

same clutch size distribution was found among the four nests at the WFVZ.

The current taxonomic placement of the Large-footed Finch is in the monotypic genus *Pezopetes*, although it has been suggested to be more appropriately placed in *Atlappetes* (Paynter and Storer 1970). The known nest and egg characteristics of *Pezopetes* are not inconsistent with such placement. Some species of *Atlappetes* lay spotted or blotched eggs, although all of the Middle American members of this genus lay unmarked white or pale blue eggs (Paynter 1978).

There is not yet enough information on nest-building behavior to aid in making taxonomic decisions regarding these finches. Our observations suggest that only one sex does the nest-building in *Pezopetes*, although both sexes are active in defense (Wolf 1976). There is no information in the literature regarding nest-building behavior in *Atlappetes*, but only female *Atlappetes torquatus* incubate the eggs (Paynter 1978).

M. Sc. Guillermo Canessa Mora, Servicio de Vida Silvestre, Ministerio de Recursos Naturales, Energía y Minas, granted permits to work in Costa Rica. Funding for Klein was provided by the Bird Division, Museum of Zoology, The University of Michigan, and a Block Grant from the Department of Biology, The University of Michigan, Ann Arbor, MI. Marin and Kiff would like to acknowledge the field assistance of F. Gary Stiles and Maxine Kiff, and thank D. Scott Wood for the loan of egg specimens from the Carnegie Museum of Natural History.

LITERATURE CITED

- CARRIKER, M. 1910. An annotated list of the birds of Costa Rica, including Cocos Island. Ann. Carnegie Mus. 6:314-915.
- PALMER, R. S. 1962. Handbook of North American birds, Vol. 1. Yale University Press, New Haven, CT.
- PAYNTER, R. A., JR., AND R. W. STORER. 1970. Emberizinae. In R. A. Paynter, Jr. and E. Mayr [eds.], Check-list of birds of the world. Vol. 13. Museum of Comparative Zoology, Cambridge, MA.
- PAYNTER, R. A., JR. 1978. Biology and evolution of the avian genus *Atlappetes* (Emberizinae). Bull. Mus. Comp. Zool. 148:323-369.
- SKUTCH, A. F. 1967. Life histories of Central American highland birds. Publ. Nuttall Ornith. Club, no. 7.
- STILES, F. G., AND A. F. SKUTCH. 1989. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, NY.
- WETMORE, A., R. F. PASQUIER, AND S. L. OLSON. 1984. The birds of the Republic of Panama, vol. 150, Part 4.
- WOLF, L. L. 1976. Avifauna of the Cerro de la Muerte Region, Costa Rica. Amer. Mus. Novit. 2606:1-37.

The Condor 93:448-452
© The Cooper Ornithological Society 1991

GEOGRAPHIC VARIATION IN THE ONTOGENY OF BEAK COLORATION OF GRAY-BREASTED JAYS (*APHELOCOMA ULTRAMARINA*)¹

A. TOWNSEND PETERSON²

Committee on Evolutionary Biology, The University of Chicago, Chicago, IL 60637

Key words: *Gray-breasted Jay*; *Aphelocoma ultramarina*; *beak coloration*; *ontogeny*; *maturation*; *geographic variation*; *sociality*.

The three species of jays in the genus *Aphelocoma* have been the subject of interest among ornithologists during recent decades. Aspects of geographic variation (Pitelka 1951), genetic differentiation (Peterson 1990), ecology (Edwards 1986; Peterson and Vargas, in press), and social behavior (Woolfenden and Fitzpatrick 1984, Brown 1974, Brown and Brown 1985) have been stud-

ied. Comparative studies linking different aspects of the jays' biology are now being conducted with rewarding results (e.g., geographic variation and social behavior, Brown and Horvath 1989; social behavior and genetic differentiation, Peterson, in prep.). A detailed base of information on all aspects of *Aphelocoma* jay biology is critical to these integrative studies.

A question linking behavioral biology and morphology is the effect of delayed maturation of coloration on social behavior (reviewed in Lawton and Lawton 1985). Several investigators have suggested that retention of juvenile coloration by subordinate individuals allows improved group cohesion by reducing aggression among individuals (e.g., Hardy 1961, 1974; Lawton and Lawton 1985). Because Gray-breasted Jays (*A. ultramarina*) exhibit geographic variation in both the ontogeny of beak coloration (Pitelka 1945, 1951) and in social behavior (Ligon and Husar 1974, Strahl and Brown 1987, Brown and Horvath 1989), geograph-

¹ Received 31 August 1990. Final acceptance 30 November 1990.

² Present address: Museum of Natural Science, Louisiana State University, Baton Rouge, LA 70803.

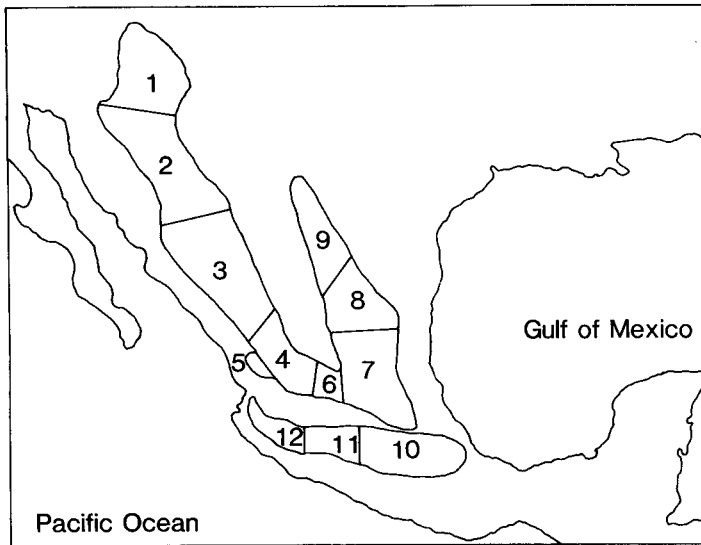


FIGURE 1. Distribution of the Gray-breasted Jay, showing the 12 regions into which the samples were divided. See Table 1 for further descriptions of regions.

ic patterns in the species have been used in tests of the above hypothesis (e.g., Hardy 1961, 1969; see discussion in Brown and Horvath 1989).

The purpose of this note is to analyze in detail the patterns of geographic variation in the ontogeny of beak coloration in Gray-breasted Jays. Adults of all forms of the species have black beaks; nestlings have beaks completely or partly whitish, pinkish, or yellowish. Populations differ strikingly in the rate of change from light to dark, with beaks of northeastern populations turning black approximately at the time of fledging, and western and southern populations taking as much as three years to mature completely.

Previous investigators apparently operated under the reasonable assumption (e.g., Hardy 1961, 1969; Ligon and Husar 1974; Brown and Horvath 1989) that geographic variation in beak color maturation in Gray-

breasted Jays consists of a discrete step between fast- and slow-maturing forms. This idea springs in part from comparisons of the two northern extremes of the range, both of which touch into the United States (in Arizona-New Mexico and Texas), with no information available on intermediate populations in México. The discrete variation idea is also founded in the belief that the three sections of the species' range (Fig. 1: regions 1-4, 7-9, and 10-12) are disjunct, although intermediate populations in the southern Chihuahuan Desert are known to exist (Pitelka 1951, 1961; Peterson 1990). The results presented below indicate that the "step" does not exist, and that the transition between the fast-maturing populations of Texas and the slow-maturing populations of Arizona in the species' U-shaped range in the mountains of north and central México is gradual.

TABLE 1. Summary of regions used in the analyses of geographic variation of beak color maturation rates in Gray-breasted Jays.

Region	Subspecies	n	Regression		
			Slope	Intercept	R ²
1. Arizona, New Mexico	<i>arizonae</i>	454	-18.6	82.9	0.671
2. N Sonora, N Chihuahua	<i>arizonae</i>	59	-17.3	73.2	0.695
3. S Chihuahua, Durango, Sinaloa	<i>wollweberi</i>	78	-15.8	64.9	0.645
4. Zacatecas, NE Jalisco	<i>wollweberi</i>	25	-0.7	3.2	0.098
5. NW Jalisco, Nayarit	<i>gracilis</i>	16	-9.9	39.2	0.936
6. Aguascalientes, Guanajuato	<i>wollweberi-potosina</i>	54	-1.6	6.0	0.315
7. San Luis Potosí, Hidalgo	<i>potosina</i>	68	-2.2	8.4	0.411
8. Nuevo León	<i>couchii</i>	63	-0.8	3.2	0.184
9. Texas, Coahuila, Tamaulipas	<i>couchii</i>	141	-0.6	2.5	0.526
10. Veracruz, México, Morelos	<i>ultramarina</i>	59	-18.6	85.6	0.589
11. Michoacán	<i>ultramarina</i>	59	-20.9	92.4	0.672
12. Colima, S. Jalisco	<i>colimae</i>	62	-20.7	89.6	0.612

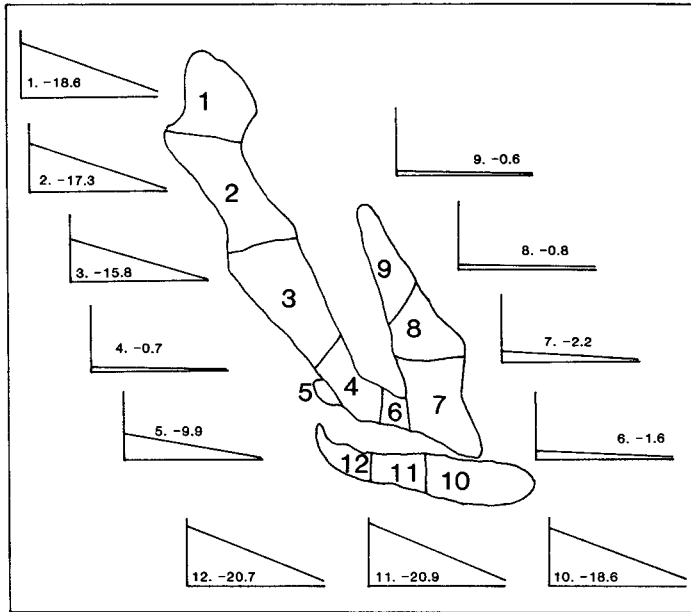


FIGURE 2. Geographic variation in beak color maturation rates in Gray-breasted Jays in 12 regions, shown as regressions of percent of mandible light-colored on age class. Regression slopes are given for each graph.

METHODS

I studied 1,138 specimens of Gray-breasted Jays in the museum collections listed in the Acknowledgments. Based on the general pattern of morphological variation across the species' range (Pitelka 1951), I grouped the collection localities into twelve regions (Table 1, Fig. 1). Regions were designed to minimize both heterogeneity within regions and the total number of regions necessary to cover the range.

For each specimen, I determined the age as juvenile (designated age class "0"; age 0–3 months; having the soft, juvenal plumage), second-year (classes "1," "2," and "3," see below; age 3–15 months; adult coloration, but retaining the remiges, primary coverts, and rectrices from the juvenal plumage), or after second-year (class "4"; age > 15 months), using molt-sequence descriptions in Pitelka (1945). Because molt schedules seem fairly uniform across the species' range (Pitelka 1951, pers. comm.; pers. observ.), second-year individuals were divided into three additional age classes: specimens collected September through December are designated age class "1," those from January through April are age class "2," and those from May through August are age class "3."

Because coloration patterns of the maxilla and mandible are correlated (Pearson's product-moment correlation across all individuals in the study, $r = 0.684$), and because maxilla coloration is less variable, I analyze here only data on mandible coloration. I estimated the percent of mandible surface area that was light to the nearest 5% by visually dividing the mandible surface in four sections, scoring each as light, partly light, or black, and combining the scores into an overall estimate.

RESULTS AND DISCUSSION

Sexual differences in maturation rates in the region for which the largest samples were available (region 1: Arizona and New Mexico) were not significant in the first four age classes (Mann-Whitney U -tests, $P > 0.20$), but were highly significant in adults (males with more light area on beak; Mann-Whitney U -test, $P < 0.0005$). This result is consistent with the findings of Brown and Brown (1990) that male Gray-breasted Jays generally must wait longer than females before acquiring breeding status. Based on the absence of sex differences in maturation rates during subadult stages, however, sexes are combined in the analyses that follow.

Geographic differences among populations are evident. Although statistical comparisons of the entire coloration-age distributions are difficult, beak colors in the 57 individuals of age two (approximately midway through the maturation process) available from eight of the twelve regions differ significantly among regions (Kruskal-Wallis test, $P < 0.005$). In general, beak color matures slowly in northwestern and southern populations, more rapidly in central-western populations, and very rapidly in eastern populations (Fig. 2).

Within the northern part of the range, contrary to the stepped pattern assumed in the literature, maturation rates change in a smooth cline from very slow to very rapid (Fig. 2). Much of the turnover occurs between the southern Chihuahuan Desert (e.g., Guanajuato, San Luis Potosi) and the Sierra Madre Occidental in Durango. However, maturation rates gradually approach the slow, northwestern extreme between Durango and Arizona, and occasional individuals with traces of light coloration in the beak are found in the eastern portion of the range. (The apparent break in

this cline between regions 3 and 4 is most likely due to a paucity of specimens from the southern part of region 3.) Hence, the transition from fast to maturation of beak color appears to be gradual across all of northern México, with a step between the northern mountains (Sierra Madre Oriental and Sierra Madre Occidental) and the mountains of the Transvolcanic Belt of central México.

The disjunct distribution of delayed beak maturation in the species is interesting. The slowest maturing populations are found in the northwestern (regions 1–3) and southern (regions 10–12) parts of the range. The same geographic pattern appears in allozyme characters, in which southern and northwestern populations (i.e., those from regions 1 and 12) are more similar than either is to intermediate populations (regions 2–5; Peterson 1990). A potential explanation is that the southern populations have been effectively isolated genetically for a long period of time, and so new characters arising subsequently in the northern populations (in this case, in northeastern populations) might spread among northern populations, but would not reach the southern part of the range.

The pattern of geographic variation in beak color maturation documented above has implications for the question of whether social group size and maturation rates are related in this species. Mean group size almost doubles from north to south (Brown and Horvath 1989, pers. observ.) without any slowdown in maturation rates, suggesting that a close relationship does not exist. However, comparing the group-size data of Brown and Horvath (1989) with maturation rates presented above (Table 1), a significant positive relationship is evident (Fig. 3; Spearman Rank Correlation, $r = 0.721$, $P < 0.05$). Brown and Horvath (1989) rejected the hypothesis of a relationship between maturation rates and group size because their two-state characterization of maturation rate showed no relationship with social group size. The added detail of quantitative measures of maturation rates shows the western population *gracilis* to be intermediate in the spectrum of maturation rates, leading to a better correlation with group size than found by Brown and Horvath (1989). (Brief observations of seven groups on 29–31 March 1989 near Villa Guerrero, Jalisco by myself and two colleagues, however, suggest that the *gracilis* population may not actually have smaller groups as suggested by the data of Brown and Horvath [1989]. The cautions of Felsenstein [1985] on interpreting correlations in comparative studies are also relevant to all such comparisons.) Although further and more detailed field studies of geographic variation in social behavior (i.e., information on more populations concerning group size, age at first breeding, beak coloration when breeding status is attained, social interactions of dark-billed vs. light-billed breeders, etc.) are clearly necessary, my analyses of geographic variation in ontogeny of beak coloration in Gray-breasted Jays suggest that the possibility of a maturation rate-social group size correlation in Gray-breasted Jays should be considered.

The curators of the following collections kindly provided access to specimens under their care: Moore Laboratory of Vertebrate Zoology, Occidental College; University of California at Los Angeles; Western Found-

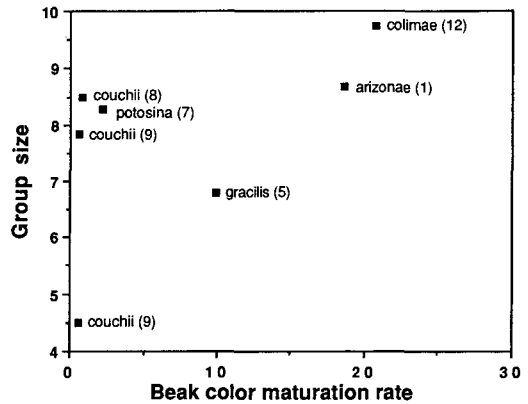


FIGURE 3. Relationship between beak maturation rates (present study) and group sizes (Brown and Horvath 1989). Beak maturation rates are presented as the additive inverse of the slope of a simple linear regression of percent of the mandible light on age. Region numbers are given in parentheses.

dation of Vertebrate Zoology; Los Angeles County Museum of Natural History; Colección Ornitológica, Universidad Michoacana San Nicolás de Hidalgo; Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México; Instituto de Biología, U.N.A.M.; Museum of Comparative Zoology, Harvard University; Delaware Museum of Natural History; United States National Museum; Academy of Natural Sciences, Philadelphia; American Museum of Natural History; Peabody Museum, Yale University; Carnegie Museum of Natural History; Museum of Zoology, University of Michigan; and Field Museum of Natural History.

I am grateful to my companions in museum studies, H. Benítez D., P. Escalante P., and A. Navarro S., and field work, A. Peterson, H. Benítez D., Noé Vargas B., and S. Baker, for companionship and interest throughout these studies. Special thanks to A. Peterson for patience and support during the last five years, to T. Schulenberg and two anonymous reviewers for critical comment on the manuscript, and to F. Pitelka for encouragement and help in designing the methodology employed. My field work was supported by grants from the National Science Foundation, National Geographic Society, Sigma Xi, American Museum of Natural History, Field Museum of Natural History, and the University of Chicago.

LITERATURE CITED

- BROWN, J. L. 1974. Alternative routes to sociality in jays—with a theory for the evolution of altruism and communal breeding. *Am. Zool.* 14:63–80.
- BROWN, J. L., AND E. R. BROWN. 1985. Ecological correlates of group size in a communally breeding jay. *Condor* 87:309–315.
- BROWN, J. L., AND E. R. BROWN. 1990. Mexican jays: uncooperative breeding, p. 267–288. *In* P. B. Stacey and W. D. Koenig [eds.], *Cooperative breeding in birds*. Cambridge Univ. Press, Cambridge.
- BROWN, J. L., AND E. G. HORVATH. 1989. Geographic

- variation of group size, ontogeny, rattle calls, and body size in *Aphelocoma ultramarina*. *Auk* 106: 124-128.
- EDWARDS, T. C., JR. 1986. Ecological distribution of the Gray-breasted Jay: the role of habitat. *Condor* 88:456-460.
- FELSENSTEIN, J. 1985. Phylogenies and the comparative method. *Amer. Natur.* 125:1-15.
- HARDY, J. W. 1961. Studies in behavior and phylogeny of certain New World jays (Garrulinae). *Univ. Kans. Sci. Bull.* 42:13-149.
- HARDY, J. W. 1969. A taxonomic revision of the New World jays. *Condor* 71:360-375.
- HARDY, J. W. 1974. Behavior and its evolution in Neotropical jays (*Cissiloph*a). *Bird-banding* 45: 253-268.
- LAWTON, M. F., AND R. O. LAWTON. 1985. Heterochrony, deferred breeding, and avian sociality. *Curr. Ornithol.* 3:187-222.
- LIGON, J. D., AND S. L. HUSAR. 1974. Notes on the behavioral ecology of Couch's Mexican Jay. *Auk* 91:841-843.
- PETERSON, A. T. 1990. Evolutionary relationships of the *Aphelocoma* jays. Ph.D. diss. University of Chicago, Chicago.
- PETERSON, A. T., AND N. VARGAS B. In press. Ecological diversity in the Scrub Jay (*Aphelocoma coerulescens*). In T. P. Ramamoorthy, J. Fa, and R. Bye [eds.], *The biological diversity of México*. Oxford Univ. Press, Oxford.
- PITELKA, F. A. 1945. Pterylography, molt, and age determination of American jays of the genus *Aphelocoma*. *Condor* 47:229-260.
- PITELKA, F. A. 1951. Speciation and ecologic distribution in American jays of the genus *Aphelocoma*. *Univ. Calif. Publ. Zool.* 50:195-464.
- PITELKA, F. A. 1961. Comments on types and taxonomy in the jay genus *Aphelocoma*. *Condor* 63: 234-245.
- STRAHL, S. D., AND J. L. BROWN. 1987. Geographic variation in social structure and behavior of *Aphelocoma ultramarina*. *Condor* 89:422-424.
- WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1984. *The Florida Scrub Jay: demography of a cooperative-breeding bird*. Princeton Univ. Press, Princeton, NJ.

The Condor 93:452-454

© The Cooper Ornithological Society 1991

THE EFFECTS OF SUPPLEMENTAL FOOD ON NEST DISPERSION IN BLACK-BILLED MAGPIES¹

ERIC STONE AND CHARLES H. TROST

Department of Biological Sciences, Idaho State University, Pocatello, ID 93209

Key words: Magpie; *Pica pica*; supplemental food; nest dispersion; nesting density.

Nest dispersion patterns among bird species range from uniform ("spaced") distributions to clumped. The relative costs and advantages of particular patterns of nest distribution have been examined in several species through the use of conceptual and theoretical models as well as empirical studies (Brown 1964, 1969). In some cases this has been accomplished by examining variability in nest dispersion patterns within a single species at different geographic locations within its range (Lott 1984). These costs and benefits might also be examined in the same population over a period of several years.

Factors which lead to high nest densities are limited nesting habitat (Veen 1977, Burger 1982), variable food resources (Horn 1968), or abundant food resources (Knight 1988). Advantages of high nesting densities or clump nest distributions within an intraspecific population include reduced risks of nest predation through group defense (Veen 1977, Burger 1982) or increased

foraging efficiency (Ward and Zahavi 1973). Competition for resources may be greater in higher density habitats (Fretwell and Lucas 1969, Fretwell 1972) as is the probability of interference from conspecifics (Brown and Brown 1988).

Horn (1968) suggested that when the resources are unpredictable, territory defense should not persist and nests should be clumped, but according to Brown (1969) this might also occur when resources are economically undefendable. Economic undefendability might occur if resources are distributed sparsely and are ephemeral but what if resources are predictable, superabundant and found at a single source such as might be found in many supplementally-fed populations? It might be expected that population density would increase in the vicinity of the supplemented resource, but will territoriality and nest dispersion patterns persist or change?

We examined the influence of food abundance on nest distribution patterns in a discrete population of black-billed magpies (*Pica pica*). Black-billed magpies are a useful species in which to examine the factors that lead to different nest distribution patterns. While magpies in Europe have been described as territorial with nest distributions being uniform or "hyperdispersed" (Birkhead et al. 1986), Knight (1988) suggests that black-billed magpies in North America nest in varying densities. Furthermore, local food resources

¹ Received 13 September 1990. Final acceptance 19 November 1990.