

VOCAL REPERTOIRE AND ITS POSSIBLE EVOLUTION IN THE BLACK AND BLUE JAYS (*CISSILOPHA*)

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The 4 allopatric Middle American jays of the taxon *Cissilopha*, which I treat as a subgenus of *Cyanocorax* (Hardy 1969), are communally social year round (Hardy 1976, Raitt and Hardy 1976). The species are the Yucatan Jay (*C. yucatanica*), Bushy-crested Jay (*C. melanocyanea*), San Blas Jay (*C. sanblasiana*, with 2 distinct races, see Hardy and Raitt 1977), and the Beechey Jay (*C. beecheyi*). Their displays as a group are distinctive although not very elaborate (Hardy 1974b). Their vocal repertoires superficially seem small, as short-term experiences in the wild usually allow the observer to hear only 1 or 2 call types and these mainly from excited groups. Each form has a more extensive vocabulary.

In this paper I describe the known vocalizations, assign them to behavioral or motivational contexts, show some context patterns in tabular form, and speculate on the possible nature of evolution of vocabulary in the group.

METHODS

As described in detail elsewhere (Hardy 1973, 1974a, b, 1976; Raitt and Hardy 1976) all these jays were studied in the wild and in captivity. Recordings were analyzed on a Kay Electric Company Sona-Graph, Model 7029A, for sonograms (all wide band) presented here. All recordings or exact copies of them are deposited in the Bioacoustic Archive of the Florida State Museum's Department of Natural Sciences. The 4 tables showing context and pattern of vocalizations are based entirely upon tape recorded sequences in the Archive. In the discussion of the vocalizations, I have used my aural experience in many additional field hours with the birds in an attempt to compensate for the bias inherent in a quantitative approach to repertoires based only on recorded sound specimens.

RESULTS

In this section each species' vocalizations are treated separately.

Yucatan Jay.—The Yucatan Jay apparently has the largest active vocabulary of the 4 species. That is, more of its known vocalizations can be heard in the normal course of events while the birds are studied in the breeding season (Table 1). A description of the vocabulary of this species provides a basis for comparative consideration of the sounds of the remaining 3 species.

My 1969 paper showed narrow band sonograms of vocalizations of *C. yucatanica*, and Hardy (1974a) illustrated calls including one shown in both papers. These and several other calls are illustrated in Figs. 1 and 2. I have revised the phonetic interpretation of 2 vocalizations (from *clok!* to *clank!* and from *crook* to *chook*); 1 vocalization in Fig. 1, line 5, H of Hardy

TABLE I
PATTERNS AND CONTEXTS OF YUCATAN JAY VOCALIZATIONS

Call type	Contexts 1-9 (Contexts 3, 5, 6, treated only in footnotes)											
	1		2		4		7		8		9	
	N	%	N	%	N	%	N	%	N	%	N	%
Chatter	32	27.8	5	7.1	6	10.7	10	58.8	7	53.8	10	19.2
“Fear”							1	5.7				
Rattle	2	1.7									1	1.9
<i>Caah</i>	2	1.7							6	46.2		
<i>Chook chook</i>	1	0.8			50	89.3					1	1.9
Pump-handle	1	0.8	8	11.4			2	11.8				
Guttural												
tin-horn piping	1	0.8										
Clear tin-horn												
piping	5	4.3										
Metallic yelp	7	5.6										
Foggy bell	19	16.5										
Clanks	21	18.3	51	72.8							29	55.8
Peeps	24	20.9	6	8.6			4	23.5			1	1.9
<i>Peer</i>											6	11.5
<i>Woooh!</i>											2	3.8
<i>Coo-caa</i>											2	3.8
Total calls	115		70		56		17		13		52	
Total time (sec)	1864		95		180		130		38		260	

¹ Group of 6-10 birds, attending army ant swarm, April, dry season. Seven recorded sequences at 1 sitting. Jays 2-10 m away.

² Same as 1, except July, wet season, with juveniles in group. Birds along roadside.

³ Group of 10-15 birds mobbing fox on ground, April. Chatter only. 45 sec (N=4, %=100).

⁴ Two birds foraging in brushy field along forest edge, often out of sight of each other, mostly unaware of observer, April. Sequence twice interrupted briefly.

⁵ General bird-human encounter. No specific circumstances, July. Continuous chatter only. 35 sec in single burst (%=100).

⁶ Same as 5, but at nest-site. Observer immobile, July. Chatter only. 120 sec, 85 and 20 sec bursts.

⁷ Same as 6, but observer trying to examine nest contents with mirror on pole, July.

⁸ Group with fledglings. Humans searching for young, July.

⁹ Bird-human encounter, group having ¾-grown juveniles in it, July.

(1969) is now considered to be a variant of the *clank!* call. *Sotto voce* song is not illustrated here.

Three related loud harsh calls are spectrographically noisy. All were used in the general context of alarm. The staccato, rapid-fire, harsh “chatter” (Fig. 1A) was the call most frequently heard in the wild and is the Yucatan Jay’s most obvious species-specific vocalization. “Chatter” is a social-alarm call. Birds chattered when discovering potential danger on the ground or in a tree. A fox, human, or squirrel readily stimulated such calling. A jay’s

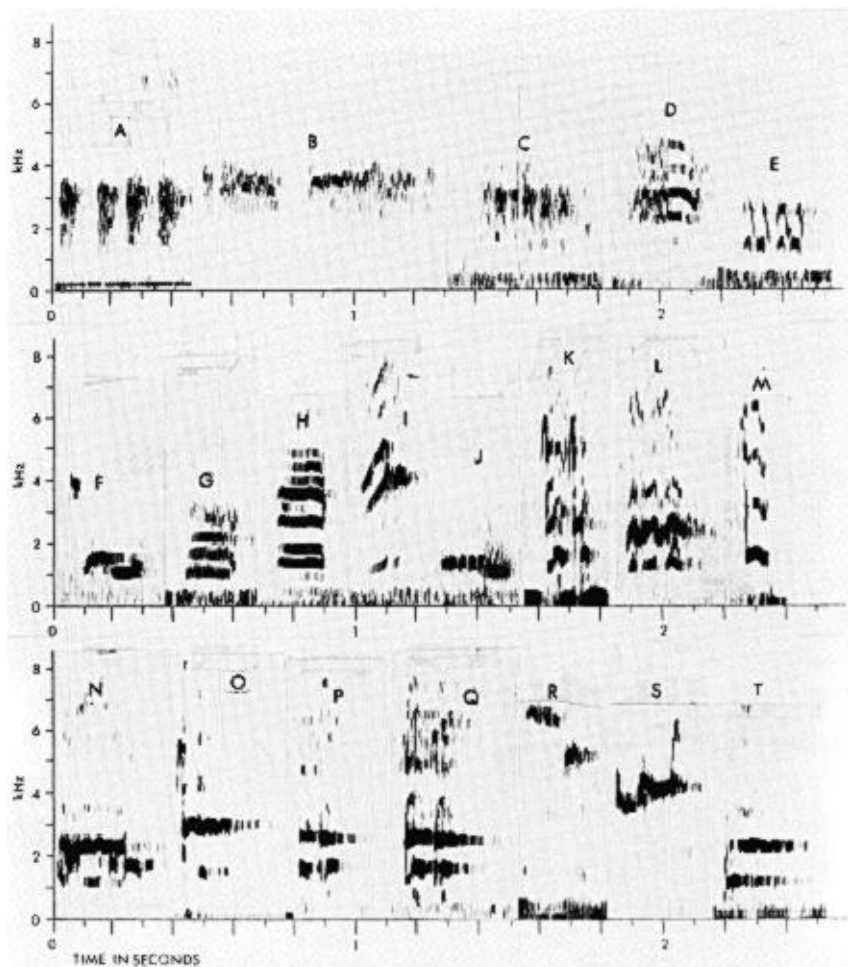


FIG. 1. Sonograms of vocal specimens of Yucatan Jays. Specimens are designated by their Moore Laboratory of Zoology (MLZ) master tape catalog numbers, Florida State Museum (FSM) master tape cut and species cut numbers, and recording dates. All recordings by J. W. Hardy, at Zoh Laguna, Campeche, Mexico, except B and T, recorded at Moore Laboratory of Zoology. (A) Chatter (MLZ 29, FSM 47-10-8, 9 April 1968); (B) "fear" call (MLZ 42, FSM 55-2-11, 23 May 1969); (C) rattle (MLZ 30, FSM 48-2-10, 13 April 1968); (D) begging *caah* (MLZ 42, FSM 55-2-11, 23 May 1969); (E) *chook chook* (MLZ 31, FSM 48-16-10, 14 April 1968); (F) "pump-handle" (MLZ 29, FSM 47-10-8, 19 April 1968); (G) guttural "tin-horn piping" call; (H) clear "tin-horn piping" call; (I) metallic "yelp;" (J) "foggy bell;" (K-Q) variants of resonant *clank* or *clank-clank*; (R,S) *tsi-peep, p-pee-eeep* (G-S, all MLZ 29, FSM 47-10-8, 9 April 1968); (T) *peyook* (MLZ 44, FSM 55, no cut assigned, no date given).

chattering alerted other jays, which also usually gave the call and/or rapidly moved to the scene of the potential danger. When we played recordings of chatter it regularly caused jays to approach us. In fact, we used this method in censusing the population. "Chatter" occurred in all 9 contexts shown in Table 1. In context 1, however, it was not given by birds actively attending the army ant swarm but only by arriving birds that discovered us. After "chatter" has been used to notify of danger, a convention of jays uses the same vocalization in mobbing. Cadence varied from regular to the achievement of a rolling effect; rate of utterance increased with level of stimulation, grading, in 1 kind of circumstance, into the "fear" call (Fig. 1B). This call is thinner and less structured. The "fear" call was typically evoked by a predator or human touching the eggs or young in the nest (Table 1, context 7), and was accompanied by pecking or threats of attack. "Chatter" also grades into the rapid "rattle" (Fig. 1C) that resembles "chatter" in internal structure and tonal spectrum, but is more diffuse with a less staccato quality or a less steep wave front to the successive call components. This feature of the rapid "rattle" plus the approximately 2 kHz lower frequency limit are ascribed by Marler (1956) to effective avian-predator alarm calls. I had more difficulty locating birds giving this call, thus it may give a measure of protection to the caller while giving a warning signal to its cohorts. I heard this call given at Zoh Laguna, Campeche, Mexico, when a Collared Forest Falcon (*Micrastur semitorquatus*) flew fast and low over a flock of Yucatan Jays foraging at an army ant swarm (as in Table 1, context 1). I also heard it given twice by my captive flock when a Red-tailed Hawk (*Buteo jamaicensis*) soared overhead.

The begging *caah* (Fig. 1D), such as that given by the adult ♀ on the nest, was accompanied by slight wing fluttering and gaping; response by other birds was to feed the begging bird (Table 1, contexts 1, 8). In late incubation such calling was regular and probably encouraged increased visitation to the nest by other flock members and their readiness to bring food. More intense versions of this call have a squawk quality. Young birds often gave such begging "squawks" when feeders approached. These "squawks" (not illustrated) seemed to stimulate such approach.

The complex *chook chook* (Fig. 1E) was the second most often heard call, although Table 1, based on tape sequences only, does not reflect this. It is composed of 2 or 3 figures and was given as a social contact call by birds foraging or moving slowly in a loose group. At such times the birds were not so close together as to be regularly in visual contact. Each then gave occasional *chook* calls as it moved and fed. When I saw birds giving these calls, they were busily intent on feeding and unaware of our presence (Table 1, context 4). Playback of *chook* calls evoked no visible response.

The “pump-handle” (Fig. 1F), is a simple, mellow, low-pitched call, which sounded to the human ear as if composed of 2 parts, *pleeop*. Spectrographically 3 figures are revealed. I recorded and heard it 3 times (Table 1, contexts 1, 2, 7). This type of call is widespread in the “Ornate Line” of New World jays (Hardy 1969) that includes *Cyanocitta* and *Cyanocorax (sensu lato)*. The context in which I heard it is discussed below; this call suggests a low intensity conflict of motivations.

Resonant calls are the guttural and clear “tinhorn piping” calls, the metallic “yelp,” the “foggy bell,” and the *clank* or *clank-clank* calls, of which there are many variants. These are shown in Fig. 1G–Q. I (Hardy 1974a) have heard the piping calls, “yelp,” and “foggy bell” only from birds attending an army ant swarm (Table 1, context 1) and speculated that they might be specialized for that context. It seems possible (though my experience does not support the view) that any situation where excitement and marked motivational conflict occur could evoke these calls, as well as the “pump-handle” that was also heard at an army ant swarm. Such motivational conflict is otherwise characterized by sleeked plumage, quick jerky movements, tail flicking, slight bobbing, and sudden, short back-and-forth flights, as when taking insects from an army ant swarm. Resonant calls were usually given abruptly by individuals that were otherwise almost silent.

High-pitched, pure tonelike calls sound like intensive “peep” notes, but, as Fig. 1R and S shows, they are structurally more complex, with either 2 or 3 components. The first may be written phonetically as *tsi-peep* and the second as *p-pee-eeep*. They were noted in context with the resonant calls discussed above (Table 1, contexts 1, 2) as well as in other situations in which motivational conflict seemed likely (Table 1, contexts 7, 9). The 2 forms of “peep” notes are not distinguished from each other in Table 1. One sonogram (not illustrated) showed a *clank* followed quickly by a *p-pee-eeep!* We noted that 1 recorded example of *tsi-peep* was accompanied by a deep bobbing motion and an aspect of intense alertness. The food discovery call (Fig. 1T) may be written *peyook*. When the captive flock or one of its members discovered a new food supply, they gave this call. I did not hear this call in the wild.

Fig. 2A, B, C shows sonograms of 3 calls heard and recorded only once (Table 1, context 9) in which a group of jays were tending nearly grown juveniles. On this occasion the jays gave social alarm “chatter” calls at me, and then when I did not approach, they uttered the resonant *clank-clank* (Fig. 1K–Q) throughout the rest of the recording period. Interspersed among these calls were 2 each of the *wooh!* calls and the *coo-caa* and 6 of the *peer* calls (Fig. 2A–C), given in a context of apparent motivational conflict.

Fig. 2D is a sonogram of the location call of a young fledgling. It is not shown in the tabulation of contexts. The structure of such calls is poorly

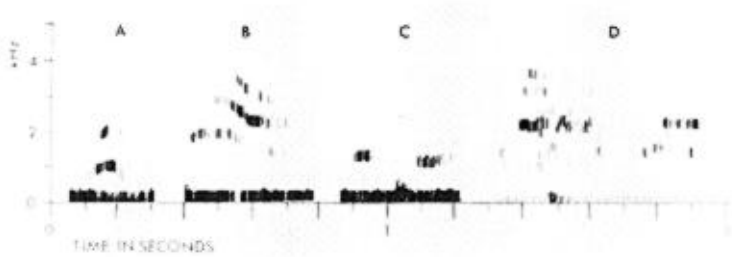


FIG. 2. Sonograms of additional vocal specimens of Yucatan Jays. See Fig. 1 for catalog number code. (A) *Woooh*; (B) *peer*; (C) *coo-caa* (A–C, all FSM 5-5-3, 12 July 1973); (D) fledgling location call (FSM 9-5-4, 23 July 1973).

defined and sounds to the ear like developmental stages of the “chatter” call. Fledglings of species treated below have aurally similar calls but these have escaped my recording.

Sotto voce song is rare in this species. I have not heard it in free birds but did so occasionally in captives. The song and associated display is described under the San Blas and Bushy-crested jays, which regularly perform them. Rarity in the present species may be associated with dark irides and the consequent lack of the constricted pupil display (Hardy 1974b).

San Blas Jays.—*C. sanblasiana* has 2 well-differentiated races, the nominate form (Southern San Blas Jay) and *nelsoni* (Nelson San Blas Jay), not in geographic contact at present and having social/alarm calls distinguishable from one another (Hardy and Raitt 1977). The extreme of differentiation of these calls is illustrated in Fig. 3A and B. In comparison to the “chatter” call of the Yucatan Jay, those of the San Blas Jays are nasal and less staccato. There is considerable variation in pitch and cadence in the utterance in different individual birds. Some are consistently shrill and very rapid (Fig. 3B) and others softer and sustained, *cacaah*, with an oft-repeated stereotyped pattern (Fig. 3C). As in *C. yucatanica* “chatter” is the most frequently heard call included in almost any context (Table 2).

A sustained, soft, begging *caah* (Fig. 3D) is given by incubating or brooding ♀♀ and also by food-begging juveniles (Table 2, contexts 2, 7). This is comparable to the Yucatan Jay’s begging call (Fig. 1D). During extreme stimulation, as when an observer attempts to examine the nest, the chatter call grades into a “fear” call (Fig. 3E, Table 2, contexts 5, 6).

C. s. sanblasiana has an overhead predator “rattle” call (Fig. 3E, Table 2, context 9), but in our study area, hawks were virtually absent and thus the call rare. I have tape recorded it only once, when a group of 3 or 4 jays responded to a Grey Hawk (*Buteo nitidus*) flying overhead at tree top height.

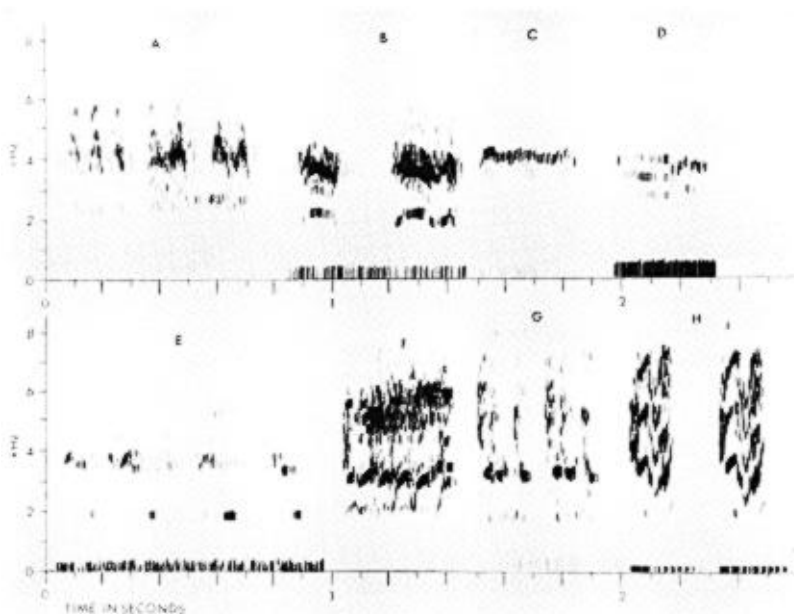


FIG. 3. Sonograms of vocal specimens of *Cyanocorax sanblasiana*. See Fig. 1 for catalog reference numbers code. *Cyanocorax s. nelsoni*: (A) "chatter" (MLZ 39, FSM 53-24-7, 26 June 1970); *C. s. sanblasiana*: (B-D) "chatter" (more sustained figures) (FSM 29-1-1, 27 June 1975); (C) social alarm call of 1 bird showing distinctive constant variant form from most frequently given form (FSM 161-19-10, 24 June 1976); (D) sustained *caah* (FSM 29-1-1, 27 June 1974); (E) "rattle" (FSM 324-4-15, 6 July 1977); (F) "fear" call (FSM 162-4-11, 7 July 1976); *C. s. nelsoni*: (G) *chank chank* contact call (MLZ 38, FSM 53-20-6, 18 June 1970); *C. s. sanblasiana*: (H) resonant *clank-clank!* (FSM 161-20-11, 24 June 1976).

Fig. 3G shows the 2-note counterpart of the *chook chook* calls of the Yucatan Jay (Fig. 1E). Both races of San Blas Jay utter this 2-note counterpart, a more resonant *chank chank* sounding call. Its function seems to be the same as in the Yucatan Jay—a social contact call given by birds that cannot see one another (Table 2, context 1). In situations where high levels of motivational conflict would be predicted, a complex, resonant call (Fig. 3H) similar to the Yucatan Jay's metallic "yelp" or to its resonant *clank!* is given by individuals of the nominate race (Southern San Blas Jay). It is rarely given; we heard it uttered by an adult excitedly watching us remove a jay from a mist net, and also from parent birds when we disturbed nests while viewing their contents (Table 2, contexts 5, 6).

The *sotto voce* song is part of a display in which the pupils are constricted

TABLE 2
PATTERNS AND CONTEXTS OF SAN BLAS JAY VOCALIZATIONS

Call type	Contexts 1-9 (Contexts 3, 4, 8 treated only in footnotes)											
	1		2		5		6		7		9	
	N	%	N	%	N	%	N	%	N	%	N	%
Chatter/caw	18	85.7	24	88.8	27	17.0	11	57.9	78	91.8	4	67.7
Sustained caw			3	11.2					6	7.1		
Begging (juvenile)									1	1.0		
Rattle "Fear"					120	75.5	3	15.8			1	33.3
Chank chank	4	14.3										
Clank-clank!					12	7.5	5	26.3			1	33.3
Total calls	21		27		159		19		85		6	
Total time (sec)	120		155		90		90		190		15	

¹ Immediately after a period of mobbing of unseen animal. Near nest, June.

² Foraging bird. Chattered at observer, then gave 4 two-note contact calls, June.

³ Adult male near nest, observer close by, July. Chatter/caw only. 35 sec (N=35, %=100).

⁴ Two or 3 birds mobbing unseen animal, near nest, June. Chatter/caw only. 35 sec (N=35, %=100).

⁵ Two observers operating nets near nest with young, catching jays and marking them, also examining nest contents, July.

⁶ Observers near nest with eggs or young, July.

⁷ Loose group feeding half-grown juveniles or fledglings. Observers in sight, June.

⁸ Same as 7. Chatter/caw only. 12 sec (N=12, %=100).

⁹ Small group of foraging birds. Grey Hawk sails overhead.

(see Hardy 1974b). The song is complex and melodious and occurs in situations where conflict of motivation might be expected, as in courtship, but also it can be evoked by the suddenly detected presence of a human (or other "predator?"). Such song in another species is illustrated in Hardy (1969).

Bushy-crested Jay.—This jay has a repertoire similar to that in the San Blas Jay. The harsh loud social alarm "caw" (Fig. 4A) is neither staccato nor nasal as in San Blas or Yucatan jays. Instead, it is intermediate to these and the sustained cawing of *C. beecheii* (Fig. 4E). To my ear and by sonogram the sound more closely resembles the social alarm call of the Beechey Jay. Context is like that of social alarm calls of the other species (Table 3, contexts 1, 2, 4, 5). I have not heard an overhead predator "rattle" or the rapid "fear" call in this species.

A soft begging "caw" in *C. melanocyanea* is shown in Fig. 4B. It is comparable to those already described, and is given in the same circumstances by brooding or incubating females (Table 3, contexts 3, 4). The short "caw"

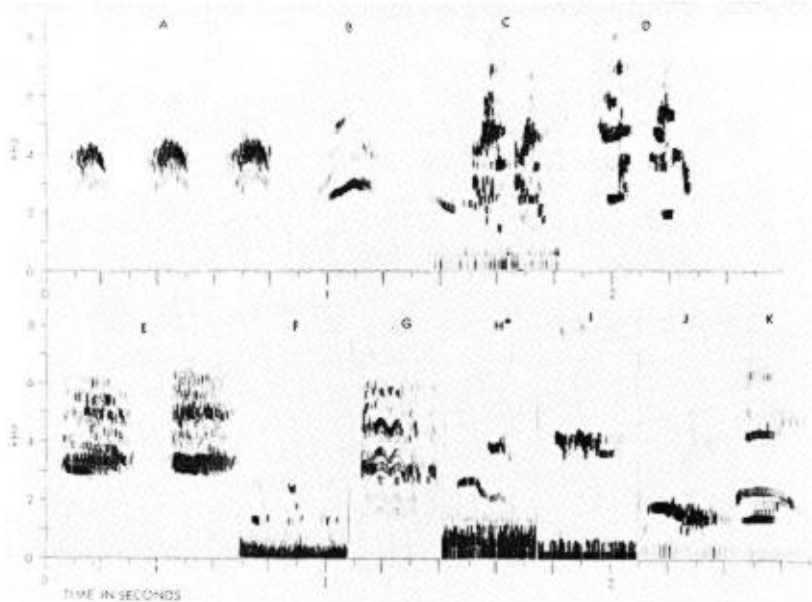


FIG. 4. *C. melanocyanea*, *C. beecheii*, *Corvus sinaloae*. *C. melanocyanea*: (A) social alarm "caw" (MLZ 34, FSM 50-7-1, 14 June 1976); (B) begging "caw" of ♀ on nest (MLZ 35, FSM 51-12-4, 19 June 1969); (C) *chank chank* (MLZ 35, FSM 51-12-4, 27 June 1969); (D) resonant *chank chank* of captive bird (MLZ 40, FSM 54-4-9, 24 March 1971); *C. beecheii*: (E) social alarm "caw" (FSM 160-3-3, 14 June 1976); (F) *clock clock clock* (FSM 327-15-8, 6 June 1977); (G) "quavering caw" (FSM 32-11-2, 24 June 1974); (H*) "crying" call (FSM 65-11-4, 3 December 1975); (I) intense *peep!* (same data as H); (J) *pook* (MLZ 44, FSM 55, no cut assigned, no date given); *Corvus sinaloae*: (K) social call *weer* (FSM 160-7-1, 14 June 1976).

of juveniles (not illustrated) combines elements of begging and location (Table 3, contexts 2, 5, 7).

The basic 2-note contact call, *chank chank*, of the Bushy-crested Jay (Fig. 4C) is similar to that of the San Blas Jay, being more resonant than that of the Yucatan Jay. In my experience, this call is rarely given. I recorded it twice in the wild—I believe the only times I heard it in a 3-week study (Table 3, contexts 2, 5). I heard an often given variant of the call from a captive bird (Fig. 4D).

Sotto voce song is common in this species. As in the San Blas and Beechey jays it is associated with a display in which the pupils are constricted (Hardy 1974b). As in other jays that give this song, it is barely audible a few m

* Frequency scale on 4, H is 40–4000 Hz.

TABLE 3
PATTERNS AND CONTEXTS OF BUSHY-CRESTED JAY VOCALIZATIONS

Call type	Contexts 1-7 (Contexts 1, 3, 6, 7 treated only in footnotes)					
	2		4		5	
	N	%	N	%	N	%
Caw	1	1.4	2	50.0	7	77.6
Begging caw			2	50.0		
Short caws (juveniles)	63	88.7			1	11.2
<i>Chunk chunk</i>	7	9.9			1	11.2
Total calls	71		4		9	
Total time (sec)	290		25		30	

¹ Loose group of 10-15 adults with full-grown juveniles. Response to human squeaking sounds, June. Caw only; 135 sec (N = 8, % = 100).

² Same as 1, June.

³ Three or 4 birds near nest, including 2 juveniles, June. Begging caw only; 61 sec (N = 5, % = 100).

⁴ Same as 3, June.

⁵ Full-grown juvenile perched near nest with young. Adults coming and going, feeding young, June.

⁶ Begging female on nest with 3 eggs; male feeds her and she leaves. Begging caw only; 70 sec (N = 16, % = 100).

⁷ Group of 3 or 4 almost grown juveniles moving in understory along trail in forest, giving short begging and cawing calls. Short calls (of juveniles only); 230 sec (N = 37, % = 100).

away, is complex and melodious, and is given in courtship situations as well as by isolated birds. Sudden sight of me by captive birds often evoked such song from 1 individual. It may be associated with conflict of motivation, as in courtship.

Beechey Jay.—*C. beecheii* seldom utter any sounds except harsh "cawing" sounds (Fig. 4E). These are variable in cadence, amplitude, and configuration, differing little if any from bird to bird but more with respect to context and level of apparent motivation. The call in a social alarm context (as figured) is very *Corvus*-like. This is intriguing, since the small Sinaloa Crow (*Corvus sinaloae*) with which the jay is syntopic, has a very uncrow-like call *weer* (Fig. 4K) very much like that found in several *Cyanocorax* species (see Hardy 1969). The harshness of the call in the Beechey Jay is typical for *Cissilopha*. Therefore, if character displacement (Brown and Wilson 1956) has operated in the area of sympatry between Sinaloa Crows and Beechey Jays, it seems it is the crows' calls that have been altered. Further evidence for this belief is the fact that the social alarm calls of all other North American crows are harsh. This includes the call of the very similar Tamaulipas Crow (*Corvus imparatus*), which Davis (1972) describes as "a frog-like *gurr*." Davis' apt description of the call of the Sinaloa Crow

TABLE 4
CONTEXTS AND PATTERNS OF BEECHY JAY VOCALIZATIONS

Call type	Contexts 1-3					
	1		2		3	
	N	%	N	%	N	%
Caw	43	77.0			19	61.3
Quavering caw	10	23.0				
<i>Clok klok klok</i>					12	38.7
Plaintive cry			3	42.9		
Two-note peep!			4	57.1		
Total calls	53		7		31	
Total time (sec)	225		36		120	

¹ Adult pair at nest, observer at base of nest tree.

² Flock of 6 to 8 birds, moving and foraging in forest, aware of stalking observer, out of sight, December.

³ Three observers at nest, eggs newly missing, adult pair owners of nest ca. 100 m distant, 1 calling caw and the other the *clok klok klok* call.

also lends support to the theory presented here: "A relatively shrill ceow . . . very much like that of the Brown Jay of e. Mexico."

Selective advantage of character displacement and resulting dissimilarity of the social alarm calls of the jay and the crow seem clear: the vocalizations in both cases have only intraspecific significance, signaling members of the same species to convene. Dissimilarity avoids confusion of the signals.

A distinct variant of the social alarm call is the "quavering caw" (Fig. 4G) comparable to the "fear" call of the other species and given under similar circumstances (Table 4, context 1). *Sotto voce* song is common in the specific context of courtship in this species, again associated with a display as described in Hardy (1974b). The song as in the other species is complex and melodious.

Other calls of the Beechey Jay are so rarely given that I have thus far recorded only 3 in the wild and each of these only once. The contact call (and sharply resonant variants) is usually of 2-figure structure and resembles those of the other species. The basic version (Fig. 4F, Table 4, context 3) is soft with a marimba-like quality (*clok klok klok*) most like that of the Yucatan Jay (Fig. 1S) but of similar character to my ear. The behavioral and motivational context of these 2 calls are not known.

My captive Beechey Jays gave a food discovery or expectancy call (Fig. 4J) that may be described as a mellow *pook* sound. It was given in the same context as the somewhat higher-pitched *peyook* (Fig. 1T) of the captive Yucatan Jay nearby, and like that note, only when food was being placed in the aviary.

DISCUSSION

Only the social alarm call ("chatter" and "caw") is a really common vocalization, though it has many variations, in all of these jays. In the Yucatan Jay the contact call is infrequently uttered in the wild, yet is heard daily. In the Beechey Jay the call is so rarely uttered that, as previously mentioned, I only once tape-recorded it. If one is in the field for 4 h a day from approximately 06:00–10:00 throughout the breeding season I estimate that he would hear the call an average of less than once a day. Begging calls are to be heard from incubating or brooding females, but not all such birds give these calls regularly, and they seem to be restricted to that context.

Only in the Yucatan Jay are other calls such a frequent part of the repertoire that one can expect to hear and record them in a period of a few days' time. With the exception of the calls so far heard only in the context of army ant swarm attendance (Table 1, context 1) and from jays tending juveniles when the observer was nearby (Table 1, context 9), the Yucatan Jay's actual repertoire is also its active repertoire. Under circumstances of stress, where motivational conflict can be predicted, this jay displays an unusual variety of other calls compared to its close relatives. In my personal experience, the repertoire, as with Magpie-jays (*C. formosa*) and Blue Jays (*C. cristata*), seems to be expandable at a given moment by individual invention of call types. The Collared Jay (*Aphelocoma viridicyana*) is another tropical latitude jay that has a bewildering number of calls, some of which I naively called non-jay-like calls (Hardy 1967) and tried to relate to habitat density and association with other species in mixed flocks. Certainly the Yucatan Jay has a visually more restrictive habitat than that of its close relatives treated in this paper; thus, perhaps the large repertoire bears some relationship to habitat character.

Highly unusual circumstances such as those already described seem also to evoke greater variety of sounds in the Bushy-crested and San Blas jays, while in the Beechey Jay no situation that one can easily contrive, such as examining the nest contents, can be depended upon to evoke other than the harsh cawing sound; the rare components of the vocabulary seem to be given almost at random, although this is unlikely to be the case.

Elsewhere (Hardy 1969) I have discussed how I believe the main pathway of evolution of plumage pattern and ornamentation in the New World jays of the Ornate Line has proceeded from complex to relatively simple. Thus, I regard species such as the elaborately and boldly plumaged Tufted Jay (*Cyanocorax dickeyi*) and Plush-crested Jay (*C. chrysops*) to be phenotypically least derived from the ancestor of this group. Intermediate forms include the Cayenne Jay (*C. cayanus*) and Black-chested Jay (*C. affinis*). Four of the phenotypically highly derived forms are the subjects of this

paper; others are the Brown Jay (*C. morio*), Azure Jay (*C. caeruleus*) and Purplish Jay (*C. cyanomelas*).

The evidence in phenotypes and ontogeny of plumage and soft part coloration (Hardy 1973) is that the "simplification" process has not been a simple one. Thus in the Black and Blue jays (subgenus *Cissilopha*) different disappearing ancestral traits are to be found in different species. The Yucatan Jay reveals the white-tipped tail in the first year stage; the Bushy-crested Jay retains the feature of black chest divided from paler abdomen, and the San Blas Jay has the prominent tufted fronto-nasal crest, well-developed in the juvenile, and gradually less so in yearling, 2-year-old and adult stages of the nominate form and virtually absent after the yearling stage in the race *nelsoni*.

It is my judgment that something similar to this simplification process is occurring in vocal repertoire. The Yucatan Jay retains the most elaborate actively-used vocabulary, while the other species seem to have simpler active ones, with some vocalizations being used infrequently in certain unusual contexts that would be expected to evoke fear and conflict of motivation or, rarely, in seemingly haphazard form and context.

I believe that the small size of the active vocabulary in the Beechey Jay is related to its lesser degree of sociality (Raitt and Hardy 1979). The size of this species' social breeding units is smaller by at least half that in the other species.

There is general support for this hypothesis in another New World species the Dwarf Jay (*Aphelocoma nana*) (Hardy 1971), which to my knowledge is the least social of all New World jays. Breeding pairs in the nesting season are solitary and essentially nonvocal. They can usually be provoked to call only by extreme measures, such as tampering with the nest. Ordinarily there is only 1 vocalization, the doubly inflected *shrééup!* When the nest is touched, the birds utter the harsh rasping rage call, but otherwise only variants of the *shrééup!* are to be heard. Nonbreeding flocks are small and slightly more vocal, but also utter only variations of the *shrééup!* call.

SUMMARY

The 4 species discussed are the closely related allopatric Yucatan, Bushy-crested, San Blas and Beechey jays of the genus *Cyanocorax*, usually grouped in the taxon *Cissilopha* (here considered to be a subgenus). The Yucatan Jay has the largest vocal repertoire—24 call types are illustrated and discussed—about $\frac{1}{3}$ of which is active, that is, employed frequently in "everyday" situations in the breeding season. Harsh staccato chatter constitutes the social alarm call and is the commonest utterance. The 2-note call seemingly serves as a contact call between individuals of a group not within sight of each other. Other calls include distinctive variations of the 2-note, overhead predator call, fear call, and a variety of calls that along with the 2-note variants seem to be typical of motivational conflict associated with unusual contexts.

The San Blas Jay has 2 races that differ in 1 consistent way in vocalizations. The Southern San Blas Jay (n nominate subspecies) has the social alarm call composed of simple regular nasal figures plus more complex sustained figures; the Nelson San Blas Jay utters only the simple figures. In the Southern San Blas Jay individuals may have consistently identifiable deliveries of the social alarm call. Besides a "fear" call and this call, others are 2 variants of the 2-note call.

The Bushy-crested Jay has a social alarm call that may be described as a short cawing figure, intermediate in length between the short calls of the above 2 species and that of the Beechey Jay. A begging call and 2 variants of the 2-note call are shown and discussed.

The Beechey Jay possesses the smallest active vocal repertoire. The only commonly heard call is a crow-like cawing without much interindividual variation but considerable variation in rate of delivery and cadence, depending on context. A distinct variant of this call is the "quavering caw" representing the "fear" call in this species. A contact call is seldom heard, and the soft cry and a 2-syllable peeping are rare. The former was heard mostly from birds that had just lost nests and eggs, presumably to predation. The Beechey Jay's very small vocabulary may be related to its smaller degree of sociality when compared to the other species considered in this study.

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LITERATURE CITED

- BROWN, W. L. AND E. O. WILSON. 1956. Character displacement. *Syst. Zool.* 5:49-64.
- DAVIS, L. I. 1972. A field guide to the birds of Mexico and Central America. Univ. of Texas Press. Austin, Texas.
- HARDY, J. W. 1967. The puzzling vocal repertoire of the South American Collared Jay, *Cyanolyca viridicyana merida*. *Condor* 69:513-521.
- . 1969. A taxonomic revision of the New World jays. *Condor* 71:350-375.
- . 1971. Habitat and habits of the Dwarf Jay, *Aphelocoma nana*. *Wilson Bull.* 83:5-30.
- . 1973. Age and sex differences in the black-and-blue jays of Middle America. *Bird-Banding* 44:81-90.
- . 1974a. Jays as army ant followers. *Condor* 76:102-103.
- . 1974b. Behavior and its evolution in Neotropical jays (*Cissilopha*). *Bird-Banding* 45:253-268.
- . 1976. Comparative breeding behavior and ecology of the Bushy-crested and Nelson San Blas jays. *Wilson Bull.* 87:96-120.
- AND R. J. RAITT. 1977. Relationships between the two races of the San Blas Jay. *Bull. Br. Ornithol. Club* 97:27-31.
- MARLER, P. R. 1956. Über einige Eigenschaften tierlicher Rufe. *J. für Ornithol.* 97:220-227.

- RAITT, R. J. AND J. W. HARDY. 1976. Behavioral ecology of the Yucatan Jay. *Wilson Bull.* 88:529-554.
- AND ———. 1979. Social behavior, habitat, and food of the Beechey Jay. *Wilson Bull.* 91:1-15.

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