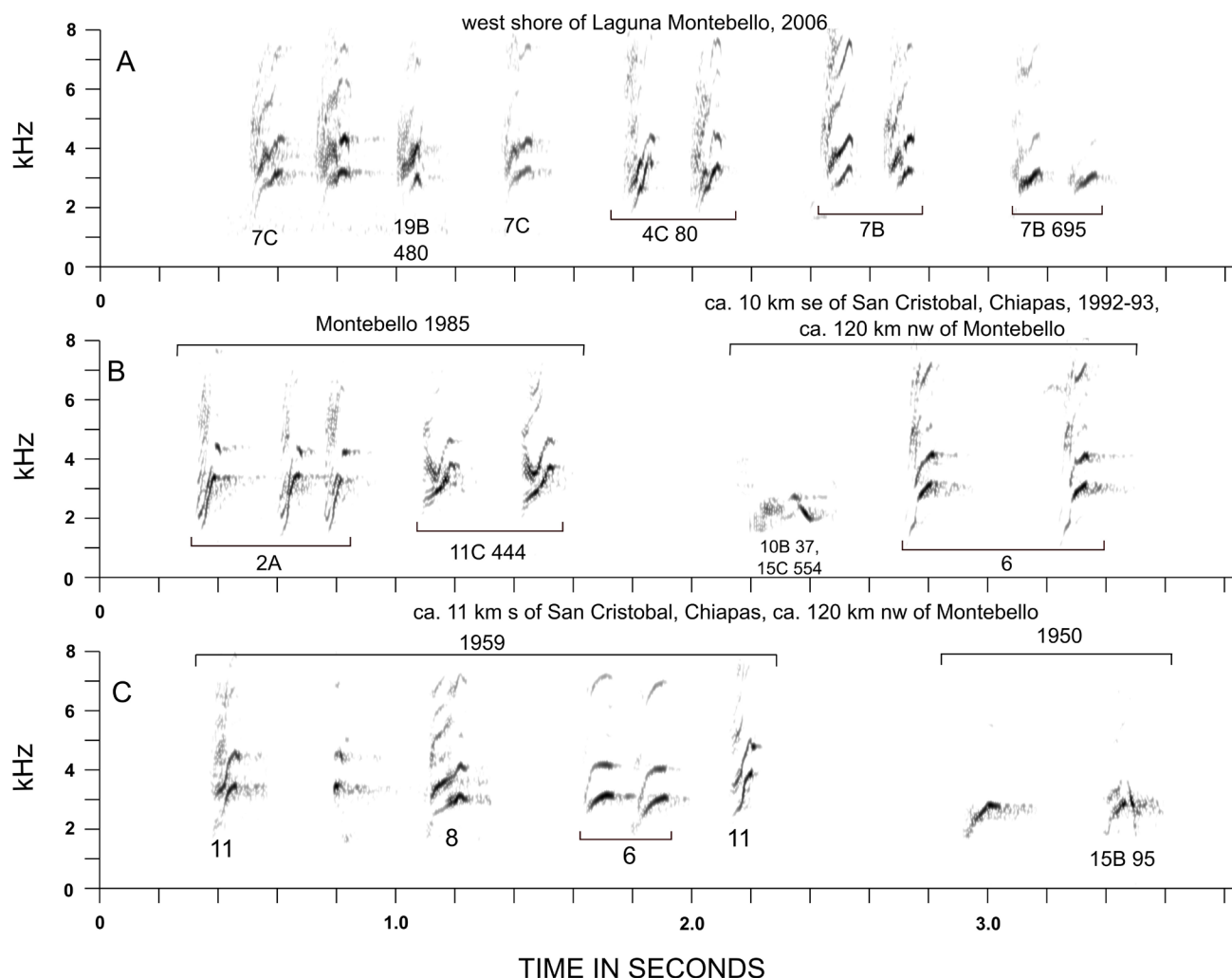
**Figure 23.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. Calls of volume lower than those in Figure 2 through row B of Figure 21. We do not show an exhaustive inventory of the variation we recorded in such relatively short-range calls. Row A, left, variety in kuks. These are similar to calls given by *A. coerulescens* (Barbour 1977) and *A. californica obscura* (Webber 1984). Row A, right, two examples of poits. *A. c. obscura* has several similar calls. The jays used kuks and poits at close range as they and other group members perched or flew, especially when distances between the calling birds were changing. Row B, left, calls that share some characteristics of kuks and poits. Some of these are remarkably similar in form to loud long-range Unicolored Jay calls, but we do not group them with those calls, for these, like the other calls in this figure, are delivered sotto voce. Row B, right, two examples of anxiety gutturals, a low-volume call given while the jays perched in pauses between loud calling and display flights during boundary defense. These are similar to calls given by *A. coerulescens* (Barbour 1977) and *A. californica obscura* (Webber 1984), who use them in similar circumstances. Row C, whisper song. This is a small part of a much longer performance; it is a single uninterrupted sequence of sounds given by one bird, similar in form to the whisper songs of *A. coerulescens* (Barbour 1977) and *A. californica obscura* (Webber 1984), who use them in similar ways.



**Figure 24.** Sonograms of Unicolored Jay vocalizations at Montebello, Chiapas, Mexico, January-May 1987. Rows A and B, a variety of calls from fledgling or juvenile jays within two months of leaving the nest. None is a match for any particular adult call shown in the series from Figure 2 through row B of Figure 21. The resemblances range from close to distant, and some show a similarity only to a broad range of adult calls. A number and letter directly below a call indicate the figure and row with a range of adult sonograms that the call resembles in a general way. For instance, the call designated 4C here is generally like the calls in row C of Figure 4, and an arrow designates the sharp downward inflection of a band in call 15A that places it near similar calls in row A of Figure 15. The calls labeled 18A show a certain similarity to those in row A of Figure 18, but resemble more closely the calls of adult *A. californica obscura* that Webber (1984) has called zhraanhs. A few calls show closer similarity to a particular adult call, but without matching it. We designate these with a number and letter followed after a space by the number of the particular call it most resembles. For instance, 10C 43 resembles most closely call 43 of row C in Figure 10, with the notable exception of the clicks preceding it (arrow). Some calls are so unlike any adult calls that we cannot place them in any figure or row, so these are not marked with letters and numbers. Row C shows a continuous multi-part food-begging call from a single juvenile, similar to those of *A. coerulescens* (Barbour 1977) and *A. californica obscura* (Webber 1984).

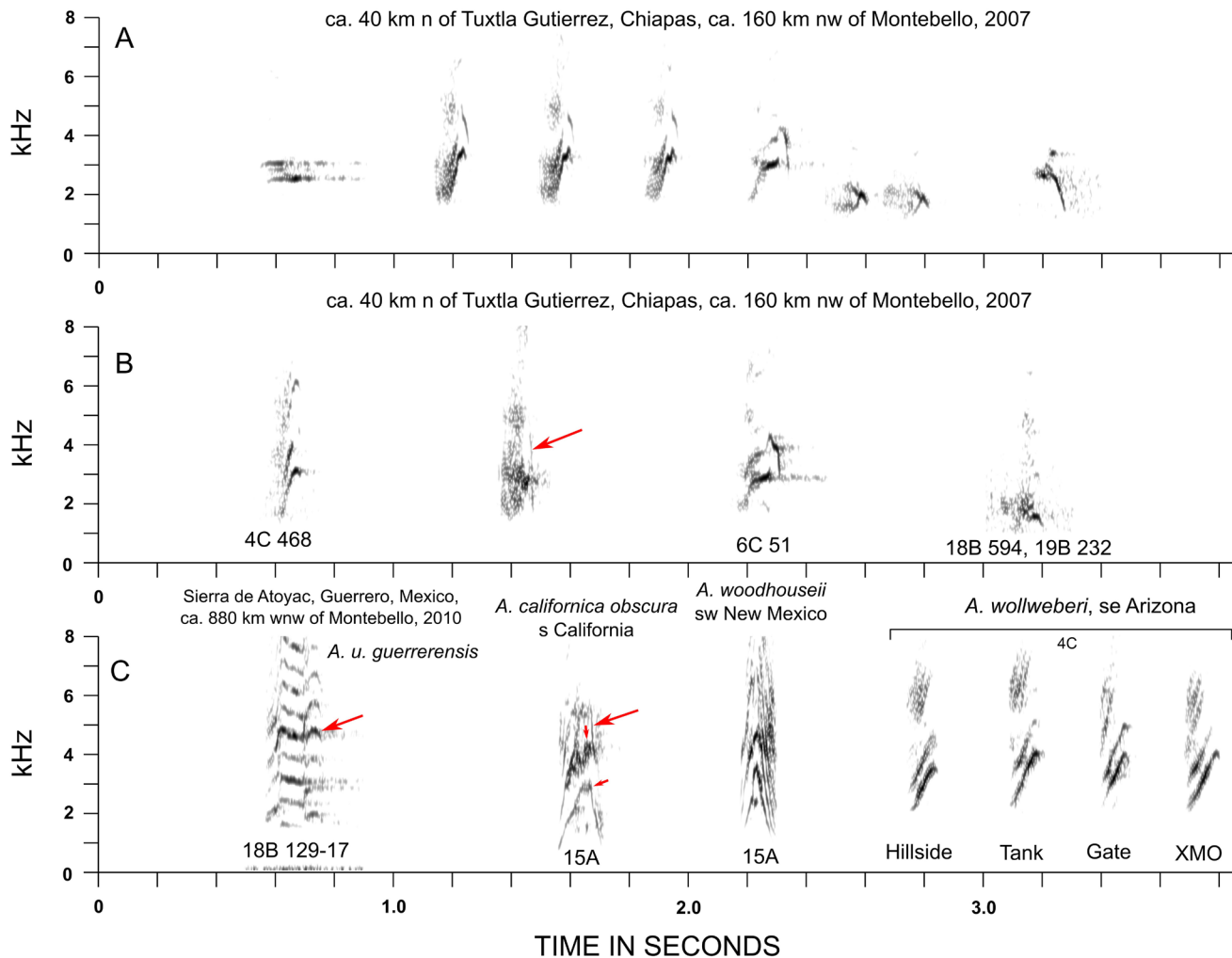


**Figure 25.** An outline of one way in which the relationships of the 1987 Montebello long-range calls (Figs. 2-20) can be represented in a branching pattern. Dots represent individual calls, marked by their number and the figure and row in which they appear. Each horizontal black line terminated by dots represents a continuous segment of the linear series of calls that runs through sonogram Figures 2-20. Within a line all the named calls appear in the same left-to-right order in which they appear in those figures. The isolated dots at the ends of lines represent calls not readily placed within the series, for instance the three calls at the right end of row A in Figure 12 (blue arrow A). Red lines connect calls that link non-adjacent series in the sonogram figures. For instance, call 2 in row B of Figure 2 links to call 5 of row C in Figure 4 (blue arrow B). These connecting calls are marked in the sonogram figures with the notation “cf.,” and the name and location of the call to which they link. Here we do not show all the links marked with “cf.” in Figures 2-20, and therefore this figure does not show all possible ways the calls could be arrayed.

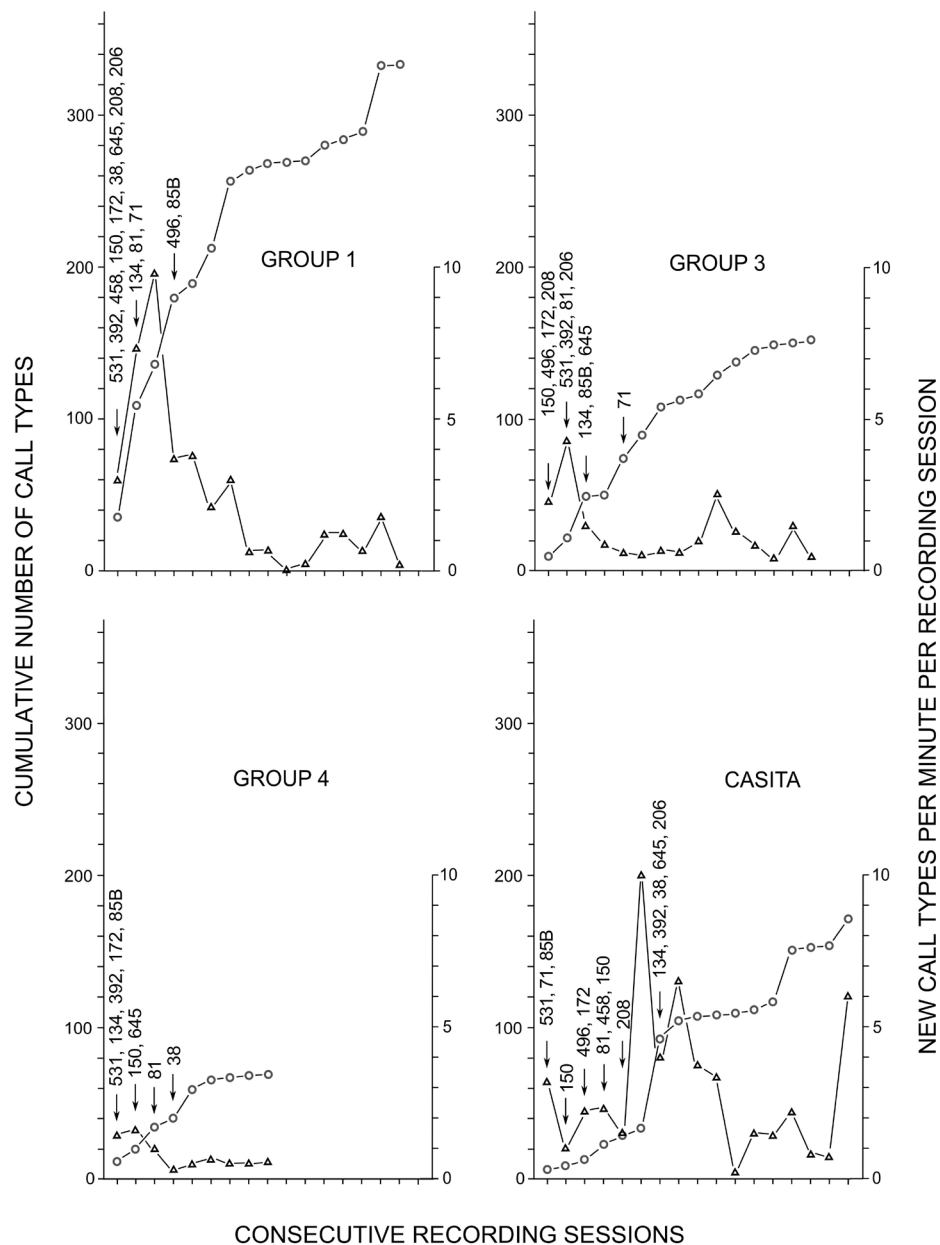


**Figure 26.** Calls of Unicolored Jays at Lagunas de Montebello and other sites in Chiapas, Mexico. Row A, Unicolored Jay calls recorded in 2006 on the west shore of Laguna Montebello, in what had been the territory of our jay Group 1. Recordings by and courtesy of Nathan Pieplow. Rows B and C, calls recorded at an unspecified location at Montebello and near San Cristobal, Chiapas, in the years shown. None is a match for any particular adult call we recorded at Montebello in 1987. The resemblance ranges from distant to fairly close. A number below a call indicates that the call resembles in a general way the sonograms in the figure of that number. For instance, the calls marked 6 at the right of row A resemble overall the calls in Figure 6. A number and letter directly below a call indicate that it resembles in a general way the sonograms in that figure and row. For instance, the call marked 7C at the left of row A resembles the sonograms in row C of Figure 7. A number after a figure-row combination indicates a particular call the sonogram most closely resembles, and the figure and row in which it is illustrated. For instance, the call marked 19B 480 at the left of row A most closely resembles call 480 in row B of Figure 19, though it is not close enough for us to have counted it as a rendition of that call if it had occurred among our recordings from 1987. Calls not marked by any number or letter (e.g., the call second from the left in row A), are so unlike any of our 1987 Montebello calls that we cannot place them in any particular figure.





**Figure 27.** Calls of Unicolored Jays at several sites other than Lagunas de Montebello, Chiapas, Mexico, and certain calls of some other *Aphelocoma*. None of the Unicolored Jay calls here is a match for any individual call we recorded at Montebello in 1987. A number and a letter directly below a call indicate that it generally resembles the sonograms in that figure and row; in particular, the calls in row C marked 15A are similar to those in row A of Figure 15. The number or numbers following a figure-and-row combination indicates the individual call or range of calls the sonogram most resembles. For instance, the call marked 18B 129-17 at the left of row C most closely resembles calls 129 through 17 in row B of Figure 18; the resemblance includes a terminal flourish (arrow). Calls not marked by any number or letter (e.g., all the calls in row A), are so unlike any of our 1987 Montebello calls that we cannot place them in any particular figure. Even though the second call from the left in row B is unclassifiable in any category of Figures 2-20, it shows a downswept trace (arrow) similar to those in calls of Figure 14 row C, and Figure 15 row A. Row C, center, shows two calls of scrub-jays with certain detailed resemblances to the Unicolored Jay calls of Figure 15, row A; in the call from *A. californica obscura*, note the sharp downwardly inflected trace (larger arrow), and the two peaks of the main bands (smaller arrows). Row C, right, shows four calls of *A. wollweberi* from a single locality in southeastern Arizona. Each call is from a different communal family group, denoted by the names below the calls. Hopp et al. (2001) showed through playback experiments that the jays could distinguish these calls from one another. These calls resemble in a general way the Unicolored Jay sounds of Figure 4 row C. Recordings by and courtesy of Steven Hopp.



**Figure 28.** Cumulative number of call types recorded from four Unicolored Jay groups, Lagunas de Montebello, Chiapas, Mexico, January-May 1987. The curves connecting circles show the total number of call types known for each group (scale on the left). The curves with triangles show the number of new call types that appeared per minute in each recording session (scale on the right). Here we show data for each group rather than for the study population as a whole to avoid the confounding effect of new calls added merely through sampling of new family groups. The ticks at the bottom of the axes represent the separate recording sessions for each jay group. These show the consecutive sessions in which we recorded each group (e.g., nine sessions for jay Group 4, 17 for Casita group); we do not name the individual recording sessions as in Figures 29-31. Arrows with numbers indicate the first session for each jay group in which we recorded an example of the call groups we defined in Figures 2 through 20. For instance, in Group 4, the second recording session was the one in which we first recorded examples of call groups 150 and 645 for this jay group (not necessarily the first in any jay group). See Table 1 for the distribution of our recording sessions in each jay group from January through May.



### EPISODIC INTRODUCTION OF NEW CALLS

The jays sometimes produced spates of many novel closely related calls in a single recording session, instead of distributing them more evenly among the sessions. For example, in recording session 8, Group 1 gave the first renditions we recorded of calls 173, 203, 200, 196, 191, 23, 199, 119, 204, 197, 194, and 193 (call group 458, Fig. 8 rows B and C, Fig. 9 row A; Fig. 29). None of these calls occurred in any later sessions. We observed this pattern of related-new-call production and lack of repetition in three of our most-recorded jay groups (Figs. 29–31). Figure 7 row C illustrates an extreme example, in which all except two renditions of these 12 call types given by jay Group 1 are from a single recording session.

A contrast that helps to illustrate this pattern is the way Group 3 spread the calls of call group 85B over a relatively wide variety of recording sessions (Fig. 30).

### DISTRIBUTION OF CALL TYPES AMONG JAY GROUPS

The individual calls and even the call groups were not evenly distributed among the jay groups on our study site. 552 individual call types occurred in one jay group only, 74 in two only, 29 in 3 only, 10 in four only, 3 in five only, and 5 in six only, the largest number of groups in which any single call type occurred (Fig. 32). All jay groups shared only a portion of their calls with any other group, none higher than 0.52, and most much lower (Table 2).

Some entire call groups did not occur in every jay group. We recorded seven of the 14 call groups in each of our four best-sampled jay groups, six of them in three of those groups, and one in two of them (Figs. 33, 35–39).

The distances between the jay groups may be reflected in the extent to which they shared calls. One plausible example is the scarcity of sharing between the southeasternmost Cinco Lagos (CL) group and any of the groups to its west (see Fig. 1). The only group with which CL shared calls was its nearest neighbor from which we have a sample, Group 1. The small size of the sample from CL probably contributes to this effect, though all the western groups with similarly small sample

sizes (E, CE, G5, P, WG, and G) shared calls with other western groups. The number of jay groups with substantial sample sizes is small, but there is another inkling of a distance effect in the sharing of the abundantly recorded Group 1 and all other western groups: the highest shared proportion is for a pair of western groups (Groups 3 and 4), while all combinations of Group 1 and the other banded western groups show the lowest proportions of any pairs (Table 2).

To judge whether our sample shows that a call or cluster of related calls is truly restricted to one or more jay groups, it is necessary to assess the evidence that these calls do *not* occur in certain other jay groups. We consider a call to be a better candidate for being truly absent from a jay group using these criteria: 1) the larger our total recording sample from that group; 2) the more distinctive the form of the call, so that it could not be confused with any calls the jay group is known to have; and 3) if the jay group seeming to lack the call performed other kinds of calls in the particular contexts where the candidate calls occurred (i.e., in gray cells of Figs. 35–39; see the explanations of these figures below in RESULTS and in their captions). Using these criteria, we list the following calls or clusters of calls as candidates for being distributed in a truly discontinuous way among the jay groups on our study site:

*Calls that may occur in only one jay group or two neighboring jay groups:*

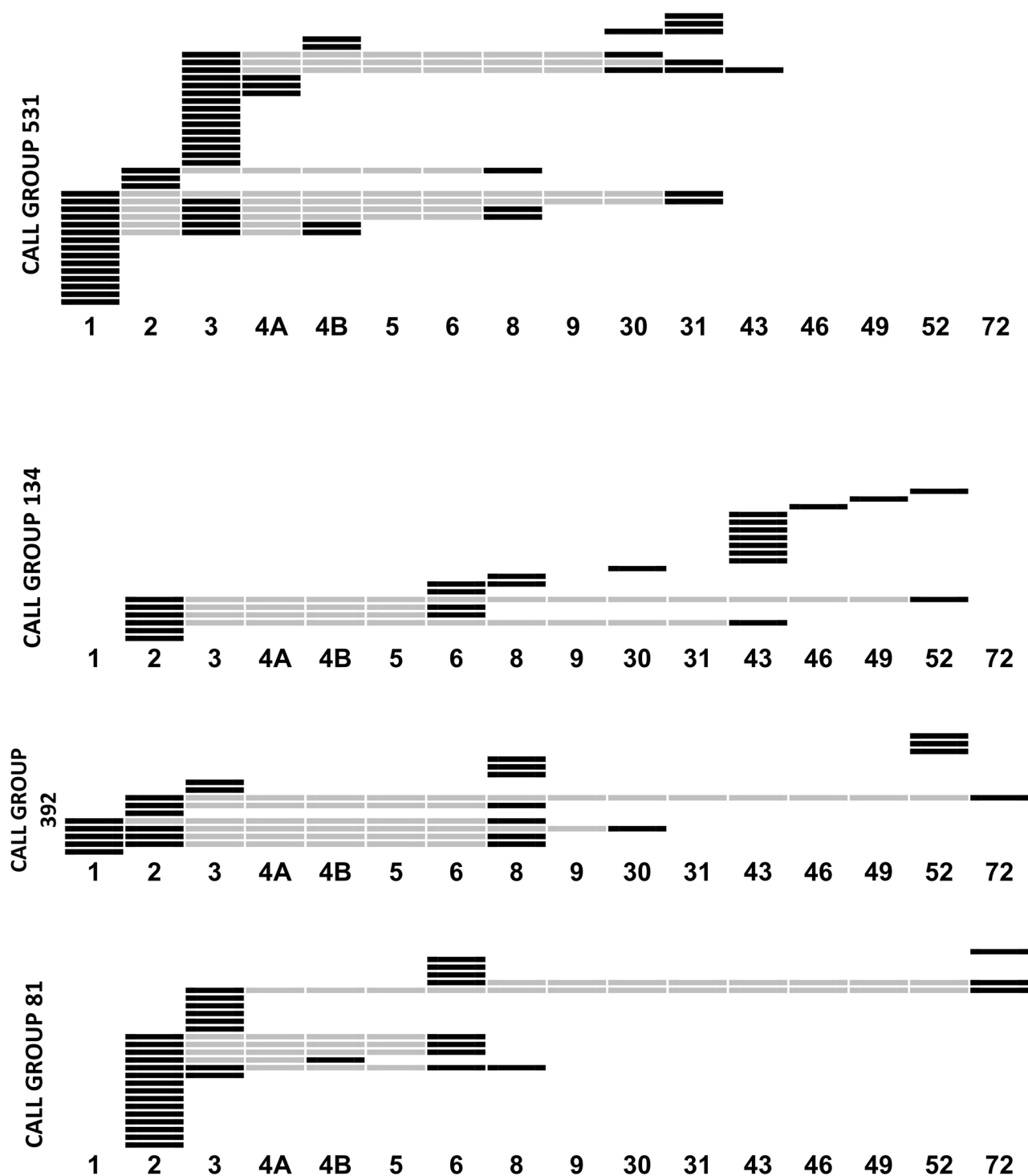
**134** (Fig. 4 row B). Group 1 only; 55 renditions in four sessions.

**242 through 432** (Fig. 5 row C). Only in Group 3 (common; multiple recording sessions) and in another northwestern group, West of Grutas (a few renditions). Distinctive.

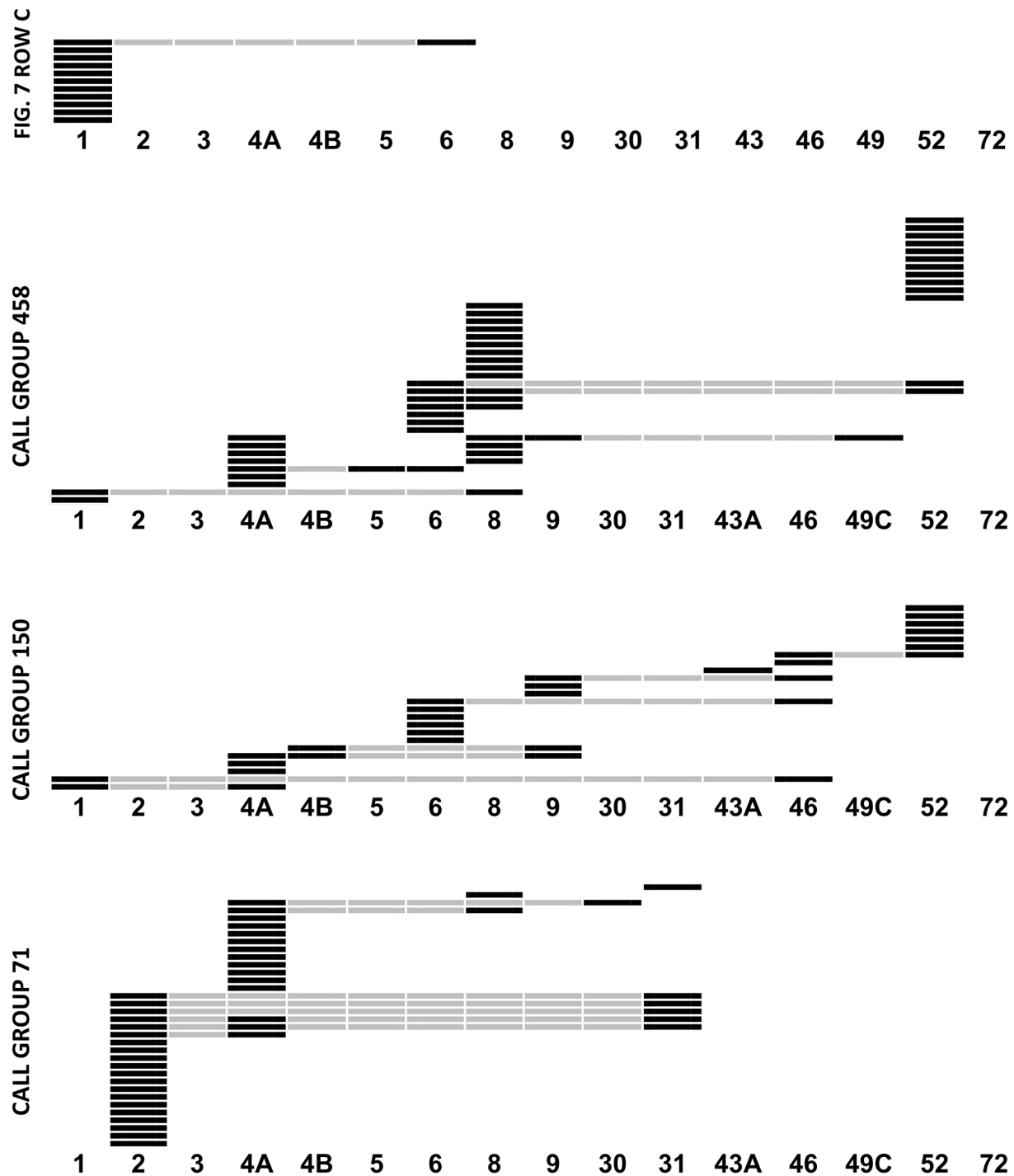
**416 and 417** (Fig. 8 row B). Casita group only. Not abundant, but with a distinctive multi-banded structure seen in no other calls.

**371 through 369** (Fig. 10 row B). Agua Tinta group only. In structure these are intermediate between the calls of groups mostly farther to the west (254, 349, 252), and those of Group 1 and Cinco Lagos (408, 192 through 37).

**192 through 453** (Fig. 10 row B). All from Group



**Figure 29.** Episodic appearance of new Unicolored Jay Group 1 calls among the sessions in which we recorded them, Lagunas de Montebello, Chiapas, January-May 1987. This and Figures 30-31 illustrate the way in which the jays often gave many new closely similar calls in a single recording session, rather than evenly spacing the production of new calls among the sessions. Many of the calls produced in these episodes of plural novelty occurred only rarely or not at all in later recording sessions. We group the data by the call groups defined in Figures 2-20, with the names of those groups shown at the left. We show data only for call groups in which we recorded at least 10 call types. [caption continued next page]



**Figure 29.** Continued. At the bottom are the names of the sessions in which we recorded the calls. Each individual call type (not identified separately by number) is assigned to only one row in each of these compilations. Within that row, a black cell indicates that we recorded that call in the session indicated. If a call occurred in more than one session, the black cells are connected by gray cells. For instance, reading the entries for call group 531 from the bottom up, 15 individual call types occurred together for the first time in session 1; of these 15, two also occurred in sessions 3 and 4B, two in 3 and 8, one in 3 and 31, and one in 31.

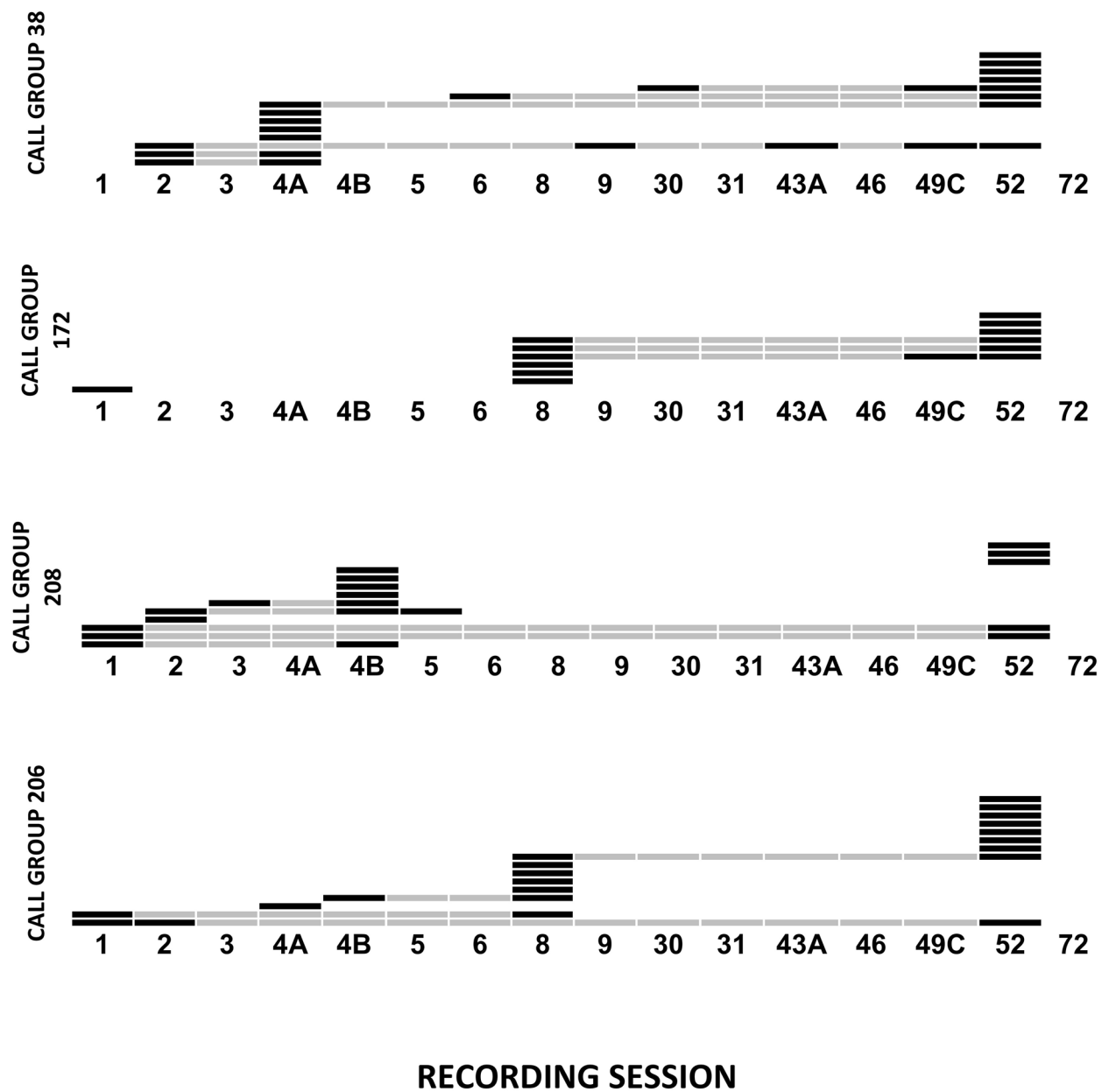
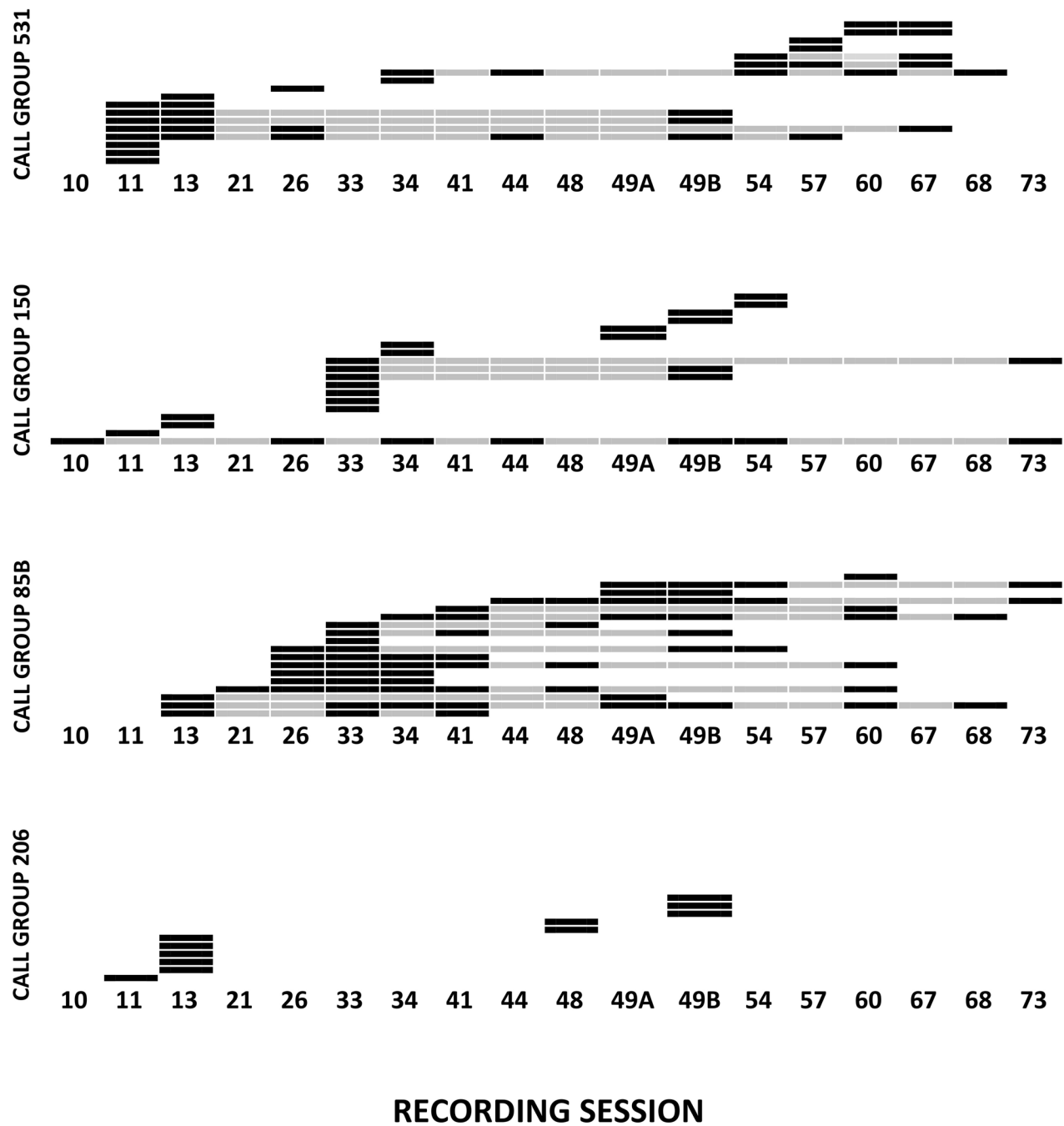
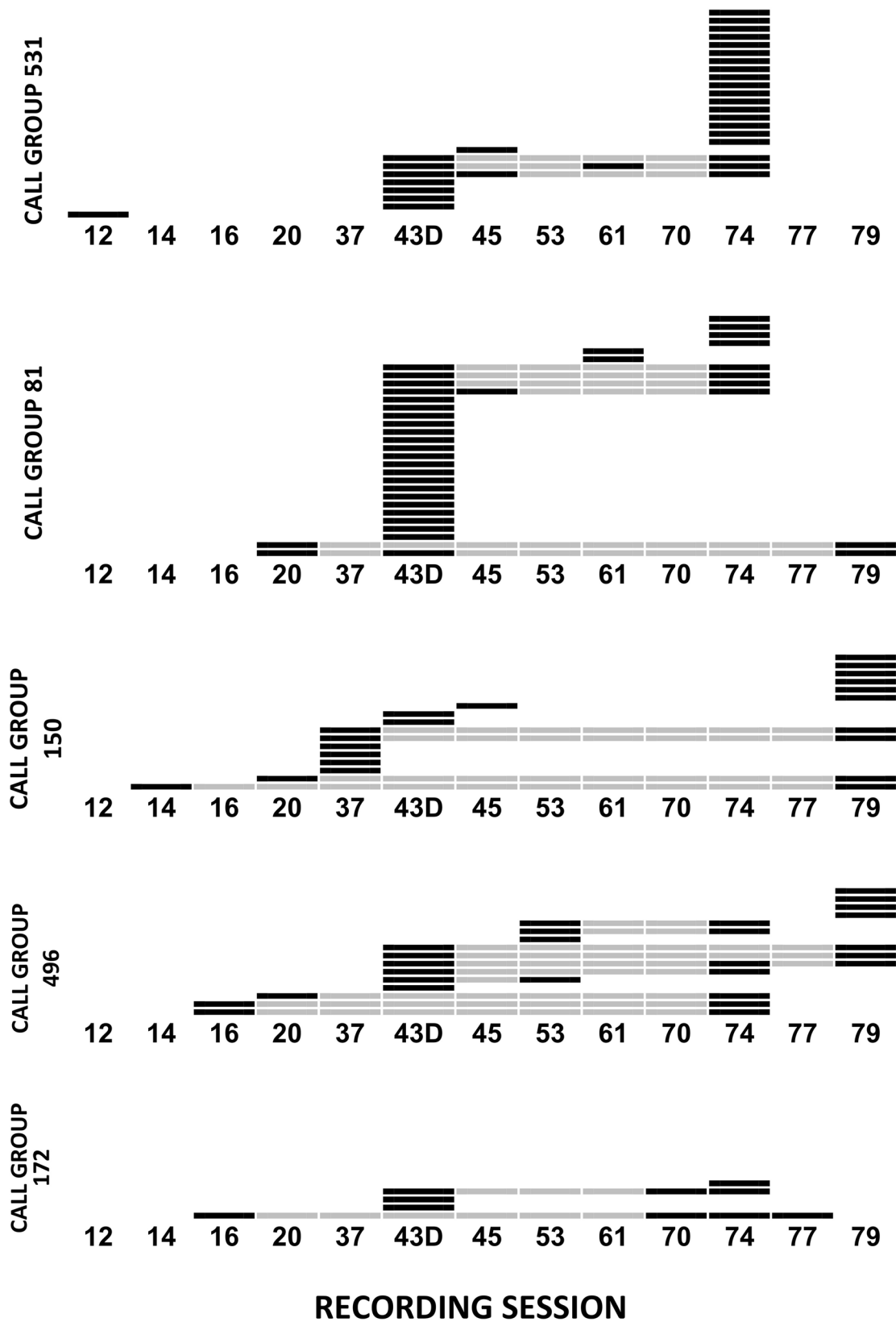


Figure 29. Continued.



**Figure 30.** Episodic appearance of new Unicolored Jay Group 3 calls among the sessions in which we recorded them, Lagunas de Montebello, Chiapas, January-May 1987. Format as in Figure 29.





**Figure 31.** Episodic appearance of new Unicolored Jay Casita group calls among the sessions in which we recorded them, Lagunas de Montebello, Chiapas, January-May 1987. Format as in Figure 29.



1 and the birds to the east at Cinco Lagos. Call 453 is most like call 37 (see DISCUSSION—Distribution of Call Types Among Jay Groups).

**37** (Fig. 10 row B). Common in jay Group 1, and recorded or heard nowhere else except perhaps from the adjacent Group 2. Highly distinctive in sonograms and one of the few single call types (as opposed to a range of related calls) we could easily identify by ear. We phoneticize it as *dzee-oo*.

**450 through 63** (Fig. 11 row C). All from the southeastern Group 1 and Cinco Lagos group.

**518** (Fig. 12 row A). Recorded only from the adjacent groups Casita and Grutas; of peculiar form.

**212** (Fig. 12 row C). Only from Group 3, in two recordings sessions. Quite unlike any other calls.

**38** (Fig. 15 row B). Group 1 only; 11 renditions in seven recording sessions.

**174 through 725** (Fig. 15 row C). Common in Group 1, occurring in three recording sessions; recorded nowhere else. Distinctive in their combination of short, delicate, downwardly inflected parts of the lower bands, with simplified semi-detached upper bands.

**554 and 266** (Fig. 15 row C). Common in the Casita group, occurring in two recording sessions; recorded or heard nowhere else. The sonograms are distinctive in their cloud-like traces at the beginning (arrow, 554), followed by short and dark ascending upper bands and descending lower bands.

**668 through 413** (Fig. 16, and Fig. 17 row A). This long segment consists entirely of calls from Casita and its neighbor West of Grutas, except for one (195, Fig. 16 row A) from Group 1, which differs in overall frequency from the other calls in the series.

**129 through 17** (beginning of call group 208, Fig. 18 row B). Group 1 only. Relatively short calls with wide frequency range and heavy, distinct banding.

**19** (Fig. 18 row C). Group 1 only; in three recording sessions.

**238 and 214** (Fig. 18 row C). Both only from adjacent jay groups 3 and Casita. Distinctive rapidly modulated banding, introductory clicks, and a downwardly inflected terminal flourish.

**329 and 552** (Fig. 19 row A). Casita group only. These two distinctive and closely similar calls each

appeared in multiple sessions.

**18** (Fig. 20 row A). Group 1 only; 38 renditions in four recording sessions.

**475** (Fig. 20 row A). Group 1 only. Few renditions, but not closely resembling any other calls.

*Calls occurring in more than two jay groups, but not occurring in one or more of our four most heavily sampled groups:*

**458 through 193** (Fig. 8 rows A through C, and Fig. 9 row A), all 45 calls in call group 458. Most given by jay Group 1, with others by Casita, Agua Tinta, and groups 4/5. We have no examples from the abundantly recorded jay Group 3, in the midst of western jay groups that did give these calls.

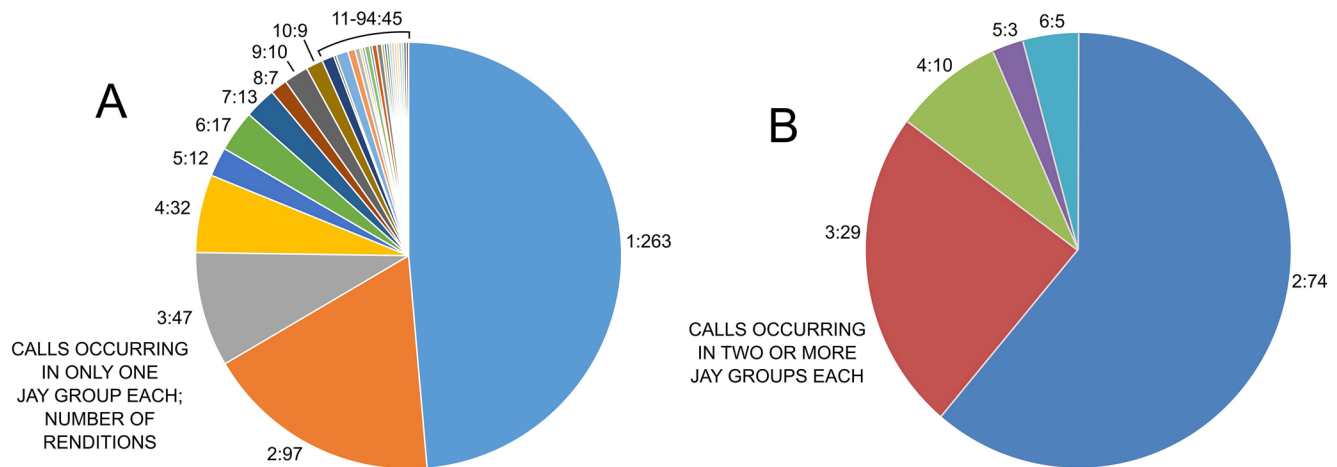
**327 through 270B** (Fig. 14 rows B and C), all 13 calls in the latter half of call group 85B. We recorded these only from the western groups on the study site; none from jay Group 1. See the caption of Fig. 14 for details of the differences between these 13 sounds and the others in this call group. Note, though, that the western jay groups also gave calls distributed throughout the entire call-group 85B series.

**478 through 231** (Fig. 19 rows B and C; Fig. 20 row A), all 33 calls in call group 206. Recorded from jay groups 1, 3, Casita, and 5, but not from jay Group 4. It should be noted however that Group 4 is the least recorded of our four best-sampled groups.

*Calls occurring in only two or three non-neighboring jay groups.*

These are mainly the repeated instances in which we recorded certain calls only in Group 1 and Casita, at nearly opposite corners of the study site. Though the samples in each case are small or highly uneven (many renditions from one jay group, few from the other), we consider the occurrences to be unequivocal and frequent enough to be noted.

**590 through 134** (Fig. 4 rows A and B). Recorded only from jay Group 1, with the exception of two renditions of call 315 from distant jay Group 4. Most individual calls are not abundant but these are numerous as a group, from multiple recording sessions. These make up the extreme end of the call-group 134 series, with tails of the sonogram traces strongly curved.



**Figure 32.** Distribution of individual call types among Unicolored Jay groups, Lagunas de Montebello, Chiapas, Mexico, January-May 20 1987. A) Unicolored Jay calls each recorded in only one jay group, and the number of renditions we recorded of each. The number before the colon indicates the number of renditions, and the number after the colon indicates the number of call types occurring with that frequency. For example, we recorded 263 individual call types once each, and ten call types nine times each. At the upper left the figure summarizes the abundance of 45 call types we recorded from 11 to 94 times each. See Appendix A for the names of the calls, the call groups to which they belong, their location in the sonogram figures 2-20, the number of sessions in which we recorded them, and the jay groups that gave them. B) Unicolored Jay calls each recorded in two or more jay groups. The number before the colon indicates the number of jay groups in which the calls occurred, and the number after the colon indicates the number of call types occurring in that category. For example, we recorded 74 call types in two jay groups each, and 29 call groups in three jay groups each. See Appendix B for the names of the calls in all particular combinations of jay groups, their locations in the sonogram figures 2-20, and the call groups to which they belong. The total number of calls shown here does not come to 697 (the total number of calls we recognize in Figures 2-20) because we could not assign some of them to a particular number of jay groups. For instance, if we recorded a call from two jay groups calling simultaneously, we may not have been able to tell which group or groups gave the call.

**60 through 708** (Fig. 7 row C). Group 1 gave all of these calls except for two by Casita.

**113 through 284** (Fig. 10 row C). Group 1 and the distant Group 3 gave all of these calls.

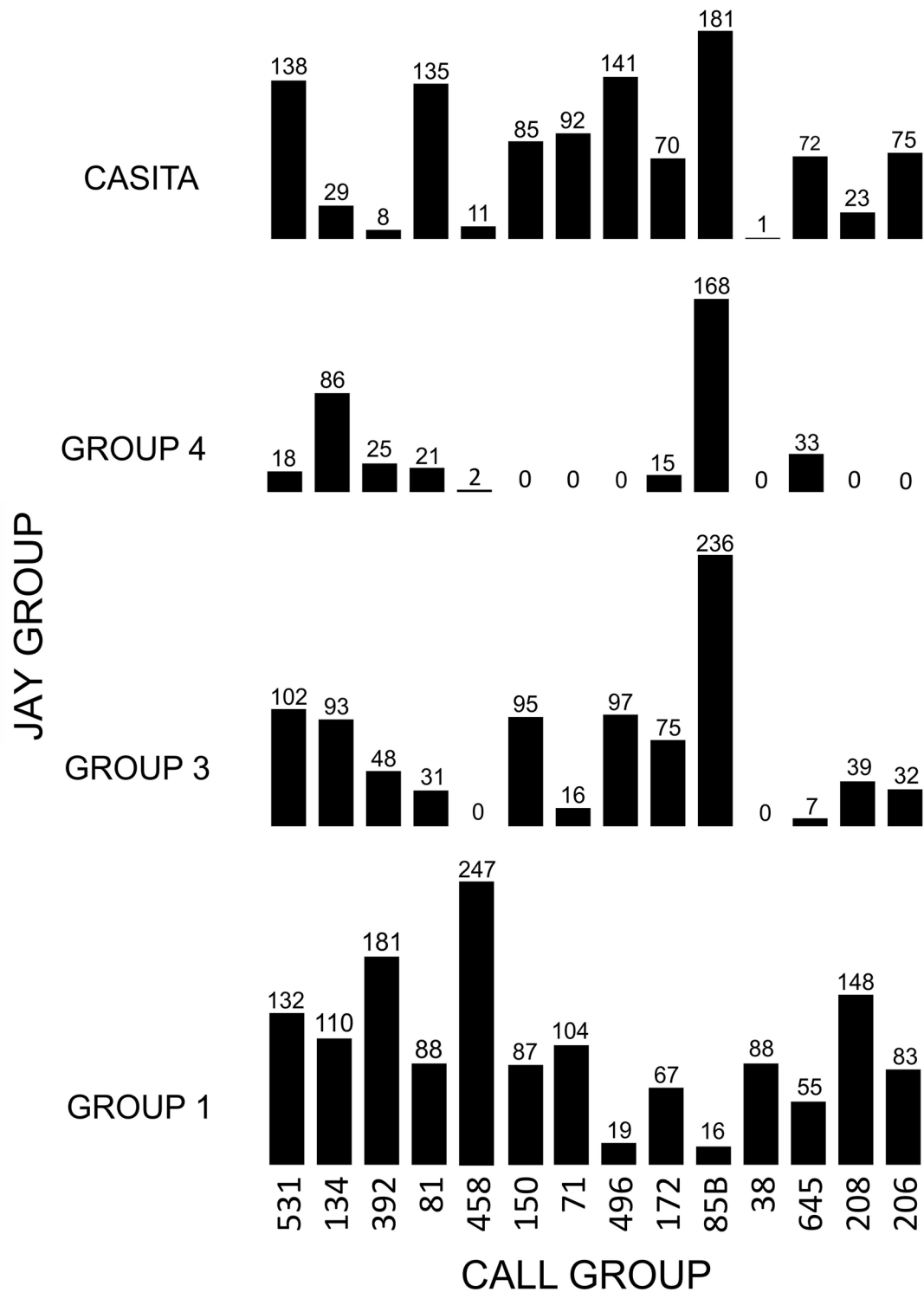
**133** (Fig. 14 row A). Group 1 gave this call 48 times in four sessions, Casita once.

**Call group 38** (Fig. 15 row B). Group 1 gave all renditions of all these call types except for a single rendition of call 464.

**668 through 413** (Fig. 16 rows A through C and Fig. 17 row A). Group 1 and the distant pair of groups Casita and West of Grutas gave all of these calls.

**66** (Fig. 18 row B). Group 1 gave this call 65 times in three recording sessions, Casita once.

We have little information to help determine whether these apparent differences between groups may have represented the peculiarities of particular individuals or were typical of all the birds in a group. The numbers of calling birds, the density of the forest, and the steepness of the terrain in many cases kept us from identifying individual calling birds in territory defense or other contexts in which many birds gathered and moved about. Our recordings of more isolated birds do indicate that some particular individuals produced the only known



**Figure 33.** Summary of Unicolored Jay call groups and the jay groups that used them, Lagunas de Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Form and Variety of Calls and Figures 2-20 for delineation of the call groups. Each bar shows for a major jay group the total number of renditions of all call types they gave in all contexts of each call group, listed on the horizontal axis. For instance, we recorded a total of 138 renditions of calls in call group 531 from the Casita jay group, and no calls of call group 150 from jay Group 4.



examples of certain call types (Table 3).

We did not notice any tendency for jays to match one another's calls in territory boundary defense or in long-range contact calling.

#### OTHER CALLS, USED AT SHORT- TO MEDIUM RANGE

In addition to their loud projecting calls, Unicolored Jays, like other *Aphelocoma*, produced a variety of softer sounds audible (to us) at no more than about 20 m (Figs. 21 row C through Fig. 24.) These calls do not fit in any of the call groups we have defined, so they are not included in call-context figures 35 through 39. These calls are commoner than would appear from their representation in our recordings because they are hard to record.

**Rattle.** Unicolored Jays gave two kinds, slow (Fig. 21 row C), and fast (Fig. 21 row C, Fig. 22 row A); some have a squeaky flourish at the end (Fig. 22 row A). Only females gave these calls. Rattles were usually intermediate in loudness between the long-range calls of Figures 2–20 and the quieter sounds, Osprey through whisper song below.

**Osprey calls.** Short, usually gradually inflected pure tones (Fig. 22 row B) given in series, not mixed with dissimilar elements as in whisper song. So named because to Webber's ear they sound like some calls of Ospreys (*Pandion haliaetus*).

**Peeps.** Pure tones shorter than the Osprey calls, and tending to be paired (Fig. 22 row C.).

**Kuks.** Flat scratchy sounding bursts of noise, some with an overall rising inflection (Fig. 23 row A). Barbour (1977) coined this term for a similar call of *A. coerulescens*.

**Poits.** Pure-sounding, with rapidly rising tones and a terminal downward flourish (Fig. 23 row A). Webber (1984) used this onomatopoeic name for a similar call of *A. californica obscura*.

**Kuk-poit combinations.** A variety of calls incorporating various characteristics of kuks and poits (Fig. 23 row B).

**Anxiety gutturals.** Somewhat screechy-sounding calls with a rising inflection overall (Fig. 23 row B). Barbour (1977) used this term for a similar call of *A. coerulescens*; it is the only exception to our practice of not naming calls after inferred

internal states of the birds.

**Whisper song.** A low-volume continuous series of sounds that in our few recordings are not closely similar to most other parts of the vocabulary (Fig. 23 row C).

Juveniles up to about two months out of the nest performed rambling bouts of miscellaneous sounds (Fig. 24 rows A and B), none of which matched closely any calls we recorded from adults.

Juveniles gave food-begging calls, and adults gave similar calls in courtship (Fig. 24 row C). These and the juvenile practice calls were also intermediate in loudness between the broadcast calls of Figures 2–20 and Osprey calls through whisper song above.

#### THE BEHAVIOR OF CALLING JAYS

We distinguish 38 categories of behavior the jays performed while calling, and assign to each a number or number-and-letter combination in the list below and in Figures 35–40. Some of the numbers in the list below are not in numerical order (for instance, context 32 appears between contexts 7B and 1C), because after we originally assigned numbers to the contexts in our database we rearranged them in this list to appear next to the other contexts most similar to them. We group these categories here and in Figures 35–40 into broader classes of similar behavior, such as long-distance calling within the flock (contexts 1A through 25) and exchanges between jay groups (contexts 1C through 9); we call these broader classes "context groups."

The calls associated with these contexts in Figures 35–39 are loud long-range calls. We present the contexts of the shorter-range calls in Figure 40.

#### *Long-distance flock calls*

1A. Flock contact calls, general. Calls directed toward other members of the flock, when we neither saw nor heard members of other jay groups. The jays could be dispersed over as much as 150 m in their territory as they called, seemingly in response to one another. Context 1A includes instances in which the recordist did not specify whether the calling jays perched or moved together (cf. contexts 1B and 2).

**Table 3.** Calls known from individually identified Unicolored Jays, Lagunas de Montebello, Chiapas, Mexico, January-May 1987. The first column lists the identified jays, their sex, status in the group, and the groups they belonged to. In the second line of the entry for each individual, the first item is the age of the bird in years in the spring of 1987, the second is its sex if known, and the third its status in the the flock. B = breeder (for females; the bird that incubated and brooded), P = primary (for males, the dominant male in the flock and main consort of the female breeder), S = secondary (for males, the subordinate males in the flock), ? = sex unknown. For instance, Y of jay Group 3 (the fourth row) was at least two years old, female, and the incubator and brooder. See Webber and Brown (1994) for more on the the ages, sexes, and status of the jays in the various flocks. The second column lists the call types in our recordings known only from the bird identified in the first column (and not any others in its group). The third column lists the call types recorded only from the identified individual *and* one or more other members of its jay group.

Individual, status, jay group	Calls unique to individual	Calls unique to individual and others in group
XXns ≥3 M S G3	424	426
WW 1 F G1	421	11, 150, 178, 26, 27, 320, 323, 420, 88
Y ≥2 F G1	398, 399, 401, 402, 403, 404, 406	11, 38, 396, 397, 400, 405
Y ≥2 F B G3	295, 334, 345, 346, 347, 349, 350, 392, 393, 504, 505	242, 270B, 299, 331, 332
Y ≥3 F B G4	422, 423, 722, 388, 423	
BB ≥3 F B G1	10, 131, 319, 324, 325, 326, 67, 68, 71, 8, 86, 9	11, 318, 323
Dayglo ≥2 ? G1	419, 467, 468, 469, 470, 471, 472, 475, 478, 479, 76, 481, 482, 484, 485, 486, 581	162, 18, 36, 441, 473, 474, 477, 149, 19. 457, 458, 460
Dayglo ≥3 M S G4	223, 391	390
XXsp ≥3 M P G3	710	222

- 1B. Long-distance flock contact calls, perched.
- 2. Long-distance flock contact calls, moving.  
The jays often called as they moved together, often foraging, sometimes separating into sub-groups.
- 3. One bird calling at long distance as it left other group members, sometimes pausing to perch and call in the direction of the other birds.
- 4. One bird calling at long distance while it remained stationary and the other group members flew away from it.
- 5. A lone jay calling as it foraged, or perched at a vantage point looking out, sometimes performing the *Aphelocoma* "bobbing" movement (Webber, 1984, Webber and Brown, 1994). This category does not include the calling behavior of incubators or brooders on or near the nest.
- 25. A lone jay calling at discovery of a rich source of food such as tortillas or peanuts, in a way similar to *A. californica obscura* (Webber, 1984).

#### *Perched calling conventions*

- 7A. Perched calling conventions, general. We observed many, and recorded several, instances in which all members of a jay group perched together within the approximate diameter of a single tree canopy and called together for as long as 20 min. The jays called in normal perching postures, and we could not find any proximate object of the calling such as a predator, another jay group, or a source of food.
- 7B. Perched calling convention, with a nearby rich source of food.
- 32. Perched calling convention, with fledglings present.

#### *Exchanges between jay groups*

- 1C. Long-distance calling that seeming to be directed toward, or in response to, another jay group, but without drawing up at the territory boundary (see context 9). At times the jays counter-called with neighboring groups when they were not in view of one another, from deep within their territories.
- 8. Perched calling, after boundary defense. At times, after a bout of close-range territory defense (see context 9), the jays in one group would perch

and continue to call in a close bunch after their opponents had departed.

- 9. Boundary defense. Unicolored Jays actively defended the boundaries of their all-purpose territories against other jay groups. They gathered at the boundary opposite the neighboring groups and called repeatedly while perched or performing display flights parallel to the boundary. Such boundary skirmishes could last as long as 1 h 15 min, and all adult group members seemed to participate (Webber and Brown, 1994).

#### *On and around the nest, including nest-building*

The vicinity of a nest under construction was busy and noisy, as various members of the group built the nest, competed for dominance, and sought mating opportunities (Webber and Brown, 1984). During the nest-building, incubation, or brooding stage, females often broadcast calls from the nest that we could hear more than 100 m away. During some of these call bouts we saw no other flock members and heard no response from any other jays.

- 10. A lone jay calling on the nest, not adding or shaping nest material.
- 11. A lone jay calling on the nest, while adding or shaping nest material.
- 12A. On the nest, and calling to a distant calling jay. The bird in the nest and one or more other jays, far enough to be out of view but near enough to be considered members of the same flock, called in a way that gave the impression they were calling in response to one another.
- 12C. An adult fed on the nest. Flock members fed the breeding female as she sat in the nest while incubating or brooding (Webber and Brown, 1994). The females called as the feeders perched on the nest (cf. context 13).
- 12D. An adult on the nest, with other flock members nearby; general nest-building in progress. The females often called on the nest with most or all their group gathered within 50 m (Webber and Brown, 1994).
- 13. A jay on the nest calling as another approached it. The arriving birds carried nest material or food as they approached in flight or along a

branch.

14. An incubator or brooder calling near but not on the nest. Females often interrupted their brooding or incubating sessions to move about through the branches near the nest, sometimes foraging as they went. Other jays may have been in view.
16. A jay flying unaccompanied (cf. context 17) to or from an active nest. This category includes calls in flight, calls given while perched during pauses on the way, and on the nest after arrival or before departure.
17. Flights to the nest by two or more jays together. During nest construction several jays, one or more carrying nest material, often flew rapidly together to the nest site over distances of as much as 30 m, and one or more called as they went. These display flights were similar to those of *A. californica obscura* (Webber, 1984).
- 18A. Rivalry near the nest: calls by subordinates. During late nest-building and early incubation, subordinate males approached the breeding female in the vicinity of the nest in an attempt to copulate with her, and the dominant male confronted them to keep them away (Webber and Brown, 1994).
- 18B. Rivalry near the nest: calls by the dominant bird as he confronted a subordinate (cf. context 18A).
- 18C. Rivalry near the nest: calls by the dominant bird after he confronted a subordinate and the subordinate left.
- 18D. Rivalry near the nest: calls by a subordinate bird, dominant bird, or both; the recordist could not distinguish among these.
19. Nest-building by various group members, general. This category includes incidents in which the recordist's narration provided no further details such as those in contexts 12A through 18D.
20. One or more jays calling, sometimes foraging, in the vicinity of an occupied nest.
22. A lone sentry calling above a nest. Often one member of the flock perched in the tree canopy above a nest while the other members were elsewhere. This is in contrast to context 14, in

which a female called during a respite from incubating or brooding.

#### *Various other general flock activities*

- 24A. A jay calling, apparently in response, as another flock member approaches it at close range while the group moved about the interior of its territory, far from any active nest site, in contrast to contexts 18A through 18D. Such an approach may be considered to be a potential intrusion upon the space of the calling bird, and thus a low-level expression of dominance (Huntingford and Turner, 1987, pp. 46, 49; Hurd and Enquist, 2001).
- 24B. A jay calling as it flew toward another flock member at close range, while the group moved about the interior of its territory, far from any active nest site (cf. context 24A).
28. Unseen birds calling, their activities unknown, such as the birds we recorded along the Cinco Lagos road.

#### *Mobbing*

23. Jays scolding the observers in the aftermath of banding. When we caught jays in traps and banded them, their flock mates gathered to scold us, and continued to call in place for as long as 15 minutes after we released the newly banded bird.
29. Jays watching and scolding the recordist other than in context 23. Most of the time the jays ignored the observers, but some directed their attention toward them and called while in normal perching postures or with the head-forward bobbing display of other *Aphelocoma* (e.g., *A. californica obscura*, Webber, 1984).
35. Sham mobbing, or mobbing a subject the recordist was unable to see. We sometimes saw jays go through all the motions of vigorously mobbing a predator, but despite close and long scrutiny we could not find anything that might have been the object of their attention. In some cases it may have been an inconspicuous predator such as a snake.
36. Jays mobbing a perched Turkey Vulture (*Cathartes aura*) or buteo (probably *Buteo brachyurus*).



37. The aftermath of mobbing a Turkey Vulture (cf. context 36). After the vulture left, the jays continued to call in place for many minutes.

*In response to overhead predators*

38. Jays calling in response to a predator flying overhead (Webber and Brown, 1984). The jays used these calls in same way *A. californica obscura* use theirs (Webber, 1984). In the sonogram figures we have marked the few calls (218, Fig. 2 row A; 215, Fig. 6 row B) we recorded in these uncommon encounters.

OCCURRENCE OF LONG-RANGE CALLS AMONG CONTEXTS

To simplify the otherwise unwieldy associations of all call types with their behavior contexts, we first show how the call *groups* of similar sounds (Figs. 2–20) are distributed among the contexts in each of our most intensively recorded jay groups: 1, 3, 4, and Casita (Fig. 34). To show these data in more detail, in Figures 35–39 we list across the top all the contexts individually as well as the broader categories into which we sorted them in the section just preceding and in Figure 34, which categories we refer to as *context groups*. The black bars show the total number of renditions of any call type we recorded in each combination of call group, jay group, and context. The height of each cell represents 50 renditions. A cell is gray if the jay group in its row ever gave calls of *any* call group in the context represented by the cell's column. A cell is white if the jay group in its row never gave any calls of the indicated call group in that context. For instance, in Figure 35 the cell for call group 531, jay Group 3, and context 12A shows a black bar indicating that we recorded any calls of that combination 25 times. The cell for the same call group, jay group, and context 11 is gray but has no black bar; this means that jay Group 3 gave no calls of call group 531 in context 11, but in the same context did give some calls of at least one other call group. The cell for the same call group, context 12A, and the Casita jay group is white, showing that the Casita jays did not give calls of any call group in this context. For the purposes of comparison in this section, if one jay group produced many

calls in a gray cell for a certain context, but another jay group has a white cell for the same context, we cannot claim that the second group did *not* give that call in the same context, because we did not in effect observe the jays behaving in that context.

The calls show abundant overlap among contexts. No call group shows an unambiguous association with any context group that is consistent among the four main jay groups 1, 3, 4, and Casita (Fig. 34). Within a single jay group, call groups that occurred in more than one individual context occurred in at least two context groups (Figs. 35–39). Individual jay groups spread single call groups over as many as 12 individual contexts (call group 85B, jay Group 4, Fig. 38) and as many as five context groups (e.g., call group 38, jay Group 1, Fig. 38).

Nevertheless the jays may have tended to use some call groups more often in certain contexts than in others. The candidates are not many. As in the discussion of the distribution of calls among jay groups, we point out differences we judge to be most plausibly real due to their larger samples and the distinctiveness of entire call groups and context groups.

*Differences that may be common to all four main jay groups:*

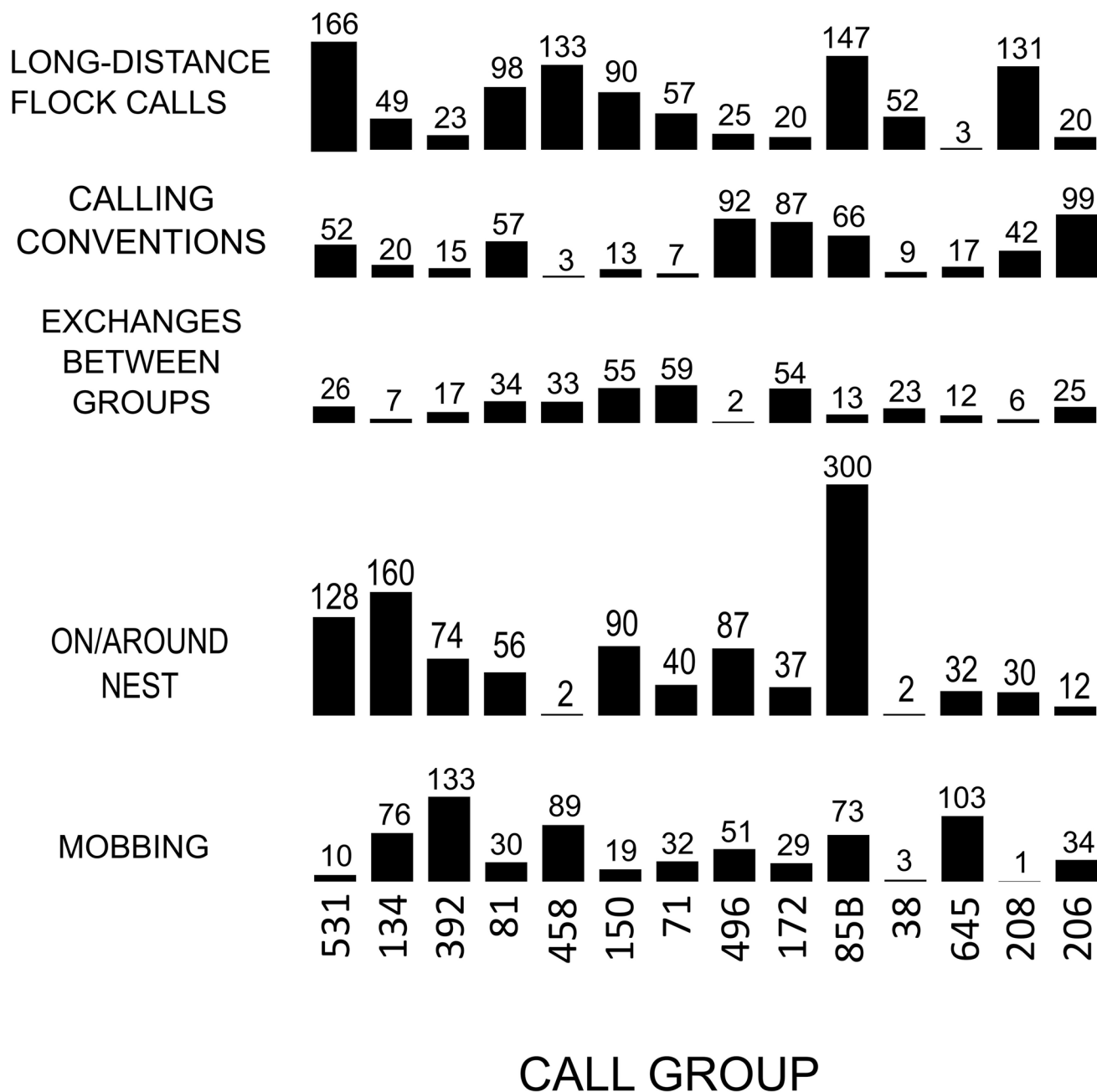
**Call group 458**, all jay groups: with the exception of two renditions, these calls did not occur in the context group On and Around Nest. In jay Group 1, which used this call group most heavily, it did not occur at all in that context group (Fig. 36).

**Call group 38**: only jay Group 1 gave many of these calls, and with the exception of two renditions, did not give them in the context group On and Around Nest (Fig. 38).

**Call group 208**, all jay groups: with the exception of a single rendition, these calls were not used in Mobbing (Fig. 39).




*Candidates for differences between jay groups in the distribution of calls among contexts:*

**Call groups 150 and 172**: jay Group 1 used these calls often in the first three context groups on the left in Figures 36 and 37, but rarely in On and Around Nest. Jay Group 3 used them rarely






**Figure 34.** Summary of Unicolored Jay call groups and the context groups in which we recorded them, Lagunas de Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Form and Variety of Calls and Figures 2-20 for delineation of the call groups, and RESULTS—The Behavior of Calling Jays for descriptions of the context groups. Each bar shows, for all major jay groups combined, the total number of renditions of all call types in each call group for a particular context group. For instance, all jay groups combined gave 166 renditions of calls in call group 531 in the context group Long-distance Flock Calls. See Figures 35-39 for the individual contexts in which each major jay group gave calls of each call group.



CALL GROUP	UJ GROUP	LONG-DISTANCE FLOCK CALLS					CONVENTIONS			BETWEEN GROUPS			ON AND AROUND NEST, INCLUDING NEST BUILDING																MOBBING										
		1 A	1 B	2	3	4	5	2 5	7 A	7 B	3 2	1 C	8	9	1 0	1 2 A	1 1	1 2 C	1 2 D	1 3	1 4	1 6	1 7	1 8 A	1 8 B	1 8 C	1 8 D	1 9	2 0	2 2	2 4 A	2 4 B	2 8	2 3	2 9	3 5	3 6	3 7	3 8
531 GROUP 	1	30	40	16			3													7	22							9					4	1					
	3	1									26			9	25					1	4	6				23		5		1								1	
	4							1										1	1		1						1		13										
	C					73			51																							6			4	1			
134 GROUP 	1	2	18			26		6				5							4												6		30	13					
	3				2						2		6	73					10												6								
	4					1		11												28		3					36							7					
	C								3																											26			
392 GROUP 	1	4	6	7		2		3	7										23														129						
	3				4						17									10	8							9											
	4							1												18		1					1	4											
	C								4																										2		2		

**Figure 35.** Unicolored Jay groups and the individual contexts in which we recorded major categories of their long-range calls, Lagunas de Montebello, Chiapas, Mexico, January-May 1987. The row headings on the left show the categories into which we grouped major segments of the spectrum-like variation in the jays' vocabulary, which we refer to as call groups, along with a sonogram showing a member of each such group. See Figures 2 and 3 for all sonograms of call group 531, Figures 3 and 4 for all sonograms of call group 134, and Figures 4 and 5 for all sonograms of call group 392. Also at the left we break down the data in each call group into the calls from each of our four most-recorded jay groups, Groups 1, 3, 4, and Casita. In the column headings we show numbers for each of the behavior contexts described in RESULTS—The Behavior of Calling Jays. We also group these context headings (except 24A-28) into broader categories of similar behavior, which we call context groups. A cell in white indicates that we never recorded calls of any jay group in the combination of call group and context represented by that cell. A cell in gray indicates that we did record birds of that jay give calls of at least *some* call group in that context—but not necessarily in the call group represented by that cell. A black bar shows the total number of renditions of all individual call types in a given call group performed by a given jay group in the indicated context; the height of a cell represents 50 renditions. See RESULTS—Occurrence of Calls Among Contexts for further details about interpreting this figure.

CALL GROUP	UJ GROUP	LONG-DISTANCE FLOCK CALLS					CONVENTIONS			BTWN GROUPS		ON AND AROUND NEST, INCLUDING NEST BUILDING																MOBBING												
		1 A	1 B	2	3	4	5	2 5	7 A	7 B	3 2	1 C	8	9	1 0	1 2 A	1 1	1 2 C	1 2 D	1 3	1 4	1 6	1 7	1 8 A	1 8 B	1 8 C	1 8 D	1 9	2 0	2 2	2 4 A	2 4 B	2 8	2 3	2 9	3 5	3 6	3 7	3 8	
81 GROUP 	1	1	20				28		15	6				2								13													1					
	3	2			1		1					7		2	4							12				2														
	4																											20												
	C						43		16	19	1		27										1														3	11	15	
458 GROUP 	1	60	6	19			45	2	2				31																				82							
	3																																							
	4																										2													
	C			1							1		2																								7			
150 GROUP 	1	36	6	1			10	2	12				15															4						1						
	3							4		1			4	21			33					12						17	3											
	4																																							
	C			1			30					6	30																							15		3		

**Figure 36.** Unicolored Jay groups and the individual contexts in which we recorded major categories of their long-range calls, Lagunas de Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Occurrence of Calls Among Contexts, and the caption of Figure 35 for details about interpreting this figure. See Figures 6 and 7 for all sonograms of call group 81, Figures 8 and 9 for all sonograms of call group 458, and Figures 9 and 10 for all sonograms of call group 150.

in these first three, but more frequently in On and Around Nest.




**Call group 85B:** jay Group 3 used this call group often in On and Around Nest, but scarcely in the first three context groups, while jay Group 4 used this call group extensively in both sets of context groups (Fig. 38).

**Call group 208:** jay Group 1 used this call group often in the first two contexts, and not in On and Around Nest, while jay Group 3 weakly showed the opposite pattern (Fig. 39).

The previous comparisons have illustrated how entire call groups are distributed among individual contexts or context groups, such as the 40

renditions of calls identified only to call group 531 that we recorded from jay Group 1 in context 1B (Fig. 35). The total number of renditions by a single jay group in such an individual context was made up of more than one individual call type, and a jay group may have given one or more of those individual call types in more than one context. Such broad dispersion of individual call types among individual contexts and context groups was typical. Individual call types occurred in as many as eight individual contexts and four context groups (Table 4).

The calls from four perched calling conventions (see The Behavior of Calling Jays, contexts

CALL GROUP	UJ GROUP	LONG-DISTANCE FLOCK CALLS					CONVENTIONS			BTWN GROUPS			ON AND AROUND NEST, INCLUDING NEST BUILDING														MOBBING												
		1 A	1 B	2	3	4	5	2 5	7 A	7 B	3 2	1 C	8	9	1 0	1 2 A	1 1	1 2 C	1 2 D	1 3	1 4	1 6	1 7	1 8 A	1 8 B	1 8 C	1 8 D	1 9	2 0	2 2	2 4 A	2 4 B	2 8	2 3	2 9	3 5	3 6	3 7	3 8
71 GROUP 	1		9	7			26		1	6			15																2					2					
	3	14																											2										
	4																																						
	C						1					44																					17				17	13	
496 GROUP 	1		8		1	1		1													2													6					
	3								10			2									7		4	20		38		16											
	4																																						
	C			5			10		1		80																										45		
172 GROUP 	1			14				2	29				5																				17						
	3									2		33	13												8		12		7										
	4							4	1					3	4														3										
	C		4							20	31		3																							1	11		




**Figure 37.** Unicolored Jay groups and the individual contexts in which we recorded major categories of their long-range calls, Lagunas de Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Occurrence of Calls Among Contexts, and the caption of Figure 35 for details about interpreting this figure. See Figures 11 and 12 for all sonograms of call group 71, Figures 12 and 13 for all sonograms of call group 496, and Figure 13 for all sonograms of call group 172.

7A, 7B, and 32) show the variety of calls given in what appeared to be a single type of activity. Here, the members of a jay group perched near one another and without visibly changing their other behavior produced long series of different call types in a variety of call groups. In the longest such bout, the Casita group gave 58 individual call types in eight call groups, and another four call types not assigned to call groups (Table 5). This jay group and jay Group 1 delivered call types by the dozens and in multiple call groups in three other transcribed conventions (Table 5). The calls the jays gave also differed from one convention to another (Table 5).

#### OCCURRENCE OF SHORTER-RANGE CALLS AMONG CONTEXTS

The jays used rattle calls (Fig. 21 row, Fig. 22 row A) in a range of contexts unexpectedly broad (Fig. 40) in comparison to *A. californica obscura*, which use them mainly during territory boundary defense (Webber, 1984). We recorded 61 of the renditions of the rattle in context 23 in a single recording session, as the jays scolded us after we had banded their group members.

Only two categories of calls in the entire Montebello vocabulary, Osprey calls (Fig. 22 row B) and peeps (Fig. 22 row C), are plainly specific to a particular set of contexts; all renditions of these

CALL GROUP	UJ GROUP	LONG-DISTANCE FLOCK CALLS					CONVENTIONS			BTWN GROUPS			ON AND AROUND NEST, INCLUDING NEST BUILDING																				MOBBING							
		1 A	1 B	2	3	4	5	2 5	7 A	7 B	3 2	1 C	8	9	1 0	1 2 A	1 1	1 2 C	1 2 D	1 3	1 4	1 6	1 7	1 8 A	1 8 B	1 8 C	1 8 D	1 9	2 0	2 2	2 4 A	2 4 B	2 8	2 3	2 9	3 5	3 6	3 7	3 8	
85B GROUP 	1			16																																				
	3												13	55		7		1	6	29	35	44		21		9				16										
	4				8	49		23		19					5		4		27			14	5					9	11											
	C			51						9	12	26																					10			53		11	9	
38 GROUP 	1	21			26			3	5	4			23		1						1																			
	3																																							
	4																																							
	C																																						1	
645 GROUP 	1						2	16		1											10													26						
	3												2	5																										
	4														1						21													11						
	C						1						5																								7	24	35	

**Figure 38.** Unicolored Jay groups and the individual contexts in which we recorded major categories of their long-range calls, Lagunas de Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Occurrence of Calls Among Contexts, and the caption of Figure 35 for details about interpreting this figure. See Figure 14 for all sonograms of call group 85B, Figure 15 for all sonograms of call group 38, and Figures 16 and 17 for all sonograms of call group 645.

calls occurred on or near the nest during the early stages of the nesting cycle (Fig. 40).

The jays gave kuks, poits, and kuk-poit combinations (Fig. 23 rows A and B) almost any time they were in one another's presence, and we suspect that their concentration in the context group In and Around Nest (Fig. 40) is due to the fact that these soft calls were easier to record there.



Our few recordings of anxiety gutturals (Fig. 23 row B; not represented in Fig. 40) are from pauses in bouts of boundary defense, much as in *A. californica obscura* (Webber pers. obs.).

Whisper song (Fig. 23 row C; not represented in Fig. 40) is also sparsely represented in our

recordings; the few segments include one instance of a bird performing the song alone.

## DISCUSSION

The sounds of Unicolored Jays on our study site exhibited several properties that appear in one or another of the few New World jays whose vocabularies are known so far in any detail: A large collection of sounds, including great variety in structure and consequent variety in tonal quality, at least as apparent to the human ear; many variants that grade finely into one another; some variation from one locality to another, suggesting that the jays learn at least some of their calls; often no clear relation

CALL GROUP	UJ GROUP	LONG-DISTANCE FLOCK CALLS					CONVENTIONS			BTWN GROUPS			ON AND AROUND NEST, INCLUDING NEST BUILDING																				MOBBING								
		1 A	1 B	2	3	4	5	2 5	7 A	7 B	3 2	1 C	8	9	1 0	1 1	1 2 C	1 2 D	1 3	1 4	1 6	1 7	1 8 A	1 8 B	1 8 C	1 8 D	1 9	2 0	2 2	2 4 A	2 4 B	2 8	2 3	2 9	3 5	3 6	3 7	3 8			
208 GROUP 	1	27	71					22			21																														
	3										8		1									1	6			6		16	1						1						
	4																																								
	C																																								
206 GROUP 	1		6	8				5				2	11																												
	3																																								
	4																																								
	C																																								

**Figure 39.** Unicolored Jay groups and the individual contexts in which we recorded major categories of their long-range calls, Lagunas de Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—Occurrence of Calls Among Contexts, and the caption of Figure 35 for details about interpreting this figure. See Figures 18 and 19 for all sonograms of call group 208, and Figures 19 and 20 for all sonograms of call group 206.

CALL TYPE	LONG-DISTANCE FLOCK CALLS										CONVENTIONS			BTWN GROUPS			ON AND AROUND NEST, INCLUDING NEST BUILDING																					MOBBING							
	1 A	1 B	2	3	4	5	2 5	7 A	7 B	3 2	1 C	8	9	1 0	1 2 A	1 1	1 2 C	1 2 D	1 3	1 4	1 6	1 7	1 8 A	1 8 B	1 8 C	1 8 D	1 9	2 0	2 2	2 4 A	2 4 B	2 8	2 3	2 9	3 5	3 6	3 7	3 8							
ALL JAY GROUPS COMBINED																																													
RATTLE	1	3	4					10		6			14																1							67	2								
OSPREY CALL														5		4		32	5									12																	
PEEP														10		13		51	44									19	4																
KUK								1	1				7							2									6																
POIT	1							1	7				5		1	3		5				1	1				1		11																
KUK-POIT COMBINATIONS	1		1									2		6		6	1	2		9								7	7																

**Figure 40.** Unicolored Jay short- and medium-range calls and the individual contexts in which they occurred, Lagunas de Montebello, Chiapas, Mexico, January-May 1987. We combine the renditions of calls for jay groups 1, 3, 4 and Casita, and do not make the distinctions between white and gray cells we observed in Figures 35-39. The height of each cell represents 25 renditions. For instance, all four jay groups together gave 14 rendition of the rattle call in Exchanges Between Groups. See Figures 21 and 22 for sonograms of rattles, Figure 22 for Osprey calls and peeps, and Figure 23 for kuks, poits, and kuk-poit combinations.

**Table 4.** Overall distribution of individual call types among individual contexts and context groups, Unicolored Jays, Lagunas de Montebello, Chiapas, Mexico, January-May 1987. See RESULTS—The Behavior of Calling Jays for descriptions of the individual contexts and context groups. Individual calls could occur not only in several individual contexts but also in several context groups. Each cell shows the number of call types occurring in each observed combination of individual contexts (counted in the heading at the top) and context groups (counted in the row at the left). For example, the first entry on the left of the second line shows that 62 calls each occurred in two individual contexts and two context groups. These calls did not all occur in the *same* two contexts and context groups.

Number of context groups	Number of individual contexts							
	1	2	3	4	5	6	7	8
1	421	42	8	10	3	1		
2		62	23	3	4		1	1
3			8	7	4	3		
4					2			

between particular contexts and particular calls; and some striking similarities with certain calls of closely related species.

#### FORM AND VARIETY OF LONG-RANGE CALLS

One approach to classifying animal sounds defines them by the categories of behavior in which they are used, and effectively imputes an internal state to the animal when using the call, for instance the *fear note* or *contentment calls* of Red Junglefowl (*Gallus gallus*; Collias, 1987). We have instead classified the sounds of Unicolored Jays strictly by structure as they appear in sonograms.

We recognize 697 variants in our full catalog of long-range calls (Figs. 2–20), and the differences among them are often subtle. Even at the end of our five months' field work at Montebello we could reliably recognize by ear only several whole categories of sounds such as call groups 85B (Fig. 14) and 208 (Figs. 18 and 19) and even fewer individual calls, such the peculiar number 37 of jay Group 1 (Fig. 10 row B). By contrast, Webber (1984) found that after about a month's daily study of *A. californica obscura* in the field he could

confidently identify and log all their calls by ear.

Mexican Jays recognize differences between calls that are slight compared to many distinctions we recognize here (Fig. 27 row C; Hopp et al., 2001). Mexican Jays use these small differences as at least one means of telling apart members of different family groups (Hopp et al., 2001).

No one knows what it is like to have perceptions as a jay would, but to judge from this experimental evidence it is conceivable that Unicolored Jays detect—in some sense—the fine differences among their many calls, and may be using them in some way. It is *possible* that much of the variation is meaningless, but so far we have no basis for *excluding* from presentation any particular calls in the vocabulary by claiming that we know the jays would find them to be unimportant.

Portraying the jays' full range of vocal variety in the detail we have presented here also has the benefit of revealing the *de facto* branching pattern that connects nearly all long-range calls in the Unicolored Jay vocabulary (see the descriptions in the captions of Figs. 2–20, and Fig. 25), which would be much harder to discern if we presented



**Table 5.** Numbers of individual call types and call groups delivered in four calling conventions of Unicolored Jays, Lagunas de Montebello, Chiapas, Mexico, January-May 1987. The headings of the rows and columns show the jay group calling, the date, the number of call types, and the number of call groups in each convention. A plus sign (+) indicates that some of the individual call types did not fall into any of our call groups. For instance, in the 30 May Casita convention (bottom row heading) the jays delivered 33 call types; these included calls in seven call groups and others unassigned. The cells at the intersections of the rows and columns show the overlap between the conventions summarized in the respective headings. The figure before the slash indicates the number of individual call types shared, and the figure after the slash indicates the number of call groups shared. For instance, the 24 May Casita convention (left column heading) and the 30 May Casita convention (bottom row heading) had in common two individual call types and four call groups. See Appendix C for the names of each call type we identified in each convention, the location of their illustrations in Figs. 2-20, the call groups to which they belong, and the number of renditions we recorded of each.

	<b>Casita, 24 May</b> 62 call types 8 call groups +	<b>Casita, 30 March</b> 48 call types 6 call groups +	<b>Group 1, 1 May</b> 34 call types 9 call groups +
<b>Casita, 30 March</b> 48 call types 6 call groups +	5/3		
<b>Group 1, 1 May</b> 34 call types 9 call groups +	1/5	1/2	
<b>Casita, 30 May</b> 33 call types 7 call groups +	2/4	3/2	1/5

only a few representatives of the broader categories.

Sounds that grade into one another are often considered to reflect graded ranges of motivation or external conditions (Suzuki, 2016); for instance, each point on a series of graded mobbing calls may correspond to a different degree of a threat's severity. The mobbing calls of White-throated Magpie-Jays (Ellis, 2008) and California Scrub-Jays (Webber, 1984) vary in this way. The Unicolored Jays did not seem to use their call variation in this manner, but recordings of individuals presented with standard stimuli, as in the experiments by Ellis (2008), may be necessary to separate out such a correspondence.

Our full inventory provides a detailed record of precisely where at Montebello the calls occurred, which can serve as a baseline for determination of long-term changes in the vocabularies of the jays at this site; we were able to make some comparisons of this sort using recordings made in 2006 on the west shore of Laguna Montebello, in the 1987 territory of jay Group 1 (Fig. 26 row A, and see below in DISCUSSION—Distribution of Calls Among Groups and Populations).

Our sample probably underestimates the full range of variation in the vocabulary of our main groups in 1987. The curves in Figure 28 show a tendency to level off but all still show at least a few

new calls appearing in the last recording session for each group. On the other hand, in each of our four best-studied groups, we found examples of all that jay group's call groups long before our last recording session (Fig. 28). The noisy nesting season had tapered off by the end of April (Webber and Brown, 1994), and this may also have contributed to the decline in the number of new calls appearing at the end of the study period.

This variety at a single small site has practical implications for attempts at sampling larger-scale variation among the regional populations of Unicolored Jays. One or two sessions at each of several different sites could easily provide unrepresentative samples of calls, even missing entire call groups. Ideally, the samples should be taken in a single season or year, with one population, such as ours, sampled intensively as a baseline. With the benefit of our large reference sample, we can say with fair confidence that certain calls in non-Montebello populations (e.g., Figs. 26 rows B and C, Fig. 27 rows A and B) did not fit even into the major call groups of the Montebello birds.

Vocabulary sizes of *Aphelocoma* (Rosa et al., 2016; Webber pers. obs.) are at present hard to compare. There is surprisingly little published, for instance, on the vocalizations of Mexican Jays, an otherwise intensively scrutinized species. Drawing on his recordings of and field experience with five species in the genus, Webber estimates with some confidence that *A. unicolor* has by far the largest vocabulary, *A. wollweberi* of Arizona and New Mexico has the smallest, while *A. californica obscura* of southern California, *A. woodhouseii* of Colorado, and *A. coerulescens* of Florida have intermediate vocabulary sizes. All except *A. californica obscura* and *A. woodhouseii* are cooperative breeders, with roughly the same group sizes.

Reports of such large numbers of sounds in the vocabulary or repertoire of a single bird species are not novel. One population of White-throated Magpie-Jays (*Calocitta formosa*) produced at least 134 call types (Ellis, 2009). Among typically singing passerines the number of the simplest elements combined to build songs can be much higher; 893 in a population of 23 Australian Magpies (*Gymnorhina tibicen*; Brown and Farabaugh, 1997),

58 to 124 per individual Sardinian Warbler (*Sylvia melanocephala*; Luschi, 1993), and over 2,400 per individual Brown Thrasher (*Toxostoma rufum*; Boughey and Thompson, 1981).

#### DISTRIBUTION OF CALL TYPES AMONG JAY GROUPS

The significance of the differences between the jay groups is obscured by the subtleties of the distinctions between the calls and the fact that most calls occurring in only one group each were rarely performed (Fig. 32A), so their apparent limitation to those jay groups may have been the result of insufficiently large samples, or one-off production of calls in bouts of invention.

The clearest example of a single easily recognizable call occurring in only one small part of our study site is call number 37 (Fig. 10 row B at the far right), recorded abundantly from jay Group 1 and perhaps its immediate neighbor jay Group 2, but in no others, including our large samples from jay groups 3, 4, and Casita. The call most similar to it is number 453, recorded many times in a short session at Cinco Lagos and a few times from jay Group 1, suggesting a gradient of call structure (Fig. 10 row B) that includes these two calls at the east end of our study site (Fig. 1).

In other instances, clusters of several closely related calls seemed to be peculiar to one part of the study site, and also not necessarily restricted to a single jay group. These patterns could be fairly obvious, because the calls in such a cluster were distinctively different from those of other such clusters in their broad pattern of frequency inflection (e.g., calls 242 through 432, Fig. 5 row C). The patterns could also be more subtle, such as the difference in peak frequency from one part of the study site to another in the series of otherwise quite similar calls shown in Figure 14 (calls 380, row A, through 270B, row C). This too, is not unprecedented; Leader et al. (2000) found microgeographic variation defined mainly by the frequency (meaning pitch in kHz, not the rate of occurrence) of a syllable common to all individual Orange-tufted Sunbirds (*Nectarinia osea*) on their study site.

Other calls or groups of calls appeared only in non-adjacent groups (e.g., the ones shared by jay groups 1 and Casita); these could conceivably

have been propagated by movement of jays from one territory to another, though we observed only a suggestion of such movements in 1987 (see Group Size in Webber and Brown, 1994).

The recordings from our jay Group 1 territory in 2006 provide another dimension to the variety in the jays' sounds by demonstrating turnover in at least some calls the jays gave at a site no bigger than a single jay territory (Fig. 26 row A). A familial dynasty of jays continuously inhabiting this patch since at least 1987 may have changed calls, new jays with different calls may have moved in, or there may have been some combination of these events.

Aside from the vocal differences between family groups of *A. wollweberi* (Hopp et al., 2001), there seem to be few other examples known so far of microgeographic vocal differences in *Aphelocoma* quite similar to the ones we found at Montebello. Brown (1964) found pair-to-pair variation in Steller's Jay (*Cyanocitta stelleri*) calls on a scale similar to that of our Montebello study site.

The nearest comparisons from other species of birds come from the smallest units, referred to by various authors as *notes*, *elements*, or *syllables*, of typical passerine advertising song, and measured as differences between individual birds rather than entire communal groups. Three neighboring male Sardinian Warblers (*Sylvia melanocephala*) with 58 to 124 note types each shared no note types with one another (Luschi, 1993). American Robins (*Turdus migratorius*) shared an average of 25% of their song elements (Johnson, 2006). Australian Magpies (*Gymnorhina tibicen*), facultative cooperative breeders, produce two kinds of song, the *warble* and the *carol*; 33% of 893 *warble* song-syllables, and 22% of *carol* syllables were shared among 23 individuals (Brown and Farrabaugh, 1997). Clay-colored Thrushes (*Turdus grayi*) shared 28% of their syllables (Vargas-Castro et al., 2012), and White-throated Thrushes (*T. assimilis*) shared 2% (Vargas-Castro, 2015).

#### VOCAL DIFFERENCES AMONG POPULATIONS OF *A. unicolor*, AND WITHIN OTHER *Aphelocoma*

Recordings from sites other than Montebello (Figs. 26–27) show vocal differences from one

locality to another that were much more pronounced than the ones within our study site in 1987. We can be fairly confident that these differences are real because of our large reference sample from Montebello, especially when the jays at these distant sites have calls that do not correspond even to any of the Montebello call groups. These differences between sites may be expected to change over time as well, just as they did on our jay Group 1 territory.

Other species of *Aphelocoma* show large-scale vocal differences between populations. The rattle calls of *A. coerulescens* differ markedly over distances of as little as 50 miles (Webber pers. obs.). In southern California, males of *A. californica obscura* have a loud, highly distinctive “chuk” call (Webber, 1984) that they use in the same way females use the rattle call, and which is absent in *A. californica* of the California central coast (W. Carmen pers. comm.). Mexican Jays in some populations of the subspecies *A. w. couchii* have a rattle call while the other subspecies have none, and among these there is no consistent association between presence of the rattle and group size or rate of bill-color maturation (Brown and Horvath, 1989). How can calls seemingly important in one population be missing in another, without even an apparent analog to take their place?

#### CONJECTURES ON VOCAL LEARNING, IMPROVISATION, AND CULTURE DRIFT

The tendency of Unicolored Jays to produce series of similar and apparently new calls in spates, geographical variation in calls on scales small and large, and turnover in calls at a single locality may all reflect call learning, call improvisation, and the process of random vocal change referred to as *culture drift* by Podos and Warren (2007). Geographic variation on these scales can occur by accumulation of differences through imperfect learning of familial or other local calls or by outright invention, combined with dispersal limited enough to prevent homogenization. These randomly created and perhaps inevitable local copy variants are in turn the basis of further differentiation, producing progressively greater differences among populations (Podos and Warren, 2007).

Little definite is known about the extent of

vocal learning among New World jays, though the scattered evidence strongly suggests that learning plays a large role in acquisition of at least some sounds among the jays and crows in general. The clearest example yet known among *Aphelocoma* and the other New World jays was an instance in which a captive adult *A. californica* from central California learned two distinctive calls from an *A. coerulescens* of Florida (Webber and Stefani, 1990). *A. coerulescens* are expert vocal mimics, incorporating even mechanical sounds into their whisper songs (Webber pers. obs.). Blue Jays (*Cyanocitta cristata*; Smith et al., 2013; Webber pers. obs.) and Steller's Jays (*C. stelleri*; Brown, 1964) are also vocal mimics. The bell calls of Blue Jays vary over distances of tens of km (Kramer and Thompson, 1979), and this pattern may also result from those jays' proclivity for vocal learning. Common Ravens (*Corvus corax*; Enggist-Dueblin and Pfister, 2002) and New Caledonian Crows (*C. moneduloides*; Bluff et al., 2010) learn at least some of their major commonly used calls, and the patterns of geographic variation seen in their sounds are considered to reflect that practice. American Crows (*C. brachyrhynchos*) learn from one another features of their warbling low-volume song (Brown and Farabaugh, 1997).

The calls we recorded from juveniles (Fig. 24) themselves provide no particular insight into the manner in which Unicolored Jays acquire their vocabularies. Only one of the juvenal calls we recorded (Fig. 24 row B, arrow) strongly resembles any particular adult call, but all had some features we found in the adult vocabulary. These calls could represent either stages in the inexorable ontogeny of fixed sounds or ventures at learning.

We suspect that Unicolored Jays, like *A. californica* (Webber and Stefani, 1990), can learn new calls at any age. They may also invent their own calls, even as adults. Marler and Peters (1982) use the term *improvisation* to refer to the creation of sounds that are similar to a model but different enough to be considered separate sounds; these may be *elemental*, new simple elements or syllables, or *combinatorial*, re-arrangement of elements to form new phrases. Janik and Slater (2000) pre-

fer the term *innovation* for the same phenomenon. Marler and Peters (1982) use the term *invention* to refer to the creation of new signals that are not modifications of any model vocalizations.

The tendency to produce series of previously unrecorded, closely similar calls in a single recording session (see RESULTS—Episodic Introduction of New Calls) is consistent with the possibility that the jays hit upon themes and improvised on them extemporaneously as we recorded them, so the variation may be open-ended instead of consisting of a large but finite collection of sounds. Yet the flattening of the new-call curves toward the end of our stay (Fig. 28) suggests that if the jays were continually creating new calls then, they were not doing it at a high rate, perhaps because nesting activity had diminished by then, as noted earlier.

If the spates of closely spaced and closely related Unicolored Jay calls represent spontaneous and continuous improvisation or invention, there seems to be no other known instance quite like it. Examples providing warrant for the plausibility of such improvisation are from the typically singing passerines. Brown and Farabaugh (1997) attribute the abundance of unique syllables in the repertoire of individual Australian Magpies (*Gymnorhina tibicen*) to “practice, invention and improvisation.” American Robins (*Turdus migratorius*) acquire some of the individual elements of their songs by imitation of other robins, but most elements of each bird's repertoire are unique to it, suggesting that they created them through improvisation or outright invention. Some individual adult robins have been observed improvising new elements and dropping others during the breeding season (Johnson, 2006). The song of a single Brown Thrasher (*Toxostoma rufum*) may consist of over 2,400 types of syllables; Boughey and Thompson (1981) and Kroodsma and Parker (1977) suggest that that this variety results at least in part from improvisation of syllables as the birds sing. Individual White-throated Thrushes (*Turdus assimilis*) share only about 2% of their song syllables with other individuals, “suggesting that males invent most of their repertoires” (Vargas-Castro, 2015). Clay-colored Thrushes (*Turdus grayi*) share only



an average of 28% of their syllable types with other individuals, also suggesting that the singers had invented or improvised the unique syllables (Vargas-Castro et al., 2012). By one month after fledging, Budgerigars (*Melopsittacus undulatus*) build their individually distinctive collections of call syllables by adding new details to old calls, combining parts of different calls, and inventing entirely new calls (Brittan-Powell et al., 1997). Kroodsma et al. (1997) found that hand-reared Gray Catbirds (*Dumetella carolinensis*) constructed their repertoires primarily by improvising or inventing syllables, and wild adults shared few or no songs, further suggesting that they created their own song novelties rather than imitating available models, but cautioned that "...we do not know what mix of imitation, improvisation, and invention gray catbirds use in nature." Each Sardinian Warbler (*Sylvia melanocephala*) has a large collection of song syllables, none of which it shares with other singers in its vicinity, which implies that these individuals have improvised or invented their own songs (Luschi, 1993). Luschi (1993) also found that the curve of new-syllable introduction for two of his three study subjects showed no sign of leveling throughout his observations, prompting him to suggest that they "do not possess a finite repertoire of notes," and that they were creating new syllable types as he recorded them.

#### VOCAL INNOVATION AND VOCAL STABILITY

Several particular similarities between the various species of *Aphelocoma* contrast with the fertility of vocal invention we otherwise find among these jays. The Unicolored Jay calls of Figure 14 row C (especially calls 389, 361), and Figure 15 row A (especially calls 132, 189), show minutely detailed similarities to certain calls of *A. woodhouseii* (e.g., Fig. 26 row C, middle), which are also similar to the calls of *A. californica obscura* referred to as *weeps* by Webber (1984).

The Mexican Jay calls from Arizona illustrated in Figure 26 row C are quite similar to the 1987 Unicolored Jay calls from our study site shown in Figure 10 row C, especially the calls at the left end of that row. While this type of call makes up only a tiny part of the variation in Unicol-

ored Jay calls, sounds of this general form seem to make up a much larger proportion of the Mexican Jay vocabulary, to judge from the little published literature (e.g., McCormack and Brown, 2008) and Webber's unpublished recordings.

If *Aphelocoma* jays learn these similar calls, they must have maintained an exquisitely fine degree of fidelity in copying them for many generations. The ancestral line leading to Unicolored Jays split from the one leading to their nearest relatives about 3 million to 8.5 million years ago (McCormack et al., 2011). How could this kind of fidelity be maintained for literally millions of generations if inexactness in learning also produces the profusion of different call types we see within and among populations of Unicolored Jays? This continuity over long ages is similar to the multi-million-year persistence that Miller and Baker (2009) attribute to certain sounds of shorebirds, which do not learn their calls. Lachlan et al. (2018) deduce that individual learned syllables of Swamp Sparrow (*Melospiza georgiana*) song last at most about 500 years. In human languages, common ancestors of cognates can be reconstructed going back no more than about 15,000 years before present (Pagel et al., 2013).

For reproducing a core part of their vocabulary, the jays may favor an innate sound template such as the one found in many songbirds with typical advertising song (e.g., Slater, 1989, Soha and Marler, 2000), while other parts remain free to vary, perhaps even invented on the spur of the moment without any model except a general pattern such as the dual bands in call group 458 (Figs. 8 and 9). This combination of free-form innovation within boundaries seems to have a parallel among Sedge Wrens (*Cistothorus platensis*), in which individuals invent their own unique songs; they are "apparently constructed on a set of design rules, but within those prescribed limits the diversity seems almost infinite" (Kroodsma et al., 1999).

Unicolored Jays show an extraordinary degree of genetic variation from one regional population to another, apparently resulting from long isolation; Venkatraman et al. (2018) calculate that Unicolored Jays on either side of the Isthmus of

Tehuantepec in Mexico have been separated from one another for about 3.3 million years (cf. the figure for the split between *A. unicolor* and other *Aphelocoma*, McCormack et al., 2011). This suggests that vocal divergence through drift and innovation among the regional populations may have proceeded in ways only hinted at by the small sample of calls currently available from sites other than Montebello (Figs. 26 rows B and C, Fig. 27).

#### OCCURRENCE OF CALLS AMONG CONTEXTS

At most, Figures 35–39 show only weak and conjectural association between any calls and particular contexts. These apparent associations were not necessarily consistent in our sample from one jay group to another. Jay Group 1 often used call groups 150 and 172 as Long-distance Flock Calls, but not in On and Around Nest, while jay Group 3 used them rarely in the former group of contexts, but frequently in the latter (Figs. 36 and 37). We are not ready to assert that calls have different meanings for different jay groups, so we think it more likely that these differences result from sampling error, even in a compilation of recordings as relatively rich as ours.

The only common calls that did have a clear relation with particular contexts were the Osprey call and peeps, neither of which is a loud long-range call. The occurrence of rattles in contexts other than boundary defense is something of a surprise, since *A. californica obscura* use rattles mainly in territory defense (Webber, 1984). It should be noted, however, that most of the renditions in the Mobbing category were from a single perhaps unrepresentative recording session.

Aside from these few cases, we found widespread overlap and thus apparent redundancy between call groups and behavior contexts (Figs. 34–39), and on a finer scale between individual calls and behavior contexts. Calling conventions may provide the best evidence for this. In these bouts of calling, as nearly as we can tell the basic behavior context remained constant while the jays uttered a great variety of calls in several call groups. The calls vary widely not just from one time to another during a single convention but also from one convention to another (Table 4).

We have drawn the context categories finely so as to reveal possible associations between calls and rather minute categories of behavior, and we have also lumped these categories into broader parcels in case those categories are too narrow. It is still conceivable that we have not discriminated the right kinds of behavior contexts to reveal clear associations with certain kinds of calls, but we are inclined to doubt it, for these relationships can show themselves readily enough without extraordinary measures to sort them out, e.g., the calls of cooperatively breeding Australian Magpies (Brown and Farabaugh, 1997) and Smooth-billed Anis (*Crotophaga ani*; Grieves et al., 2015), as well as the Osprey calls and peeps of the Montebello jays (Fig. 40). The contexts we have considered here provide a comprehensive catalog of major events in the affairs of the jays during the breeding season; would even firm associations of calls with contexts not in this inventory be so abstruse that they would be of little importance in the lives of the birds?

This broad overlap suggests that the important part of the vocal variety produced by Unicolored Jays is not to provide a close fit between particular contexts and the messages of particular calls, but simply the ability to deliver a variety of sounds. The change in call types then could amount to a signal in itself, similar to the function of song-type switching in birds with typical territorial advertising song (Kroodsma, 2004; Catchpole and Slater, 2008). This analogy has to be used with caution, because the different song types of typical singers with small repertoires are themselves found to correspond to different social contexts (e.g., Spector, 1992; Staicer et al., 2006), and it may apply best to singers with larger repertoires.

Webber (1984) found that *A. californica obscura* used a variety of calls in a single context, and if they continued to call in long bouts, would eventually cycle through these various call types in way reminiscent of typical singing passerines shuffling through their song types (Kroodsma, 2004; Catchpole and Slater, 2008).

Ellis (2009) reported a similar degree of redundancy in the way a population of White-throated Magpie-Jays used at least 134 call types



in one context, warning in response to the presence of low-threat predators.

#### SOUND VARIETY AND SOCIALITY

It is easier to describe what the Unicolored Jay vocabulary seems not to do than it is to explain why it has its peculiar characteristics.

Barbour (1977) and Hardy (1979) entertained the commonsense view that corvids with more complex social behavior—variously defined—ought to have larger collections of sounds. Freeberg et al. (2012) elaborated the idea in more explicit form for signaling animals in general under the name *social complexity hypothesis*. They distinguish the components of social behavior, such as group size and variety in the roles of group members, that they argue should result in signals specialized for navigating them.

Some vocal group-living vertebrates do exhibit apparently straightforward relationships between social contexts and the calls specialized for them. Cooperatively breeding Smooth-billed Anis (*Crotophaga ani*) have a variety of calls each specialized for activities such as territory defense and group choruses (Grieves et al., 2015). Grieves et al. (2015) explicitly consider this to be an example supporting the social complexity hypothesis. An example that seems to fit the hypothesis even more neatly comes from group-living primates. Geladas (*Theropithecus gelada*) have calls used specifically in affiliation with their long-term female associates, while the closely related chacma baboons (*Papio ursinus*) form more transitory consortships with females and lack these calls (Gustison et al., 2012).

What in particular about group living and cooperative breeding might help to mold the vocabulary of Unicolored Jays? One context in which we might expect a vocal specialization is the rivalry between dominant and subordinate males for opportunities to mate with the breeding females, a context that does not exist among *Aphelocoma* that are not cooperative breeders. Secondary males repeatedly attempted to approach the female breeder during the egg-laying period, and occasionally succeeded in copulating with her despite the efforts of the primary male to keep them away (Webber and Brown, 1994). We do not

know whether these matings produced offspring, but such copulation attempts are common among subordinate breeding Mexican Jays, which have one of the highest rates of extra-pair fertilizations known among birds (Li and Brown, 2000). (In contrast, attempts at copulation by subordinates are not observed among Florida Scrub-Jays, in which the rate of extra-pair paternity is zero; Quinn et al., 1999). This context is a natural candidate for application of the social complexity hypothesis; secondary and primary males would seem to have a large stake in exhibiting any vocal behavior fitted to enhance their respective efforts at approach and repulsion. Yet the jays used calls from seven call groups in this behavior (contexts 18A through 18D), and used all of those call groups in a wide variety of other contexts (Figs. 35–39). Even if there were a clear relationship between certain calls and this peculiarity of group living, it could scarcely serve to explain the extravagant variety we see in other aspects of the jays' vocabulary.

Ellis (2009) proposed that the immense variety of calls White-throated Magpie-Jays use in low-intensity mobbing is the result of sexual selection upon male signals of fitness, in analogy to the often-used explanation for large repertoires among singing songbirds. This might seem at first glance to be a promising explanation for the similar profusion of Unicolored Jay call types in contexts such as calling conventions. Ellis's (2009) hypothesis, however, is specific to the singular social arrangements of the magpie-jays: subordinate males are not members of territory-holding family groups but rather float around and among territories in search of matings with both subordinate and breeding females. Ellis (2009) postulates that predator mobbing provides these floater males with their best opportunities for solicitation of matings through vocal advertising enhanced in its attractiveness by means of enlarged collections of calls. We have little information about dispersal and movements of individuals around and between Unicolored Jay groups, but we saw nothing resembling a body of male floaters such as described by Ellis (2009). In any event, Byers and Kroodsma (2009) and Soma and Garamseghi (2011) provided reason to doubt

that sexual selection is the primary driver of variety in song repertoires.

Broad-scale surveys have not borne out the idea of a strong association between measures of social complexity and repertoire or vocabulary size. Ord and Garcia-Porta (2012) found no general association of social complexity and signal complexity in a wide-ranging survey of birds, mammals, lizards, and ants. (It should be noted however, that Ord and Garcia-Porta's (2012) examples from birds are songbird song repertoires, not call vocabularies such as we have in corvids.)

In another comparison, based on the few New World jay vocabularies known and comparable so far, Rosa et al. (2016) concluded that group size in these jays is correlated with vocabulary size, but that cooperative breeders tend to have *smaller* vocabularies.

Among the New World jays one example inconsistent with the Social Complexity Hypothesis stands out: southern San Blas Jays (*Cyanocorax sanblasianus sanblasianus*) are cooperative breeders living in groups of up to 26 adults with complex mutual helping at one another's nests, and sub-territories within their group territories (Hardy et al., 1981), yet they have an effective vocabulary that corresponds in variety to at most a single call group of Unicolored Jays (Webber pers. obs.).

Among the *Aphelocoma* jays, there is no clear relation apparent so far between social group size or organization and vocabulary size. For the present time the vocabulary of Unicolored Jays stands prominently among them as a prodigious enigma.

#### MORE POINTS OF COMPARISON IN THE GENUS *Aphelocoma* AND BEYOND

We rarely recorded overhead-predator calls, and the few we captured are short sharp bursts such as calls 218 (Fig. 2 row A) and 215 (Fig. 6 row B). *A. californica obscura* employ sounds of similar explosive brevity in this context (Webber, 1984). In both species these calls are also used widely in a variety of other behaviors. They also are structurally quite unlike the classic predator-warning (as opposed to predator-mobbing) calls often described in ethology textbooks (Gill and Bierema, 2013), which are pure tones with gradual onset and

decay, and thus thought to be difficult for a predator to locate. Nevertheless the jays react to the warning calls by taking cover (Stotz and Webber, pers. obs.), so some combination of context and mode of delivery must help to distinguish their use.

Loud vocalizing on the nest by incubating females (see RESULTS—The Behavior of Calling Jays, On and Around the Nest, contexts 10 through 12A, Figs. 35–39) remains a puzzle. Because incubating birds often otherwise behave cryptically, it seems paradoxical that they would do anything to make themselves more conspicuous while on the nest. As indicated by Leonard's (2008) survey of the literature on 748 species of North American birds, however, such loud behavior is common among a wide variety of species. Of these, 48.3% are known to call or sing on or near the nest. Overall, there is little evidence that such noise-making places the nest contents at greater risk. The proposed proximate reasons for such calling include territory defense, nest defense, solicitation of a group member to take over incubation, and solicitation of feeding on the nest (Leonard, 2008). Of these, only the last seems to us to be a likely function in Unicolored Jays, but even then, it is not at all clear why parents and other relatives of the incubator and her offspring would need additional prompting to feed her, and why calling would induce them to do so. Female White-throated Magpie-Jays call loudly on and near the nest (Ellis et al., 2009), but this behavior differs in three ways from the calling we observed: 1) the magpie-jay calls are juvenal-style food-begging calls, not typical adult calls 2) when magpie-jay females broadcast the begging calls with no other jays present, they were not on the nest, and 3) when magpie-jay females gave these calls on the nest, they did so mainly when attendants arrived with food. Ellis et al. (2009) propose that the female magpie-jays use these calls to advertise both their need for added nutrition and opportunities for mating by males other than their social mate. The reason for performing these vocal displays near the nest may be the need to keep other female flock members from depositing eggs, even though the calling may incur an extra risk of predation (Ellis et al., 2009). Sub-

ordinate male Unicolored Jays copulated with their group's breeding females during their fertile period despite the dominant male's attempts to repel them, and one subordinate male copulated with all three females in its group (Webber and Brown, 1994). Nevertheless we cannot make a firm connection between such events and the females' usually unanswered calling from the nest.

The long clamorous gatherings we refer to as calling conventions have no parallels that we know of among other *Aphelocoma*, and apparently few among any other passerines. Somewhat similar are the communal caroling bouts of Australian Magpies, a group-living, facultatively cooperative breeder with year-round territories. The caroling bouts among the magpies can last up to 30 minutes, both sexes and all ages participate in them, and "In non-territorial contexts, group membership is delineated by participation in the communal vocal display" (Brown and Farabaugh, 1997).

We found no clear instances of call matching. Webber (1984) found a tendency for *A. californica obscura* to match their neighbors' calls, weak generally but stronger in long continuous bouts of boundary defense. If this is a true difference between these two species, and not an artifact of the difficulty in tallying the calls of individual Unicolored Jays, this is a major unexplained difference between the two.

Most *Aphelocoma* have a rattle call, and these calls vary widely. *A. californica obscura* has a fast rattle (Webber, 1984), *A. woodhouseii* in southwestern New Mexico has a fast rattle composed of two kinds of pulses (Webber pers. obs.), *A. coerulescens* in south-central Florida has a slow rattle composed of two kinds of pulses (Barbour, 1977), some populations of *A. wollweberi couchii* of Texas and Mexico have a fast rattle, while the western subspecies of *A. wollweberi* have none (McCormack and Brown, 2008). *A. unicolor* is the only *Aphelocoma* we know of that has both fast and slow rattles in the same population.

When comparing the vocalizations of even just the *Aphelocoma* known so far, we can see that their differences go far beyond merely providing parallel categories of sounds that accompany

behavior common to two or more species; they seem to be doing something fundamentally different with their sounds that so far has no obvious relation to the difference in their presently understood social organization.

## ACKNOWLEDGEMENTS

We again thank all the helpful persons and institutions to whom we expressed gratitude in Webber and Brown (1994). We thank Jerram L. Brown for helping to provide the means for working at Lagunas de Montebello through his grants from the National Institute of Mental Health (2R01MH 16345-05) and the National Science Foundation (BSR-87 12242). We are also grateful for the generous help of Steven Hopp, Nathan Pieplow, The Macaulay Library of the Cornell Laboratory of Ornithology, the Biblioteca de Sonidos de Aves of the Universidad Nacional Autónoma de México, Xeno-Canto, and the field naturalists who contributed their recordings to those archives. Jesse M. Ellis and John E. McCormack provided unusually detailed and thoughtful suggestions that improved the manuscript. Webber remains responsible for all defects.

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### APPENDIX 1. CALLS IN ONE JAY GROUP EACH

Unicolored Jay calls each recorded in only one jay group, Lagunas de Montebello, Chiapas, Mexico, January-May 1987. The rows are organized from top to bottom by the total number of renditions of each call type we recorded throughout the study season, as listed in the left-hand column. In the first ten lines of the right-hand column we give the total number of different individual call types that each occurred the number of times shown in the left-hand column. For example, we recorded 263 individual call types once each, and ten call types nine times each. In the following lines of the right-hand column we show how many individual call types we recorded ten or more times each. Following those numbers after the colon are the name of the call type, the call group to which it belongs, its location in the sonograms (Figs. 2–20), number of sessions in which we recorded it, and the jay group that gave it. An N indicates that the call did not belong to any of the call groups designated in Figures 2–20. For example, the last line in the table shows that in our recordings we identified 94 renditions of one call, number 266, which does not belong to any call group, is illustrated in row C of Figure 15, and occurred in two recording sessions from the Casita group. Semicolons separate the data for each call type from those of others in the same category. We summarize these data in Figure 32 part A.

Number of renditions	Number of call types. For calls with 10 or more renditions: Name of call type, call group, location in sonogram Figures 2–20, number of sessions in which recorded, and jay group
1	263
2	97
3	47
4	32
5	12
6	17
7	13
8	7
9	10
10	9: 392, 392, 4C, 1, 3; 225, 392, 5A, 2, 3; 316, 81, 7A, 1, 4; 675, 81, 7B, 1, C; 163, 458, 8A, 3, 1; 496, 496, 12B, 3, C; 39, 38, 15B, 2, 1; 90, N, 15C, 2, 1; 230, 206, 20A, 1, 3
11	5: 511, 392, 5B, 1, WG; 457, 458, 8A, 1, 1; 38, 38, 15B, 7, 1; 278, 645, 17B, 1, 4; 177, 206, 19B, 2, 1
12	1: 132, N, 15A, 3, 1
13	5: 510, 531, 2C, 1, 4; 197, 458, 9A, 1, 1; 193, 458, 9A, 1, 1; 325, 71, 11A, 1, 1; 329, 208, 19A, 4, C
15	3: 473, 172, 13A, 1, 1; 680, 645, 16B, 1, C
16	2: 21, N, 5C, 1, 1; 100, 458, 8C, 4, 1
17	1: 250, 150, 9C, 2, C
18	1: 165, N, 5C, 1, 1
19	2: 118, 458, 8C, 3, 1; 462, 208, 18B, 1, 1
20	1: 676, 81, 6C, 1, C
21	2: 242, N, 5C, 5, 3; 722, 645, 17B, 1, 4
23	2: 699, 150, 9C, 1, C; 162, 38, 15B, 2, 1
25	1: 326, 71, 11A, 3, 1
30	1: 270B, 85B, 14C, 5, 3
35	1: 11, 531, 3B, 5, 1
38	1: 18, 206, 20A, 4, 1
40	1: 267, 81, 6C, 2, C
52	1: 522, 206, 19C, 2, C
55	1: 134, 134, 4C, 4, 1
58	1: 252, N, 10B, 1, E
66	1: 226, 71, 12A, 3, C
81	1: 149, 458, 8A, 3, 1
94	1: 266, N, 15C, 2, C

## APPENDIX 2. DETAILED DISTRIBUTION OF SHARED CALLS AMONG NAMED JAY GROUPS

Distribution of call types that occurred among two or more groups of Unicolored Jays, Lagunas de Montebello, Chiapas, Mexico, January-May 1987. The left-hand column shows the names of the jay groups in which the numbered call types in the right-hand column occurred. See Figure 1 for the locations of the jay groups and the abbreviations of their names. The jay-group names in the left column are organized in categories from top to bottom according to the number of jay groups sharing the calls, from calls occurring in only two jay groups at the top to those occurring in the observed maximum of six at the bottom. Within each of these categories we arrange the combinations of jay group names in order of the groups' locations on the study site, from northwest to southeast. For example, at the top of the table in the category showing calls shared by only two jay groups, the first pair is WG, the northwesternmost jay group in the category, and Casita group, the northwesternmost jay group with which WG shared the two calls in this category. Then follows the pair of WG with jay Group 3, the next most northwesterly jay group with which it shared such calls. The order continues in this manner to the last line of the category, the combination of jay Group 1 and Cinco Lagos, at the southeastern end of the study site. We include only records of calls that we recorded from positively identified jay groups; for instance if a call occurred in a boundary skirmish between Group 4 and the Agua Tinta group in which we were unable to say which particular group(s) gave the call, we did not count the 4/AT call. In the right-hand column, the call number is given first, then in parentheses the figure and row in which its sonogram appears, followed by the call group, if any, to which it belongs. An N indicates that the call is not assigned to a call group. The calls for a given combination of jay groups are listed in order as they appear in Figures 2–20. For example, in the last line of the first category at the top of the table, the list shows that jay groups 1 and Cinco Lagos shared two calls: number 453, illustrated in row B of Figure 10 and not part of any call group, and number 446, illustrated in row A of Figure 12 and part of call group 71. We summarize these data in Figure 32 part B.

Jay groups	Calls (location in sonogram figures, call group)
WG, C	513 (3C, 134)
WG, 3	338 (5C, N)
G, C	518 (12A, N)
G, 3	517 (14C, 85B)
C, P	265 (12A, 71)
C, 3	218 (2A, 531), 508 (2A, 531), 220 (2B, 531), 352 (3C, 134), 344 (6A, 81), 343 (6A, 81), 305 (7B, 81), 502 (9A, 150), 503 (9B, 150), 382 (9B, 150), 210 (9C, 150), 333 (10A, 150), 301 (12B, 496), 213 (12B, 496), 207 (13C, N), 509 (14B, 85B), 238 (18C, 208), 214 (18C, 208), 425 (20A, 206), 435 (20A, 206), 224 (20A, 206)
C, 4	527 (2A, 531)
C, 5	531 (2A, 531), 628 (6B, 81)
C, 1	560 (6B, 81), 53 (7B, 81), 627 (12A, 71), 494 (12B, 496), 547 (12B, 496), 116 (13C, N), 133 (14A, 85B), 74 (14B, 85B), 464 (15B, 38), 155 (18A, N), 66 (18B, 208), 206 (19C, 206)
3, 4	223 (2B, 531), 244 (3C, 134), 259 (3C, 134), 245 (5A, 392) 286 (11A, 71)
3, AT	298 (13B, 496)
3, 1	181 (4C, 392), 190 (5A, 392), 182 (5A, 392), 141 (6A, 81), 153 (9A, 150), 45 (11B, 71), 300 (13B, 496), 93 (13B, N), 87 (18A, N), 171 (18B, 208)
4, AT	376 (4C, 392), 380 (14A, 85B), 360 (14C, N), 275 (18A, N)
4, 1	176 (3C, 134), 144 (6B, 81), 25 (9A, 150), 442 (11B, N), 260 (15C, N)
5, 1	615 (2C, 531), 4 (3A, 531), 30 (20A, 206)
AT, 1	200 (8B, 458), 86 (12B, 496)
CE, 1	524 (14C, N)
1, CL	453 (10B, N), 446 (12A, 71)
WG, C, 3	500 (2C, 531), 296 (14B, 85B)
C, 3, 4	219 (2B, 531), 351 (3C, 134), 257 (3C, 134), 273 (9A, 150), 272 (10A, 150)

**Appendix 2.** Continued.

Jay groups	Calls (location in sonogram figures, call group)
C, 3, 5	490 (9B, 150)
C, 3, AT	262 (12B, 496), 253 (13B, 496)
C, 3, 1	378 (10A, 150), 205 (13A, 172), 380 (14A, 85B)
C, 4, AT	313 (14B, 85B)
C, 4, 1	383 (5A, 392)
C, AT, 1	168 (12B, 496)
C, E, 1	251 (4A, 134)
3, 4, AT	354 (3C, 134), 362 (14C, N)
3, 4, 1	78 (3B, 531), 14 (5A, 392), 310 (7A, 81), 274 (9A, 150)
3, 5, 1	123 (3A, 531), 81 (6C, 81)
3, AT, CE	342 (14C, N)
3, AT, 1	55 (5A, 392), 185A (14A, 85B), 363 (14A, 85B)
WG, 3, 4, 1	311 (3C, 134)
G, C, 3, 4	335 (14B, 85B), 270A (14C, 85B), 394 (14C, 85B)
C, 3, 4, AT	85A (14A, 85B), 381 (14A, 85B)
C, 3, 5, 1	215 (6B, 81)
C, 3, AT, 1	64 (13B, 496)
C, 4, AT, 1	261 (14B, 85B)
3, 4, AT, CE	340 (14C, N)
G, C, 3, 4, CE	389 (14C, N)
C, 3, 4, AT, CE	361 (14C, N)
C, 3, 4, 5, 1	185B (14A, N)
WG, C, 3, 4, E, 1	172 (13A, 172)
WG, C, 3, 4, AT, 1	337 (14A, 85B), 85B (14B, 85B)
G, C, 3, 4, 5, AT	327 (14B, 85B), 336 (14B, 85B)

**Appendix 3.** All calls identified from each of four calling conventions of Unicolored Jays, Lagunas de Montebello, Chiapas, Mexico, January–May 1987. See RESULTS—The Behavior of Calling Jays for a description of calling conventions. For each convention we list each call type we identified, the location of its illustration in Figures 2–20, the call group it belongs to, and the number of renditions of the call we recorded during the convention. For instance, the left-hand group of columns lists the Casita group gave in a convention on 24 May; at the top is call 537, illustrated in row A of Figure 2, belonging to call group 531, and uttered twice by the jays. We list the calls according to the sequence in which they appear in Figures 2–20, not chronologically as they occurred in the call bouts. We summarize aspects of these data in Table 5.

Casita, 24 May					Casita, 30 March					Group 1, 1 May					Casita, 30 May				
Call type	Fig, row	Call group	Count	Call type	Fig, row	Call group	Count	Call type	Fig, row	Call group	Count	Call type	Fig, row	Call group	Count	Call type	Fig, row	Call group	Count
537	2A	531	2	219	2B	531	1	468	4C	392	1	257	3C	134	1				
534	2A	531	7	351	3C	134	21	76	4C	392	1	352	3C	134	1				
533	2A	531	3	257	3C	134	1	149	8A	458	1	344	6A	81	6				
541	2A	531	2	636	3C	134	2	481	8A	458	1	343	6A	81	11				
527	2A	531	6	352	3C	134	1	487	9B	150	1	559	6A	81	1				
218	2A	531	1	251	4A	134	1	488	9B	150	1	560	6B	81	1				
530	2A	531	2	637	6A	81	6	489	9B	150	2	268	6C	81	2				
536	2A	531	2	638	6A	81	2	490	9B	150	1	267	6C	81	1				
348	2A	531	2	639	6A	81	2	492	9B	150	1	568	7A	81	2				
508	2A	531	2	640	6B	81	1	420	9C	150	1	305	7B	81	1				
531	2A	531	5	628	6B	81	2	150	9C	150	1	308	7B	81	1				
528	2A	531	2	215	6B	81	11	378	10A	150	1	558	7B	81	1				
220	2B	531	1	649	11C	71	1	493	10A	150	1	551	8C	458	2				
540	2B	531	2	627	12A	71	12	491	11C	71	1	502	9A	150	2				
542	2B	531	3	666	12A	71	1	467	12B	496	2	561	9B	150	1				
499	2B	531	1	265	12A	71	2	172	13A	172	4	503	9B	150	1				
538	2B	531	1	226	12A	71	1	473	13A	172	15	382	9B	150	5				
500	2C	531	2	172	13A	172	1	477	13A	172	4	339	9B	150	3				
535	2C	531	1	642	14A	85B	3	476	13A	172	4	565	9C	150	1				
529	2C	531	1	644	14A	85B	1	474	13A	172	2	210	9C	150	2				
539	3A	531	1	327	14B	85B	3	479	15B	38	3	563	9C	150	2				
532	3A	531	1	336	14B	85B	1	162	15B	38	2	250	9C	150	11				
543	3A	531	1	313	14B	85B	4	36	15C	-	23	569	10A	150	1				
215	6B	81	1	335	14B	85B	1	164	18A	-	1	378	10A	150	1				
713	7A	81	1	509	14B	85B	1	472	18B	206	1	226	12A	71	43				





## Appendix 3. Continued.

Casita, 24 May			Casita, 30 March			Group 1, 1 May			Casita, 30 May		
Call type	Fig. row	Call group	Count	Call type	Fig. row	Call group	Count	Call type	Fig. row	Call group	Count
327	14B	85B	9								
336	14B	85B	2								
335	14B	85B	2								
238	18C	208	3								
329	19A	208	5								
552	19A	208	3								
526	19C	206	1								
522	19C	206	21								
425	20A	206	2								
435	20A	206	1								
224	20A	206	7								
fast rattle	21C	-	6								