

shortcoming of the modal method is that it estimates only the direction of activity and gives no indication of the scatter of hopping, whereas the traditional method indicates the degree of concentration of a bird's hopping (mean vector length, r). This is not often a major problem because most recent studies have relied on second-order analyses of mean directions that ignore the mean vector lengths. Indeed, at this point the biological meaning of the dispersion of a bird's hopping activity is not clear and is in part a reflection of the idiosyncracies of individual birds (Wiltschko and Wiltschko 1978, Moore 1985).

LITERATURE CITED

- BATSCHLEET, E. 1978. Second-order statistical analysis of directions. Pp. 3-24 in *Animal migration, navigation, and homing* (K. Schmidt-Koenig and W. T. Keeton, Eds.). Berlin, Springer-Verlag.
- . 1981. *Circular statistics in biology*. New York, Academic Press.
- BINGMAN, V. P. 1983. Importance of earth's magnetism for the sunset orientation of migratory naive Savannah Sparrows. *Monit. zool. Ital.* 17: 395-400.
- , & K. P. ABLE. 1979. The sun as a cue in the orientation of the White-throated Sparrow, a nocturnal migrant. *Anim. Behav.* 27: 621-622.
- CHERRY, J. D. 1984. *Migratory orientation of Tree Sparrows*. Unpublished M.S. thesis, Albany, State Univ. New York.
- EMLÉN, S. T. 1969. The development of migratory orientation in young Indigo Buntings. *Living Bird* 8: 113-126.
- , & J. T. EMLÉN. 1966. A technique for recording migratory orientation of captive birds. *Auk* 83: 361-367.
- HAMILTON, W. J., III. 1966. Analysis of bird navigation experiments. Pp. 147-178 in *Systems analysis in ecology* (K. E. F. Watt, Ed.). New York, Academic Press.
- MARDIA, K. V. 1972. *Statistics of directional data*. New York, Academic Press.
- MOORE, F. R. 1985. Individual variability in the migratory orientation of the Savannah Sparrow, *Passerculus sandwichensis*. *Z. Tierpsychol.* 67: 144-153.
- RABØL, J. 1969. Orientation of autumn migrating Garden Warblers (*Sylvia borin*) after displacement from western Denmark (Blåvand) to eastern Sweden (Ottenby). A preliminary experiment. *Dansk Ornithol. Foren. Tids.* 63: 93-104.
- . 1970. Transformation of colour degrees to number of jumps using the Emlen orientation technique. *Dansk Ornithol. Foren. Tids.* 64: 118-126.
- WILTSCHKO, R., & W. WILTSCHKO. 1978. Relative importance of stars and the magnetic field for the accuracy of orientation in night-migrating birds. *Oikos* 30: 195-206.
- WILTSCHKO, W., & K. H. SCHMIDT. 1974. Direcciones preferenciales de migrantes nocturnos (Passeres) por Almería. *Ardeola* 20: 127-140.
- , & R. WILTSCHKO. 1972. Magnetic compass of European Robins. *Science* 176: 62-64.

Received 4 February 1985, accepted 26 August 1985.

Notes on the Plumages of the Paramo Seedeater (*Catamenia homochroa*)

ROBERT W. DICKERMAN

Cornell University Medical College, New York, New York 10021 USA, and
American Museum of Natural History, New York, New York 10024 USA

Many species of nonpasserine birds, especially among the Ciconiiformes, Falconiformes, and Charadriiformes, exhibit three or more successive, pre-definitive, full basic plumages. Comparable sequences are little known among Passeriformes; for one example, Parkes and Humphrey (1963) described four age classes in male Yellow-backed Tanagers (*Hemithraupis flavicollis*), and I have found four age classes in male Altamira Orioles (*Icterus gularis*; Dickerman MS).

The acquisition of freshly collected and correctly aged specimens of the Paramo Seedeater (*Catamenia homochroa*) from Cerro Neblina in extreme southern Venezuela stimulated me to review the geographic variation in the species. In preliminary studies it was immediately obvious that the species is not only sex-

ually dimorphic, but that there are several plumage stages. Geographic variation could not be evaluated until the plumages were identified so that comparable age classes could be compared.

I obtained 107 specimens of *C. homochroa* on loan (see Acknowledgments) for comparison with the 65 specimens in the collection of the American Museum of Natural History (AMNH). Included in the series of *C. homochroa* were 5 specimens of *oreophila*, the subspecies from Cerro Santa Marta, Colombia. For the purposes of this study, all Andean specimens of *C. homochroa*, from Merida, Venezuela to Chuspipata, Bolivia, were combined and segregated by sex, and thence by plumage stage, regardless of date of collection. Similarly, all specimens of *C. h. duncani*, the subspecies from the Pantepui region of southern

TABLE 1. Comparison of postjuvenile basic plumages of male *Catamenia homochroa homochroa*. Capitalized color names with numbers indicate direct comparison with Smithe's (1975, 1981) "Naturalists' Color Guide."

	First basic	Second basic	Definitive
Crown	Prout's Brown (121A) to Sepia (219), weakly streaked with dusky	Sepia (119), streaking becomes evident in some worn specimens	Blackish Neutral Gray (82) to black, unstreaked even when worn
Interscapular area	Prout's Brown (121A) to Sepia (219), strongly streaked	Hair Brown (119A) to Vandyke Brown (121), weakly streaked, more evident in worn specimens	Vandyke Brown (121) to Blackish Neutral Gray (82), streaking obsolete when worn
Rump	Prout's Brown (121A) to Dark Brownish Olive (129)	Brownish Olive (29) to Olive Brown (28)	Sepia (119)
Throat	Buffy Grayish Horn (91)	Glaucous (79) to Dark Neutral Gray (83)	Dark Neutral Gray (83)
Flanks	Brussels Brown (121B) to Verona Brown (223B), weakly streaked	Dark Brownish Olive (121)	Vandyke Brown (221)
Belly	Cinnamon (39) to Buff (124)	Cinnamon (39) to Clay Colored (123B)	Glaucous (79)
Crissum	Kingfisher Rufous (340)	Kingfisher Rufous (340) to Mahogany Red (132B)	Chestnut (32)
Specimens used	AMNH 117056, 124964, 820576	AMNH 130474, 170034, 180700, 180699	AMNH 134129, 820632

Venezuela, were segregated by sex and plumage stage. Unfortunately, few specimens in molt are available.

Four plumages were identified and are described below for each sex of *C. homochroa*, based on comparisons of the changes in wear from fresh to worn

within each successive stage, followed by a shift in color or pattern in the next plumage group. Specimens taken year-round are not available from a single locality, or even from adjacent ranges, and because of the obvious variation in phenology over the

TABLE 2. Comparison of postjuvenile basic plumages of female *Catamenia homochroa homochroa*.

	First basic	Second basic	Definitive
Crown	Raw Umber (223) to Fuscous (21), heavily streaked	Hair Brown (119A) to Fuscous (21), heavily streaked	Dusky Brown (119) to Blackish Neutral Gray (82), streaking obsolete
Interscapular area	Hair Brown (119A), heavily streaked	Prout's Brown (121A), heavily streaked	Vandyke Brown (121) to Blackish Neutral Gray (82), streaking obsolete
Rump	Olive Brown (28) to Brownish Olive (29)	Prout's Brown (121A)	Olive Brown (28) to grayish Hair Brown (119A)
Throat and breast	Glaucous (80) to Light Drab (119C), streaking obsolete	Light Drab (119C) to Brownish Olive (29) on breast, throat weakly streaked	Glaucous (79) to brownish Light Neutral Gray (85), unstreaked
Flanks	Brussels Brown (121B) to Prout's Brown (121A)	Clay-colored (26) to Olive Brown (28), streaking obsolete	Smokey Gray (44) to Dark Brownish Olive (129), grayer when worn
Belly	Clay-colored (132B)	Pale Horn (92) to Tawny Olive (223D)	Tawny (38) to Kingfisher Rufous (240)
Crissum	Tawny (38) to Kingfisher Rufous (240)	Tawny (38) to Kingfisher Rufous (240)	Tawny (38) to Kingfisher Rufous (240)
Specimens used	AMNH 180701, 180702, 180703, 112727	AMNH 134132, 134133, 134135	AMNH 134134, 170036; CM* 70469, 70704

* CM = Carnegie Museum of Natural History.

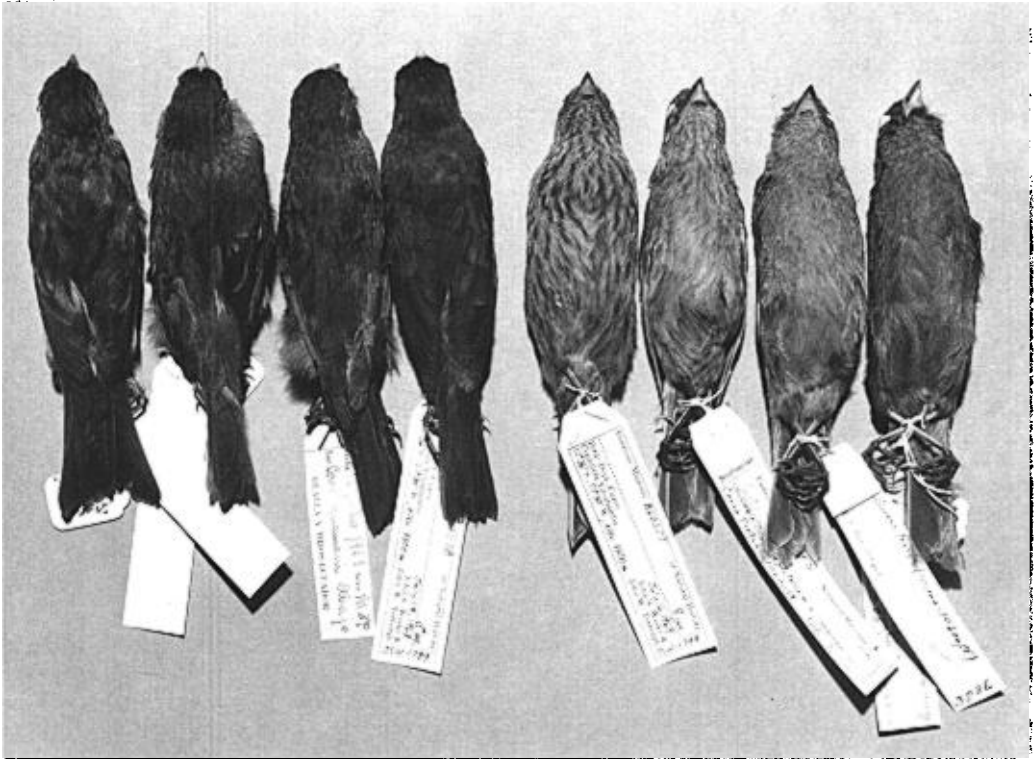


Fig. 1. Dorsal view and ventral view *Catamenia homochroa homochroa*. Left to right, males: juvenile plumage AMNH 134128 Colombia; first basic AMNH 124967 Ecuador; second basic AMNH 180705 Ecuador; definitive AMNH 820578 Peru. Females: juvenile plumage AMNH 820577, first basic USNM 375405 Colombia; second basic USNM 375410 Colombia; definitive AMNH 1314134 Colombia.

extended range of the species, specimens could not be compared based on dates of collection. Because there was no evidence of extensive (if any) prealternate molt that would be indicated by differential wear of parts of the body in worn specimens, the four stages may be called juvenile, first and second basic, and definitive basic plumages.

Having determined the plumage sequence of *C. homochroa*, I examined the specimens of *C. inornata* and of *C. analis* in the AMNH, supplemented by 19 specimens of females and males in the more confusing striped plumages obtained on loan. Sufficient males of *C. inornata minor* were available to delimit four plumage stages similar to those in *C. homochroa*. In male *C. analis analoides* (the latter supplemented with specimens of the subspecies *analis* and *alpica* in striped plumages), I could identify three plumage stages, but material was insufficient to be certain as to whether there is a second striped stage such as that represented by the first basic plumage of *C. homochroa* (described below).

Specimens of *C. homochroa* in fresh plumage or showing little wear were used for the comparisons of the postjuvenile plumages presented in Tables 1

and 2. However, the three age groups are most dramatically seen among specimens in worn plumage (Fig. 1). In all three species of the genus, there are two general trends in the plumage succession: the reduction of streaking from the juvenile to the definitive plumage, and an increase in grayness.

There appeared to be no sexual dimorphism in the heavily streaked juvenile plumage. Juvenile nominate *homochroa* are paler and less heavily, although not less extensively, streaked than are juvenile *duncani*.

When specimens of *C. homochroa* were segregated by age and sex, and when recently taken (post-1960) specimens were separated from those taken earlier, there were no comparable groups with a sufficient number of specimens in unworn plumage to be able to determine the extent of foxing over time, or the extent of geographic variation within the Andean or the Pantepui populations. I believe that foxing is not a marked problem in the species, and that geographic variation within the two regions is minor compared with the distinctness of *homochroa* and *duncani*. Specimens from the southern portion of the Andean range (Peru and Bolivia) are slightly grayer and less olive than specimens from Ecuador, Colombia, and An-

dean Venezuela, and specimens from the western tepuis of Territorio Amazonas are somewhat grayer than are specimens from the eastern tepuis of the Gran Sabana.

The definitive female plumage in the two subspecies is similar to that of the second basic male plumage of the same subspecies. Between the subspecies, the definitive male plumage of *duncani* is similar to, but still somewhat browner than, the definitive female or second basic male plumage of *homochroa*. Similarly, the second basic plumage of *duncani* is more similar to the first basic plumage of *homochroa*. Thus, reduced stripedness and gray coloration probably represent the derived condition, and heavily striped brown plumage is probably the primitive condition.

If this is true, then I would suggest that *duncani*, which inhabits the tops of the far older land mass of the tepuis, would have been the parental stock that "hopped" to and colonized the Andes after they were formed. A paler juvenile plumage and grayer definitive plumage was part of their adaptation to the drier paramo conditions.

Males of *C. h. oreophila*, the isolated Santa Marta population, in juvenile and first basic (in second pre-basic molt) and three females in second basic plumage are separable from the corresponding plumages of nominate *homochroa* in being somewhat paler brown. The type of *oreophila* was compared with the above three females by K. P. Parkes. It is distinctly grayer and probably represents the definitive basic plumage.

In contrast to our knowledge of plumage sequences for North American birds, one can generalize that such sequences are poorly known for neotropical species. The recognition of four sequential

plumages in male *Hemithraupis flavicollis* was so startling at the time that reviewers of Parkes and Humphrey's (1963) manuscript questioned the phenomenon (Parkes pers. comm.). The recognition of four sequential plumages in male *Icterus gularis* and now in both sexes of *Catamenia homochroa* perhaps indicate that a higher frequency of complex plumages is to be found among neotropical species.

I thank the curators of the following collections for the loan of material in their care: Carnegie Museum of Natural History, Field Museum of Natural History, Louisiana State University Museum of Zoology, Museum of Comparative Zoology, and the U.S. National Museum of Natural History. Mr. William H. Phelps, Jr., and Ramon Aveledo kindly hand carried the entire series of *duncani* from the Coleccion Phelps, Caracas to New York for this study. Kenneth C. Parkes reviewed the age plumage classes with me and made useful suggestions. The Photography Department at the American Museum of Natural History prepared the illustration.

LITERATURE CITED

- PARKES, K. C., & P. S. HUMPHREY. 1963. Geographical variation and plumage sequence of the tanager *Hemithraupis flavicollis* in the Guianas and adjacent Brazil. *Proc. Biol. Soc. Washington* 76: 81-84.
- SMITHE, F. B. 1975. *Naturalist's color guide, part I*. New York, Amer. Mus. Nat. Hist.
- . 1981. *Naturalist's color guide, part III*. New York, Amer. Mus. Nat. Hist.

Received 12 March 1985, accepted 26 August 1985.

Breeding-site Selection and Colony Formation in Double-crested and Pelagic Cormorants

DOUGLAS SIEGEL-CAUSEY¹ AND GEORGE L. HUNT, JR.²

¹Museum of Natural History and Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045 USA, and

²Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92717 USA

The success of a breeding pair to raise eggs to fledged birds does not appear to be uniform over an entire colony; instead, there are certain regions (central area, steepest slopes, etc.) where the occupants have enhanced reproductive success (Coulson 1968, Nettleship 1972, Ryder 1980, Panov and Zykova 1982, Kharitonov 1983b). Fretwell and Lucas (1970) proposed a mechanism by which colonial birds could assess and choose optimal breeding sites from among a range of choices. A series of habitats are identified, each ranked by a unique suitability function that is a density-dependent measure of average reproduc-

tive success. That is, the average success of breeding birds decreases through the effect of density-dependent factors such as disease, neighbor conflict, predator awareness, etc. as the density of the habitat increases. At some density, the expected reproductive success in the optimal habitat will equal that experienced in some lesser, unoccupied habitat. Incoming adults intent on breeding should then colonize both habitats at an equivalent rate, rather than saturate the optimal habitat. Where breeding must be initiated within a narrow time frame, or nest sites are changed at a loss of the previously invested time and effort,