SOCIALITY AND ONTOGENY OF COLORATION IN THE BLUE-AND-BLACK JAYS

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ABSTRACT.—To test the hypothesis that heterochronic changes in color maturation act to integrate avian social groups, the relationship between social-group size and maturation rates of four morphological characters was analyzed in the blue-and-black jays (*Cyanocorax* spp., formerly *Cissilopha*). Contrary to patterns found in the New World jay assemblage as a whole and to theoretical predictions, sociality and maturation rates are uncorrelated within the blue-and-black jays. Such a relationship is also lacking in at least one of the other two New World jay lineages that exhibit delayed soft-part color maturation. These results suggest that maturation rates do not track sociality closely and that the occurrence of delayed maturation of soft-part coloration in some New World jay taxa may best be accounted for by phylogenetic inertia. *Received 9 May 1990, accepted 10 Sept. 1990.*

Changes in developmental rates (heterochronic changes) in certain characters leading to retention of "juvenile" characters into later ages may be important in permitting group-living in animals (Hardy 1961, 1974; Brown 1963; Lorenz 1971; Lawton and Lawton 1985). Characters that may serve such a function in certain groups include plumage coloration, absence of male ornamentation, iris color, and beak color. Although several actual mechanisms have been proposed (Hardy 1961, Lawton and Lawton 1985), all share the basic idea that the juvenile character allows greater integration of groups with less aggression. Experimental behavioral studies support these ideas. Hardy (1974) demonstrated experimentally that Beechey's Jays (*Cyanocorax beecheii*) displaying the juvenile (yellow) beak coloration are subjected to less aggression from adults than those with the adult (black) beak color. Lawton et al. (in prep.) demonstrated that the juvenile yellow beak coloration in nestling Brown Jays (*C. morio*) increases food provisioning by adults. Thus, experimental evidence supports the hypothesis that juvenile appearance is an important factor in integrating avian social groups.

Hardy (1961) and Lawton and Lawton (1985) predicted a close relationship between degree of sociality and rates of maturation of characters such as beak color, iris color, and plumage coloration. The present study tests this prediction in the "blue-and-black" jays (formerly *Cissilopha*, now part of *Cyanocorax*) of México and Central America by comparing data on breeding group size with maturation rates of several character sets. This study differs from previous investigations in two regards: (1)

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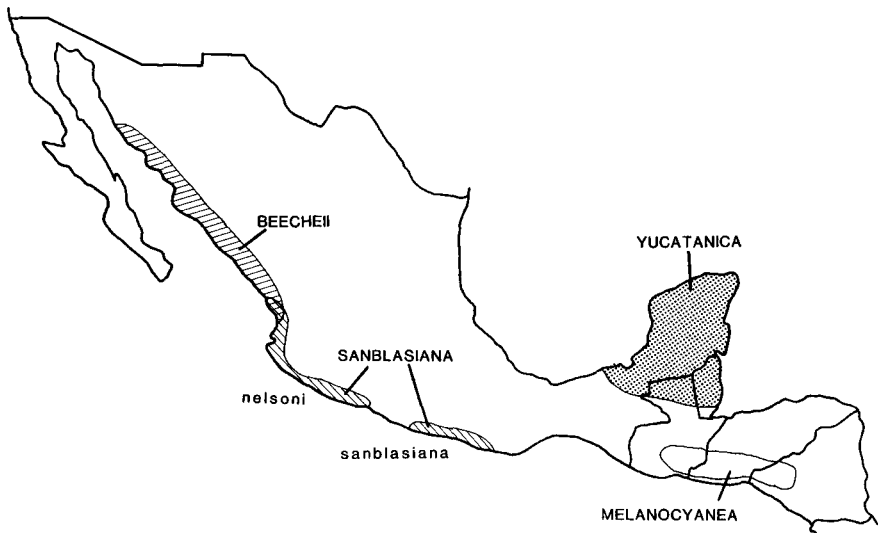
FIG. 1.   Geographic distribution of the blue-and-black jays in México and Central America.

comparisons are made within one relatively small lineage instead of across the whole family and (2) singular and plural breeding cooperative breeding systems (Brown 1987) are distinguished in discussing the patterns encountered.

The group under study consists of five largely allopatric populations of four species (Hardy and Raitt 1977; Fig. 1). Some of these populations are highly social, living in large groups that include two or more breeding pairs (plural breeders, e.g., *C. s. sanblasiana,* Hardy et al. 1981), while others live in smaller groups consisting of one pair and occasional helpers (singular breeders, e.g., *C. beecheii,* Raitt and Hardy 1979). Moreover, some populations attain the "adult" black beak coloration at the age of one year or less, while others do not exhibit the black beak color until two or more years of age. Several other characters, such as iris color, tail and body plumage color, and presence of a crest also vary in maturation rate among populations. Thus, the group exhibits marked variation in both degree of sociality and rates of maturation of several morphological characters and is ideally suited to the test.

METHODS

Information on social behavior of the blue-and-black jays was obtained from the literature (Hardy 1976; Raitt and Hardy 1976, 1979; Hardy et al. 1981; Raitt et al. 1984). Data on maturation rates of beak color, iris and circumorbital skin color, presence of a crest, and

tail and body coloration were obtained from Davis (1960), Hardy (1973), and Hardy and Raitt (1977). Because information is not available for each character set in each population of interest, and because Hardy's (1973) studies were based on captive individuals whose ontogenetic trajectories may not be representative of those of wild populations, I reviewed numerous museum specimens from each population. Because the two allopatric subspecies of *C. sanblasianus* differ markedly in social behavior (Hardy et al. 1981), they are treated separately throughout this paper. However, contrary to Hardy and Raitt (1977), it appears that delayed beak color maturation does occur in *C. s. sanblasianus*, given that the only two first-year individuals of this form examined had mandibles more than 50% yellow (Museum of Comparative Zoology 163812, 163813).

I studied 412 (39 *C. beecheii*, 157 *C. melanocyaneus*, 19 *C. sanblasianus sanblasianus*, 89 *C. s. nelsoni*, and 108 *C. yucatanicus*) specimens of blue-and-black jays in the collections of the American Museum of Natural History; Field Museum of Natural History; Museum of Comparative Zoology; Peabody Museum of Natural History; Museo de Zoologia of the Facultad de Ciencias and Colección Ornitológica of the Instituto de Biología, both at the Universidad Nacional Autónoma de México; and the Colección Ornitológica, Universidad Michoacana San Nicolas de Hidalgo. For each specimen, I determined the age as juvenile (0–3 months; having the soft juvenal plumage), first-year (3–15 months; adult coloration, but retaining the primary coverts and rectrices from the juvenal plumage), or after first-year (>15 months, AFY), using molt-sequence descriptions in Pitelka (1945). Additional categories could not be created for lack of information on molt schedules in each population.

I estimated the percent of mandible surface area that was yellow to the nearest 5% by visually dividing the mandible surface into four sections, scoring each as yellow, partly yellow, or black and combining these scores into an overall estimate. Because coloration patterns of the maxilla and mandible are highly correlated (Pearson's product-moment correlation, $r = 0.948$, $N = 412$), and for the sake of simplicity, I analyze here only data on mandible coloration.

Sexual differences in maturation rates are not evident (see Selander 1959). In the one case in which sample sizes and the pattern of variation permitted statistical testing, beak color maturation rates did not differ between the sexes (*C. melanocyaneus*, first-year, contingency test dividing above and below 50% yellow, $\chi^2 = 0.417$, df = 1, $P = 0.52$). Hence, sexes are combined in the analyses that follow.

RESULTS

Beak color maturation curves (Fig. 2) vary significantly (comparing mandible coloration in first-year individuals, Kruskal-Wallis Test, KW = 62.6, df = 3, $P < 0.001$) among the five populations of blue-and-black jays. The most rapid maturation of beak color occurs in *C. s. nelsoni, C. s. sanblasianus,* and *C. melanocyaneus* in which juveniles have nearly completely yellow beaks, but these darken rapidly, so that nearly all after first-year (AFY) individuals have completely black beaks (Fig. 2). Based on a very small sample, *C. beecheii* appears to mature more slowly. *C. yucatanicus* matures significantly slower than the other populations (Kruskal-Wallis test with multiple comparisons, $H = 63.87$, $P < 0.05$, Siegel and Castellan 1988), having completely yellow beaks until after they reach the AFY stage.

Other characters also show variation in maturation rate among blue-
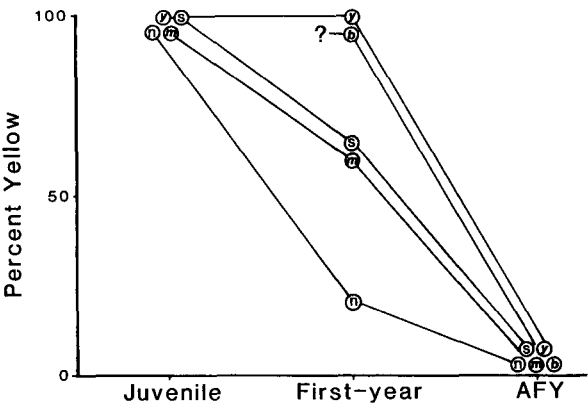
FIG. 2.   Maturation rates of beak coloration in five populations of blue-and-black jays shown as the median percent yellow of mandible surface area.

and-black jay populations, including iris color, presence of a crest, and tail and body coloration (Table 1). Maturation times (i.e., age at which adult appearance is attained) vary widely. Maturation times for iris color range between 19.5 and 39 mos (Hardy 1973). The crest requires between three and 27 mos and tail color requires between three and 15 mos. Maturation rates in different characters are not significantly concordant (Kendall Coefficient of Concordance, $W = 0.310$, $P > 0.05$, Siegel and Castellan 1988).

The degree of sociality also varies strongly in the blue-and-black jays (Table 2). Group size and breeding units per group are smallest in *C. beecheii* and *C. s. nelsoni*, intermediate in *C. melanocyaneus* and *C. yuca- tanicus*, and largest in *C. s. sanblasianus*. *C. beecheii* and *C. s. nelsoni*

TABLE 1

SUMMARY OF MATURATION RATES (AGE IN MONTHS AT WHICH MOST INDIVIDUALS ARE INDISTINGUISHABLE FROM ADULT) OF SOFT-PART COLORATION IN THE BLUE-AND-BLACK JAYS, BASED ON DATA GATHERED IN THIS STUDY, AND ON HARDY (1973) AND HARDY AND RAITT (1977). "EYE" REFERS TO COLORATION OF THE IRIS AND/OR CIRCUMORBITAL SKIN

Population	Beak	Eye	Crest	Tail
C. beecheii	15	27	3	3
C. melanocyaneus	9	19.5	3	3
C. sanblasianus nelsoni	9	39	27	3
C. s. sanblasianus	9	27	15	3
C. yucatanicus	>15	27	3	15

TABLE 2

Summary of Aspects of Sociality in the Blue-and-Black Jays from Hardy (1976), Raitt and Hardy (1976), Hardy et al. (1981), and Raitt et al. (1984)[a]

Population	Sample size	Breeding units	Non-breeders	Group size
Cissilopha beecheii	5, 7, 8, 10, 6	1.0	1.8	3.8
C. melanocyaneus	1	1.2[b]	9.0	11.0
C. sanblasianus nelsoni	2	1.0	2.5	4.5
C. s. sanblasianus	2, 2	6.1	7.0	19.0
C. yucatanicus	10, 9	1.2	7.4	11.9

[a] Individuals listed are yearling or older. Sample sizes are number of groups examined per year. Data for particular groups are averaged over years when data from multiple years are available. Number of non-breeders assumes two breeding adults per active nest (i.e., no polygamy).
[b] Sample size six.

have few non-breeding individuals. The three measures of sociality are not independent of one another (Kendall Coefficient of Concordance, $W = 0.816, P < 0.05$).

No direct relationship is apparent between the measures of sociality and maturation rates of the various characters. Fig. 3 shows the relationships between maturation rates of the four characters and three measures
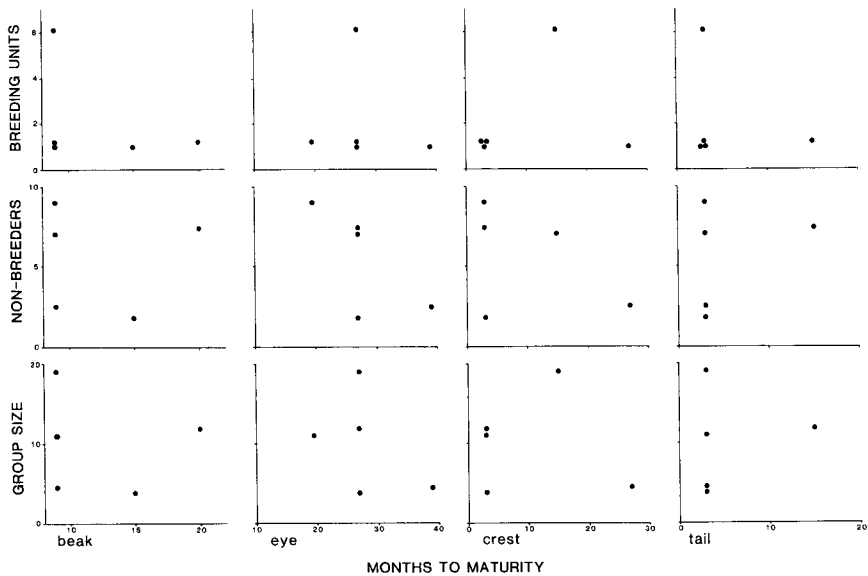

Fig. 3. Relationship between maturation rates of various character sets and degree of sociality in the blue-and-black jays.
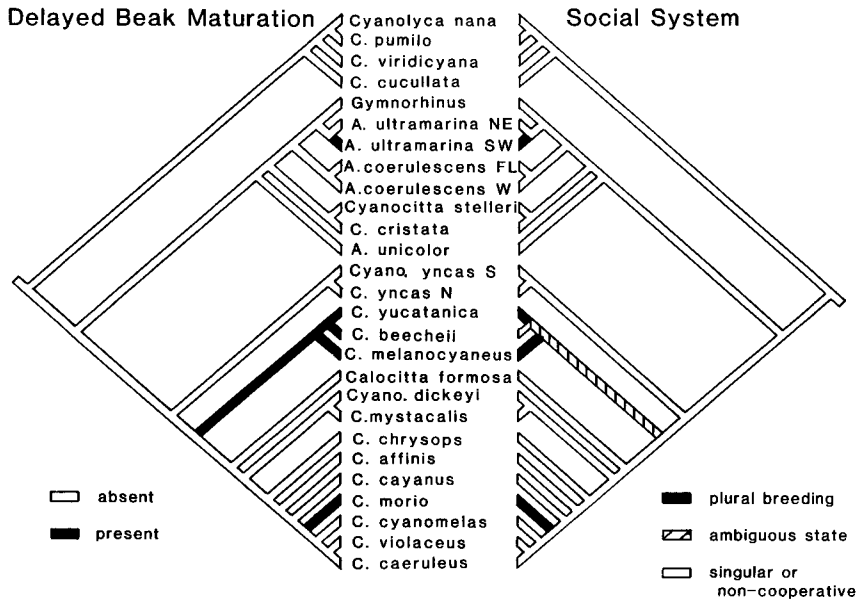
Delayed Beak Maturation   Social System

Cyanolyca nana
C. pumilo
C. viridicyana
C. cucullata
Gymnorhinus
A. ultramarina NE
A. ultramarina SW
A.coerulescens FL
A.coerulescens W
Cyanocitta stelleri
C. cristata
A. unicolor
Cyano. yncas S
C. yncas N
C. yucatanica
C. beecheii
C. melanocyaneus
Calocitta formosa
Cyano. dickeyi
C.mystacalis
C. chrysops
C. affinis
C. cayanus
C. morio
C. cyanomelas
C. violaceus
C. caeruleus

☐ absent

■ present

■ plural breeding

▨ ambiguous state

☐ singular or
   non-cooperative

FIG. 4. Relationship between phylogenetic distribution of communal breeding and de-layed beak color maturation in the New World jays. (Information on sociality is from Goodwin 1976. The phylogeny is from Hope [1989, Fig. 24b]. Reconstructions of character-state histories were produced using the MACCLADE package [Maddison and Maddison 1987].)

of sociality. None of the twelve Spearman rank-order correlation coefficients between the three measures of sociality and the four characters is significantly different from zero ($P > 0.05$). The coefficients range from -0.224 to 0.707.

DISCUSSION

In the New World jay assemblage as a whole, sociality and delayed maturation of beak color are highly correlated in their occurrence (Hardy 1961, Lawton and Lawton 1985; Fig. 4). Singular cooperative breeding (viz, one pair with helpers, Brown 1987) is widespread in the assemblage and apparently represents the plesiomorphic state (i.e., that present in the most recent common ancestor of the group). The phylogenetic distribution of singular cooperative breeding shows no obvious relation to that of delayed beak color maturation. Plural breeding (viz, more than one breeding unit per group, Brown 1987), however, is rarer in the New World jays, probably having been derived three or four times independently (Fig. 4). Interestingly, delayed beak color maturation exists only in these same lineages. The Unicolored Jay (*Aphelocoma unicolor*) is not considered to

show delayed maturation, as the delay in its beak color maturation appears to be minor (Peterson, unpubl. data). Thus, the prediction of a correlation between maturation rates of soft-part coloration and a high degree of sociality is strongly supported in the assemblage as a whole.

Why might there be a relationship between *plural* breeding and delayed soft-part maturation? Other workers who have treated these problems have either not considered the differences between singular and plural breeding (Lawton and Lawton 1985) or have assumed that individuals with "juvenile" characters were non-breeders (Hardy 1961). It is possible, however, that juvenile-like appearance may facilitate plural breeding by making it easier for a young bird to attempt early breeding inside the natal territory (R. Curry, pers. comm.). Under this view, delayed soft-part color maturation in plural breeders may act in the manner suggested for other songbirds (Rohwer 1978, Rohwer et al. 1980).

Within the New World jay assemblage, three lineages show delayed soft-part color maturation. This study focuses on variation in sociality and maturation rates within one of these lineages and finds no relationship.

In the Mexican Jay (*A. ultramarina*), a second New World jay lineage showing delayed color maturation, close correspondence between sociality and ontogenetic patterns similarly is lacking (Brown and Horvath 1989, Peterson, unpubl. data). The two populations in the United States suggest such a correlation, as Arizona and New Mexico populations breed plurally in large social groups and show delayed beak color maturation, while Texas populations are found in smaller groups (Ligon and Husar 1974, Strahl and Brown 1987, Brown and Horvath 1989) and do not exhibit delayed maturation (Pitelka 1951). However, the relationship breaks down farther south in eastern México, where social groups are large, yet color maturation is not delayed (Brown and Horvath 1989, Peterson unpubl. data).

For the third lineage showing delayed color maturation (*C. morio*), critical data on geographic variation in social-group size are lacking. Lawton and Lawton (1985) predicted that populations at the northern edge of the species' range in Texas and the state of Tamaulipas in México would be less social and show more rapid beak color maturation. However, comparing first-year individuals from Tamaulipas with similar-aged individuals from Costa Rica and Panama in the collections of the Field Museum of Natural History, I found that the northern populations actually mature significantly more slowly than those from the south (comparing percent yellow on mandible in first-year individuals, Mann-Whitney U-test, $U = 34$, $P \leq 0.005$, $N = 5, 7$). Clearly, more data on geographic variation in social-group size are needed before any predictions can be tested in this species.

Hence, in spite of a strong correlation between delayed maturation and plural breeding across the New World jay assemblage, and contrary to theoretical predictions, no such relationship exists *within* at least two of the three lineages exhibiting delayed color maturation. One potential explanation is that although delayed maturation may be an important factor in the evolution of avian plural breeding, its presence in less complex social systems may not be selected against. If the ancestral blue-and-black jay or *A. ultramarina* bred plurally, and the lower degree of sociality in some populations (e.g., *C. beecheii, A. u. couchii*) represents an evolutionary reversal, these populations may exhibit delayed soft-part color maturation as a result of phylogenetic inertia.

Thus, in spite of a close correlation in the New World jay assemblage as a whole, the current diversity of soft-part color maturation rates in the blue-and-black jays is not closely related to the degree of sociality. However, the adaptive hypothesis regarding sociality and maturation rates discussed in the introduction is not necessarily refuted. Delayed maturation rates may have been an important factor in the evolution of extreme sociality in the jays, but have not disappeared in lineages showing secondary reductions in levels of sociality.

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