BEHAVIOR AND ITS EVOLUTION IN NEOTROPICAL JAYS (*CISSILOPHA*)

By JOHN WILLIAM HARDY

The subgenus *Cissilopha* of the widespread genus *Cyanocorax* (Hardy, 1969a), consists of four allopatric species, *C. melanocyanea, yucatanica, sanblasiana,* and *beecheii.* An examination of the complex ontogeny of plumage and soft part coloration (Hardy, 1973) indicated that the four differ from each other and that each age class from juvenile to at least three years can be distinguished from adults by external features. The study also suggested that these signal features of age might be correlated with intricate social behavior in which the social role of the individual is determined by its age, which in turn is detected through external features. This is the case. Each of the first three species forms at all seasons a rather tightly knit flock and engages in some form of communal reproduction, probably as family units and probably in altruistic or mutualistic relationship. *C. beecheii,* which I have not yet studied in the wild in any detail, is seemingly much less social, forming flocks in the nonbreeding season and, I predict, nonsocial territorial pairs while breeding, possibly accompanied by young of the previous year. Studies of captive *beecheii* demonstrate that complex behavior seemingly homologous to behavior seen in that form's close allies serves in intrapair function. The variations in the character and function of seemingly homologous displays in these four jays provide a good basis for a comparative study in which hypotheses can be explored concerning the function of the behaviors and their evolution as well as the evolutionary history of *Cissilopha* itself.

PROCEDURES AND METHODS

This study was begun in April 1968, when I traveled to the state of Campeche in the Yucatan Peninsula, Mexico, to observe nonbreeding social behavior of *C. y. yucatanica,* near the villages of Xpujil and Zoh Laguna not far from the Quintana Roo border just north of highway 186. On this trip I obtained from a dealer in Merida a group of six *C. y. yucatanica,* which was of typical family composition if not in fact being a family group (as I believe it was). These were studied in captivity at the Moore Laboratory of Zoology at Occidental College until 1972. In June 1969 I studied the breeding habits of *C. m. melanocyanea* at Santa Maria de Ostuma, 6 miles north of Matagalpa, Nicaragua. Here I captured eight jays of this species which were studied at the Moore Laboratory between 1969 and 1972. In June 1970, I studied the breeding habits of *C. sanblasiana nelsoni* near Las Varas, in coastal lowland Nayarit, Mexico. Here, and at Tepic, Nayarit, I obtained six *C. s. nelsoni* from dealers for studies in captivity. These were supplemented by three birds obtained earlier in 1968 in Tepic but not studied until 1970 and two birds obtained from the Los Angeles Zoo in 1971. All of these birds were studied until early 1972. Three captive *C. beecheii* were obtained from a dealer in Tepic in 1968 and brought to Los Angeles,

Calif. Three others were obtained likewise in 1970. Study of these birds between 1968 and 1972 forms the principal basis for discussion of this species below.

Except for the information on *C. beecheii*, all behaviors discussed in this paper have been verified in the wild, and the discussion of context and meaning of the behaviors is based mostly upon their occurrences in wild birds in their natural environment. The details of description of the behavior and the illustrations of it are based on study of captive birds. Except in *sanblasiana*, I think the behavior described is species-typical. In the case of *sanblasiana* my remarks stand only for the race *nelsoni*, because there is reason to believe from facts about ontogeny of soft part coloration (Hardy, 1973) and limited observations in captivity of the behavior of the race *sanblasiana* (see p. 262 of the present paper) that it may differ in many respects from the race *nelsoni*.

Thirty-five mm still and 16 mm motion picture photographs were used to prepare the illustrations of displays and postures in this paper. Most of the descriptions otherwise are based on direct observation by me or one of my assistants (see Acknowledgments).

Captive birds were kept in cages and outdoor flight aviaries at the Moore Laboratory of Zoology. All birds were of known sex and in most cases of approximate known age (Hardy, 1973).

DESCRIPTION OF DISPLAYS AND THEIR FUNCTIONS

Agonistic Displays

Threat.—There is a strongly marked threat display only in *C. beecheii* of these four species. In it all feathers of the body and head are strongly sleeked except those of the crest, which are strongly erected. The pupils are constricted, so that the bright yellow irides are boldly evident (Fig. 1).

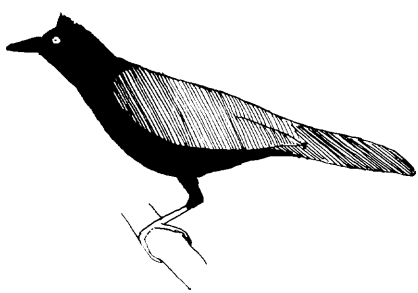

FIGURE 1. High intensity threat display of *Cyanocorax beecheii*. Note erect crest, otherwise sleeked plumage, and constricted pupils.

Strong intra- and interspecific threats seem to be identical. Dominant adult males during the time of reproductive activity are extremely hostile to all other adult males. In captivity, a dominant male maintains almost continuous threat display toward lesser males with which he is housed. This behavior is brief, for threat is punctuated by actual pecking and the mutilation or death of the

subordinant within a few days at most. I regard this as evidence for the asocial nature of this species and its division into pairs that defend territories against other breeding pairs. The crest feathers are erectile and are either decumbent or erected with other head feathers in other motivational contexts. Medium or low intensity threat by adult *beecheii* toward their mates (Fig. 2B right-hand bird) is like typical threat behavior in the other species.

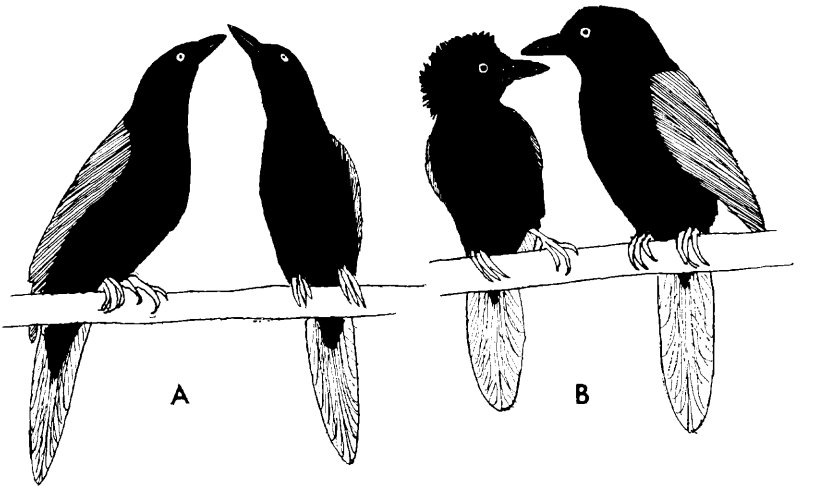

FIGURE 2. A. Mutual low intensity Sotto-voce Song display in a pair of *C. beecheii*. Note drooped tails, bills directed diagonally upward. The pupils are slightly constricted but the illustration does not show this. B. Pair of *C. beecheii* in agonistic encounter. Bird on left is in appeasement posture with fully erected head and nape feathers. Bird on right is in low intensity erect threat posture.

Threat in the other three species of jays under consideration may be discussed collectively because in all of them it is not ritualized or specialized. Although *C. sanblasiana* has a prominent crest in all but adult individuals, the crest is not erectile and not used in any expressive sense in any display. The less prominent crests of *C. yucatanica* and *melanocyanea* are likewise not of special expressive function. In all three species evidence of threat motivation is found only in a moderately sleeked rigid upright posture (Fig. 2B) or, rarely, head forward posture (directed at the victim). This is followed in actual aggression with pecking, in which the aggressor directs his pecks at the face and tarsi of the opponent.

Threat and aggression are rare in all these species except *C. beecheii*. In the others it can be experimentally induced in a flock by withdrawing one individual and re-introducing it after several days. In the first few minutes up to approximately 15 minutes the bird must endure considerable aggression from other members of the flock. If a stranger conspecific with a flock is introduced to an aviary containing that flock, even if that individual is an adult, it will not be accepted, will be threatened and pecked frequently, and usually will be killed within 24 hours.

Up-fluffing Display and Peck-preening.—It is due to the remarkable development of "Up-fluffing" that aggression and threat are so consistently rare in these jays. Up-fluffing has become highly ritualized in all of these jays in appeasement. In captive individuals of all except *C. s. nelsoni* it may be performed almost continually during periods of nonepigamic or nonreproductive activity such as preening, feeding and resting, and between any two or three or even more members (Fig. 3) that happen to be in close proximity. To illustrate an extremely high frequency of performance, on 14 January 1969 while I was observing a captive flock of 6 Yucatan Jays, I recorded in a 5 minute period 29 instances of appeasement Up-fluffing involving at one time or more 5 of the 6 birds. In 11 of these cases, the displays were mutual. Up-fluffing is exactly similar in these species in its most prevalent form, even though it is not common in *C. s. nelsoni*. In the display the neck is extended slightly to greatly, and the feathers of the neck and head are all slowly erected. This reveals the pinkish skin of the neck and the circumaural area. In the most intense form of the display, the bill is directed down-

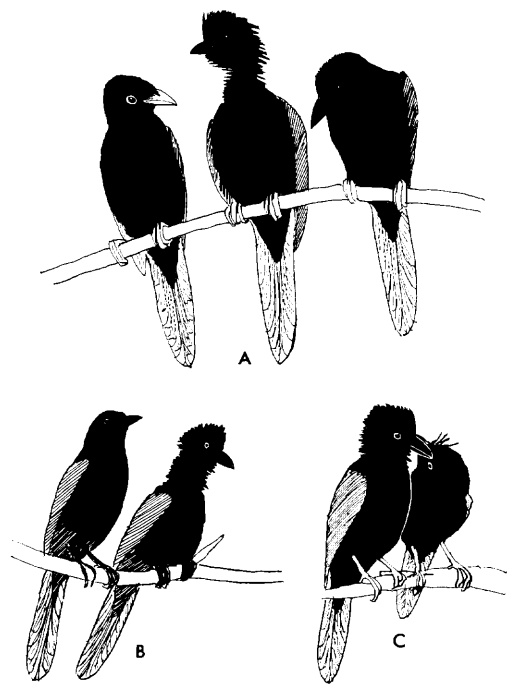

FIGURE 3. Appeasement Up-fluffing and responses to it. A. Three members of the *C. yucatanica* group. Bird in center is in high intensity Up-fluff. Bird on left is just going into the display. Bird on right is in a medium intensity version of the display in which the head is cocked forward. B. Up-fluffing behavior in *C. melanocyanea*. In B, right-hand bird in medium intensity Up-fluff as left-hand bird watches. C. Up-fluffing—Peck-preening in *C. sanblasiana nelsoni*.

ward and the head cocked slightly to one side away from the recipient of the display. In *C. beecheii* the behavior is seen almost exclusively between members of pairs, and there is an added aspect. The birds begin in a crouched position and, either together or in turn, slowly raise the body and head (Fig. 4A-C). The display has become so ritualized in all the species that it is as integral to proximity of two birds as is handshaking and smiling to humans. Like handshaking and smiling the display apparently has so completely thwarted aggression that one seldom sees it in its original function of actively accomplishing such thwarting. Instead, Up-fluffing is a substitute act for any tentative pecking or threat bout and has become a kind of greeting. Yet to call it strictly a greeting display would imply that it occurs at the moment of confrontation of two individuals that had been apart. But in these jays, the behavior may continue long after proximity has been achieved or suddenly be expressed after individuals have been sitting quietly together for some minutes. Up-fluffiing beyond its appeasive function solicits positive feedback in the form of allopreening (Figs. 3C, 4C, D, 5).

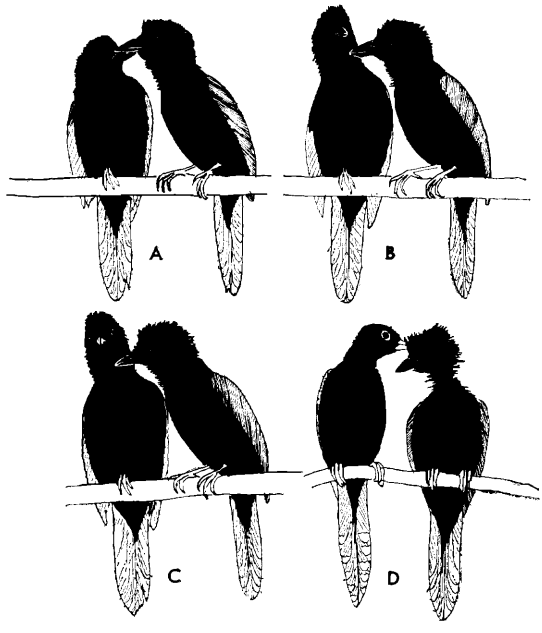

FIGURE 4. Up-fluffiing display and Peck-preening. A-C. Three stages in the behavior in a pair of *C. beecheii*. In A, left-hand bird is beginning the slow erection and fluffiing movement as right-hand bird remains withdrawn. In B, left-hand bird joins the Up-fluffing display while right-hand bird leans forward, still fluffed. In C, right-hand bird Peck-preens neck feathers of left-hand bird. D. Left-hand *C. yucatanica* Peck-preens fully Up-fluffed companion.

The cocking of the head (Fig. 5) and baring of the neck and head skin seem to evoke this. Grooming is poorly developed in comparison to that in the Psittacidae (Hardy, 1963) and usually consists only of gentle pecking at the neck and face. I must emphasize that this is not a low intensity form of aggressive pecking. Reaction to it by the recipient is completely nonevasive. I assign the term Peck-preening to this tentative form of allogrooming. Its autochthonous function might have been ectoparasite removal rather than arrangement of feathers. Successful solicitation of Peck-preening occurs in fewer than 10 percent of the occurrences of Up-fluffing. I have been unable to predict from contexts when Peck-preening will occur. There is no difference apparent to me in the Up-fluffing when Peck-preening does and does not occur.

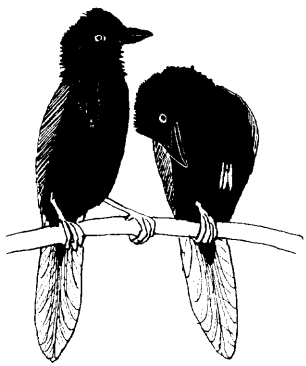

FIGURE 5. Mutual Up-fluffing in a pair of *C. beecheii*. Right-hand bird, after completing fully erect Up-fluffing, has cocked the head in Peck-preening solicitation.

From the fact that all but one of my captive flock of *C. s. nelsoni* were females, it might be concluded that my statement that Up-fluffing is rare in this species needs further study. That is, perhaps a balanced sex ratio (or at least some adult males) is necessary in *nelsoni* to stimulate normal levels of social and appeasement greeting. This seems unlikely, however, because there is no evidence from my observations of *C. melanocyanea* and *C. yucatanica* (the other two socially similar species) that sex plays a role in frequency of Up-fluffing. Moreover, my nearly three week study of *C. s. nelsoni* in the field during the time of reproduction revealed not a single instance of Up-fluffing, although such behavior was noted frequently in similar periods of observation of *C. yucatanica* and *melanocyanea* in these same periods of the life cycle. At this stage in my knowledge of *nelsoni*, I cannot suggest another basis for the low frequency of Up-fluffing.

Appeasement Gaping.—This is high intensity appeasement behavior of the general type seen widely in birds and closely resembling juvenile begging. The bird engaged in such behavior crouches, fluffs all the head feathers, and gapes at another bird

(Figs. 2B, 6), sometimes slightly fluttering the wings in the most intense state. Appeasement gaping is frequently seen in first-year birds toward adults that release the behavior by pecking severely at the tarsi or face of the appeasing bird. Such behavior is rare in established flocks of constant composition. It can be induced in the three social species in captive circumstances by introducing a strange bird to the aviary. In such cases the introduced bird may be of any age. It typically performs appeasement gaping toward the aggressive flock members as mentioned on page 255. In *C. beecheii*, first-year and older individuals subordinate to a dominant adult and forced to occupy the same cage will perform appeasement gaping at all encounters with the dominant bird. Because appeasement gaping is seen mostly under the circumstance of spatially restrictive captivity it is logical that I find it rare in wild birds.

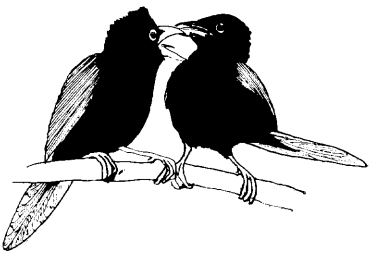

FIGURE 6. Erect threat posture and appeasement gaping in *C. yucatanica*.

I hypothesize, however, that the color of the bill, inside and out, in subadult birds in all four species of these jays is critical to intra-flock sociality. Successful employment of appeasement gaping as a signal of subordinate rank is increased if not dependent largely upon the component of pale bill color, probably especially the color of the inside of the mouth. I have experimental support for the high valence of yellow bill coloration in the thwarting of aggression by adults of *C. beecheii*, as described below.

In May 1968, I kept an adult mated pair of *C. beecheii* in a small cage beside a cage in which there was another adult male *C. beecheii*. The male of the pair spent at least half of its daylight time hammering with its bill at the bars of its cage in the direction of the other male and clinging to the cage bars toward that individual while erecting the crest and constricting the pupils of the eyes. After several days of this, I altered the appearance of the lone male by painting its bill yellow. The change in the behavior of the aggressive male was dramatic and immediate. It entirely ceased in its threat behavior and for the most part ignored the altered bird. Instead the female of the pair then displayed nonthreatening interest in the altered bird, while her feathers were fluffed and her behavior weakly resembled that of an adult toward a juvenile bird.

In a second part of this experiment, conducted immediately after the above described events, I placed the cage containing the pair on a shelf next to a mirror. Immediately the male reacted threateningly

to its own image in the mirror (Figs. 1 and 7A) just as he had toward the unaltered adult male in the nearby cage. I then painted the bill of the male yellow and allowed him to see his own image in the mirror. As before, he almost completely abandoned his aggressive behavior (Fig. 7B) and merely viewed his image in neutral fashion or ignored it.

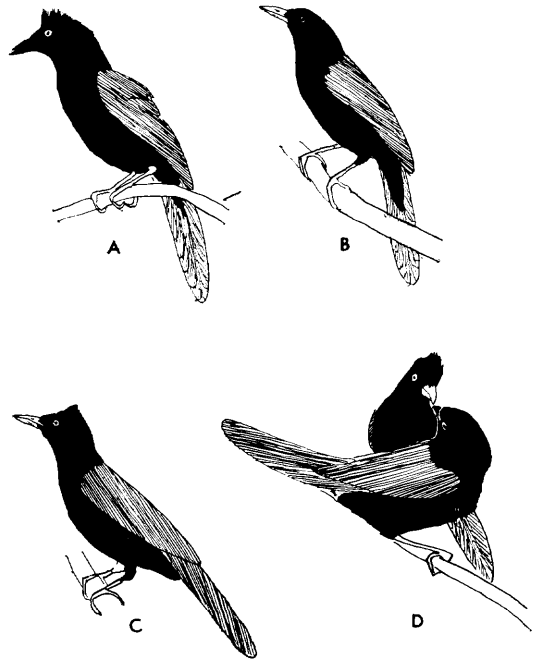

FIGURE 7. Phases in behavior of two *C. beecheii* in bill color alteration and mirror presentation experiment. A. Medium intensity threat of adult male *C. beecheii* (black bill) toward mirror-image. B. Bird of A moments later has bill painted yellow and exhibits no threat or in C low intensity threat posture to its mirror-image. D. Same adult male seemingly redirecting hostility toward mate while mirror still present and bill still yellow.

In March 1969 I repeated the mirror part of this experiment, using the same mated pair and photographed the results. The same events occurred, with the added feature that the male on one occasion redirected his aggression toward his mate (Fig. 7D) and retained strong curiosity and briefly some low intensity threat behavior toward his image (Fig. 7C) even when it was altered. In my judgment this aggression toward the female resulted from the abrupt loss of an opponent shortly before "present" (when the bill was black). The aggressive state had been stimulated, then its releaser removed. The male in an ambivalent state reacted to its mate (which possessed the exact same aggression releasing features) by attacking her.

SOCIAL AND PAIR BOND BEHAVIOR

Allofeeding.—In all four species of Black-and-Blue Jays allofeeding is prominent. In the three highly social species, it clearly functions in nonsexual social bonding and can occur between any members of the communal group without reference to sex and age. In *C. beecheii* it occurs between members of a pair throughout the year and is thus classed here as a behavior of pair bond maintenance. It is more frequent early in the reproductive cycle and occurs integrated with pre-copulatory "Song-and-Dance" display described below. In other jays that I have studied courtship feeding is by the male to the female (Hardy, 1961, for *Cyanocitta cristata;* 1971, for *Aphelocoma nana*). In *C. beecheii* either member of the pair may feed the other and the food may be passed back and forth several times before being eaten. In the three social species considered here, food may travel between several members of the flock before being eaten. In all except *C. beecheii,* no display ever accompanies allofeeding and, except that no begging occurs, to my eye it is exactly like the feeding of young by adults.

Sotto-voce Song Display.—This soft, "throaty" vocalizing occurs in all four species, is poorly developed in *C. yucatanica,* moderately well developed in *C. s. sanblasiana,* and well developed in *C. melanocyanea* and *C. beecheii;* in *C. s. sanblasiana* the performer "Switch-sidles" (Dilger, 1962) along the perch; in *C. beecheii* and possibly also *C. s. nelsoni* the display is elaborated with a dance component.

C. yucatanica exhibits this display so infrequently that at first I thought it was absent from the species. It is so rare, even so, that my notes allow no conclusion as to its context and function. In weekly observations from 1968 to early 1972, I saw the display only twice, both times by the adult male of the dominant pair in a flock. Both times it occurred about the onset of the reproductive period. The display was not directed toward the female or clearly toward any other bird in the flock. The tail was drooped and the posture little altered from a relaxed resting posture. The bird did not move about while engaged in the act. The rudimentary character of the display in this species is clear to me. The fact that the iris color is dark throughout life is probably correlated with the rarity of the display. The other three species each have yellow irides in the adults and each has the display at least moderately well developed. Dark irides are probably the derived condition in the ornate line of New World jays (see Hardy, 1969a), and therefore I theorize that the display associated with yellow irides is vestigial in the Yucatan Jay, rarely seen, poorly developed and no longer integrally functional.

C. s. nelsoni shows a slight elaboration of the Sotto-voce Song display. Besides the basic low-intensity form as seen in *yucantanica,* there is an intermediate intensity form in which the posture stiffens and the tail is slightly raised. The displayer constricts the pupils revealing the yellow irides in all intensities; in the medium intensity development, the bird crouches slightly and fluffs the abdominal feathers. The bird may also move along a perch toward the recipient of the display.

Either sex may give the display. I photographed a wild adult female engaged in this display just after she had left her nest and perched 30 cm away. No other jay was apparently nearby. In the captive flock at Occidental College, the fact that I had only female adults prevented me from knowing whether the display was used in a sexual context in this species. I saw and cine-photographed a third-year female performing the medium intensity display in the aviary (Fig. 8). She flew to a perch near another bird and began singing softly with tail down. Then she moved toward the other individual. Instead of edging forth, she hopped in the manner described as Switch-sidling (Dilger, 1962), in which the bird alternately places the left, then the right foot forward and thereby moves the tail from one side of the perch to the other. As she approached the other female, the tail was slightly raised and the belly feathers fluffed. Her bill was also raised slightly so that the back was arched. The head was not waved. The posture resembled the medium intensity display of *C. beecheii* (Fig. 10B), except there was no "dance." Another bird interfered momentarily and the displayer hopped away briefly only to turn and begin the display over. It lasted only about 30 seconds in total and was seen only this once.

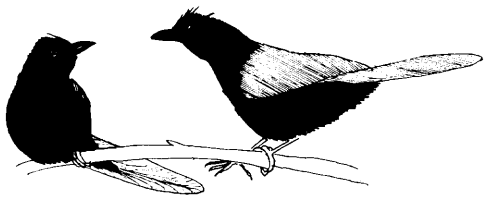

FIGURE 8. Sotto-voce Song display in *Cyanocorax sanblasiana nelsoni*. Right-hand bird Switch-sidles toward left-hand bird with tail slightly up, belly feathers fluffed, head slightly craned, and throat distended slightly in song. Displaying bird is subadult with dark irides.

Intuitively, I feel that the above observations represented a sexual display that was being conducted in the absence of males by a female toward another female.

I have been able to obtain only one captive specimen of *C. s. sanblasiana*, through the courtesy of the Los Angeles Zoo. Based on that one bird's behavior this form may have race-specific behavior. On 18 March 1971 I obtained this bird because I was intrigued by an alarm vocalization it infrequently gave and which resembled that of *C. beecheii* (instead of the rapid chatter, it gave a cawing call). On 2 April I saw this bird perform a high intensity courtship dance like that of *C. beecheii* described below.

In *C. melanocyanea*, the Sotto-voce Song display is very common in captive birds at the onset of the reproductive season. I have not seen it in the wild because I have not been present at this period in the life cycle.

The display (Fig. 9) is performed stationarily in this species. The tail is not raised at any intensity. Instead in the most intense form,

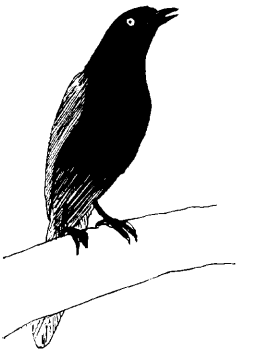

FIGURE 9. Stationary Sotto-voce Song display of *C. melanocyanea*. The tail is drooped, pupil constricted, and bill open in song.

the tail is fully drooped, the pupil quite constricted and the *head slowly waved about*. It is not a mutual display; one bird performs it toward another or, apparently in a vacuum. There is no ritualized response. Birds of either sex perform the display, but it is more intense and frequent in males. I saw both sexes perform the display in apparent vacuum; I saw only males perform the display toward other birds—always toward females.

C. beecheii has the display more elaborately developed. In this species it is performed only between members of a bonded pair. It can occur from December, following the prebasic molt, until nesting begins in April. Either sex may initiate the display. It may elicit a response in kind by the mate (Fig. 2A) or the latter may respond by Up fluffing or by sitting quietly and watching (Fig. 10B). In a captive pair in 1969, the first displays following molting were seen on 1 December. Displays were seen until mid-May when nest-building began. Most of them were mutual with neither bird clearly initiating them. In the display encounters in which one bird performed alone or clearly initiated a mutual display, it was the female 23 times and the male only 8, in 31 randomly recorded instances.

The display in some form sometimes occurred as frequently as five times in a period of four to five minutes interspersed with brief periods of resting or feeding or merely perching . Displays were more frequent in morning hours in periods of high general activity and rare in periods of low activity involving mainly rest.

Toward time of copulation, the male either initiated more displays or, in ones in which display activity was mutual from its beginning, "led" the display. This is probably correlated with the necessity for the male to be dominant at least during the brief period of mating in which copulation is successfully negotiated. In one complete observation of display and copulation as a part of a continuous activity, the female's participation in the high intensity period of the display led gradually to her copulation solicitation posture and behavior at which time the male mounted.

Degrees of intensity of the display form a continuum, but three arbitrary degrees of low, medium, and high may be designated. In

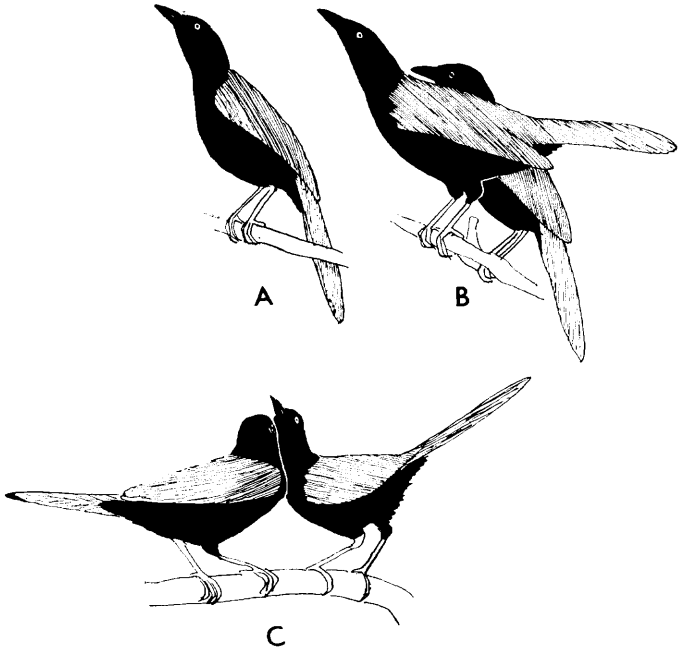

FIGURE 10. Three phases in Sotto-voce Song and Dance display of *C. beecheii*. A. Low intensity display. B. Medium intensity display with tail slightly raised. C. Mutual display with tail greatly elevated and bill almost vertical in right-hand bird while left-hand bird is in medium intensity state.

low intensity, the tail is drooped, the feet placed close together, the head directed diagonally upward, and the pupil slightly constricted (Fig. 10A). In medium intensity (Fig. 10B) the tail is slightly raised, the back straight or slightly arched, the feet more widely spaced, the bill directed at a steeper diagonal, and the pupil more constricted. In the high intensity form (Fig. 10C), the tail is raised at a diagonal, the back arched, the bill pointed almost vertically, the pupils constricted to pinpoint size, and the feet moved in a clasping—unclasping kind of dance on the perch. The head also is waved about slightly. This may or may not be accompanied by passing of food back and forth between the two birds.

Probably the apparent tendency observed within this pair for the female to initiate displays or for the displays to be mutual involving either partner performing courtship feeding is typical in this species. In 1971, when the same female was housed with another male that she had never before seen, she was even more prone to initiate displays and also dominated the male in other respects, pecking him severely and causing him thereby to engage in appeasement displays (Fig. 2B). In a period of about three months that the two were kept together the male almost never initiated displays or courtship feeding and the female often fed the male. Only when he had first been introduced to the female's cage did he attempt weak

displays on his own. It may have been that either the female's long residency in the cage or her possibly greater age influenced her strong dominance role. It may also be that old adults, which have never "met" each other before, have difficulty forming normal pair bond relationships. Incidentally, although more data are needed, males are probably not larger than females in this species and from my data on a few captives, may sometimes be smaller. Four newly captured wild males purchased from a bird dealer in Tepic, Nayarit, and held captive for three weeks prior to weighing, weighed 184.0, 182.5, 183.5, and 177.9 g, respectively, at which time my only captive female (captive for over two years) weighed 202.7 g. All of these birds appeared to be in good health, had ample food, and were fully adult.

DISCUSSION

Review of Proposed Phylogeny

All speculations concerning the primitive or derived condition of the foregoing displays in this discussion rest upon my (Hardy, 1969a) proposed phylogeny of the New World jays, to which readers are referred for details. I hold the following views, discussed in that paper, concerning this assemblage. There are two basic lines in New World jay evolution (excluding *Perisoreus*, of Old World origin or of uncertain relationships). The primitive external morphology of the Ornate Line (as opposed to the Inornate Line—*Aphelocoma, sensu lato*) is represented by such species as *Cyanocorax dickeyi*. There are slightly derived species such as *C. affinis*, and further derived ones such as *C. caeruleus* in South America, and the complex (subgenus *Cissilopha*) considered herein.

Evolution of Displays

Probably the displays described in the foregoing account are primitive in New World jays. I have seen the appeasement Upfluffing display in captive *Cyanocorax chrysops* (Fig. 11A, B), *affinis*, and between *chrysops* and *cristatellus* (Fig. 12) in the Los Angeles Zoo. I have seen low intensity Sotto-voce Song display in *mystacalis* (in wild and in captive individuals), *chrysops*, *cristatellus* (Fig. 13A), and *formosa* (Fig. 13B).

Highly social breeding habits have been confirmed in *chrysops* (Crossin, pers. comm.), *dickeyi* (Crossin, 1967), *morio* (Skutch, 1935), *melanocyanea* (Hardy, 1969a), *sanblasiana*, and *yucatanica* (Hardy and Raitt, unpublished data). Social breeding is also strongly suspected to exist in *mysticalis* and *violaceus* (Hardy, 1969b). I think these facts and probabilities suggest that this social mode of life is also primitive in the Ornate Line of New World jays, and that less social breeding, as confirmed by many workers for *Cyanocitta cristata, stelleri*, and *Cyanocorax yncas*, and for *C. formosa* based on the work of Skutch (1953), is derived.

Therefore, in the complex of four allopatric forms that are the subject of this paper, I propose that *C. beecheii* is the most derived form. For pair bond maintenance or sexual behavior it has seemingly adopted displays that are associated in the others with asexual/

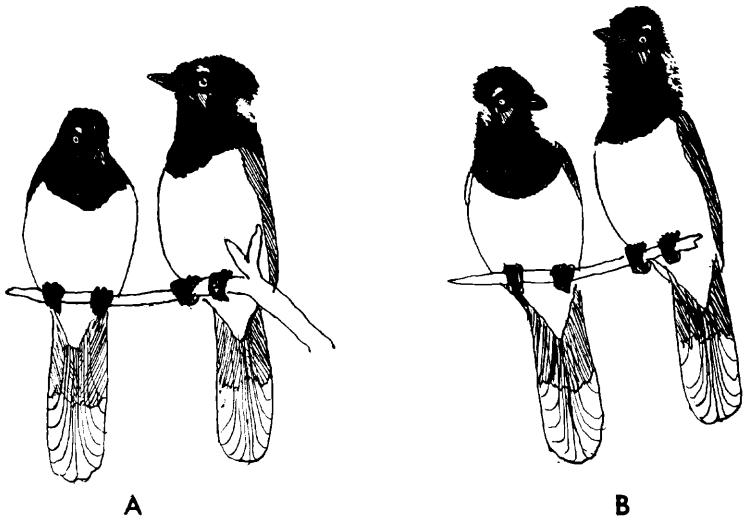

FIGURE 11. Up-fluffing displays in *Cyanocorax chrysops*. A. One bird initiates the display. B. The other bird joins in.

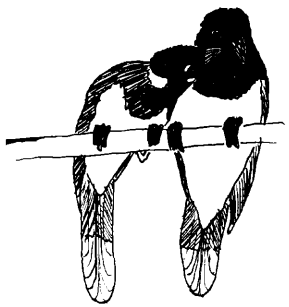

FIGURE 12. Interspecific Up-fluffing and Peck-preening response. Right-hand *Cyanocorax cristatellus* received Peck-preening from a *C. chrysops*.

social behavior. Correlated with this proposal, it seems to me, is the fact that *C. beecheii* possesses fewer of the primitive morphological characteristics (as seen in *C. chryops*, Fig. 11) than do *beecheii*'s relatives *yucatanica*, *melanocyanea*, and *sanblasiana*. Each of the latter three species possesses at least one of the following primitive features: white-tipped tails, crests persisting into adulthood, bicolored underparts.

SUMMARY AND CONCLUSIONS

The displays and postures of the four species of black-and-blue jays *Cyanocorax melanocyanea, yucatanica, sanblasiana,* and *beecheii* are described and discussed as to context, meaning, and evolution. All four species engage in appeasement Up-fluffing, appeasement

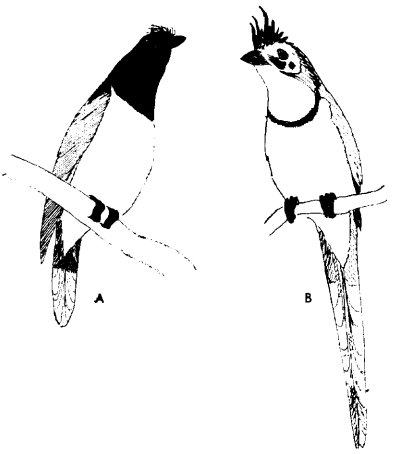

FIGURE 13. Sotto-voce Song display in A. *Cyanocorax cristatellus* and B. *formosa.*

gaping, Peck-preening, allofeeding, aggression, and Sotto-voce Song displays. In appeasement Up-fluffiing the neck is extended and the head cocked, as the feathers of these areas are erected, revealing the skin beneath. When two or more birds are in proximity to each other one may facilitate non-aggression by engaging in such a display. In response the other(s) may perform likewise or Peck-preen the displayer. The display is well developed in all but *C. sanblasiana* and is confined to intrapair behavior in *C. beecheii.* Aggression in all except *C. beecheii* is not marked by ritualized threat behavior. An aggressive bird directs itself in an erect or forward posture with sleeked plumage toward the opponent and pecks at its face or tarsi. The response to aggression is appeasement gaping in which all feathers of the foreparts are erected and the wings are fluttered as in juvenile begging. Aggression is rare except in *C. beecheii* and its rarity probably correlates with well-developed appeasement Up-fluffing and communal nature. In *C. beecheii,* probably an asocial species, aggressive motivation and threat are signalled by erection of the crest feathers, otherwise sleeked plumage, and partial constriction of the pupils revealing the bright yellow irides. Aggression is in the form of pecking at the face and tarsi. Sotto-voce Song display is rare and non-integral in *C. yucatanica* and common in *melanocyanea,* in which either sex may perform it, stationarily, with tail drooped. It is not confined to intrapair behavior. In *sanblasiana nelsoni* it is not common; the tail is slightly raised, the belly feathers fluffed, the neck craned slightly, the pupils slightly constricted, and the bird mobile in a Switch-sidling movement toward the recipient. The display's relationship to pair behavior is unknown. In *C. beecheii* it is elaborated by a dance in the most intense form, in which the tail is diagonally erect, the back arched, the bill diagonally erect, and the pupil constricted. The bird clasps and unclasps the perch in a dance. Either sex or both together may perform the display and it is often accompanied by allofeeding.

Because I have found appeasement Up-fluffiing and Sotto-voce Song display in other neotropical jays of the Ornate Line that I consider more primitive (i.e. less derived from the hypothetical ancestral form) I conclude that the displays themselves are primitive. Highly social or communal social behavior is known for several presumably primitive as well as presumably derived species of this line and is confirmed now for *melanocyanea, yucatanica,* and *sanblasiana nelsoni.* Similar, probably homologous, displays in *C. beecheii* are restricted to intrapair behavior. Adult paired males of *C. beecheii* are highly intolerant of other adult males, suggesting strong asocial, perhaps territorial behavior in the reproductive season. From this I conclude that *C. beecheii* represents the derived state in this four-species complex and in the Ornate Line of New World jays.

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