COMPARATIVE AVIAN CYTOGENETICS: A REVIEW

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ABSTRACT.—Avian cytogenetic research has, until recently, lagged far behind efforts devoted to the cytogenetics of other vertebrate groups. Avian chromosomes are inherently difficult to study because most are minute and their morphology and number are obscure. Since 1966, improved methods of culturing avian cells have resulted in more comparative chromosome studies whose quality parallels those for mammals.

Recent activity in comparative avian cytogenetics now allows us to assess such factors as the overall karyotypic variability in birds and to consider the role that chromosomal change plays in avian speciation. In the present study, chromosomal variability was assessed within and among species of the same genus and within orders of birds. Chromosomal differences among local populations appear to be associated either with mechanisms that support balanced polymorphism or frequency dependent selection and not with speciation. The data are discussed in light of current models of chromosome evolution proposed for vertebrates other than birds.

New cytological techniques coupled with interest in comparative cytogenetics have produced abundant data on vertebrate chromosomes, particulary those of mammals. Methods for examining the banding patterns of chromosomes and related procedures have transformed the cytogenetics of the 1960's into a vigorous, dynamic discipline. New efforts have been made to reassess the role that chromosomal change within a lineage can play in starting reproductive isolation, and hence the speciation process. Views concerning the relevance of chromosomal change to speciation and the processes by which this might occur have polarized (Mayr 1970, White 1978).

The number of avian species that have been karyotyped has doubled in the past decade (Shields 1980), yet no detailed review of this field exists and the earlier summaries of Bloom (1969), Ray-Chaudhuri (1973) and Shoffner (1974) are now incomplete.

My purpose here is to synthesize all available data concerning avian cytogenetics and to interpret them in light of our understanding of chromosomal evolution in other better-studied groups. To this extent the synthesis is comparative. Chromosomal variability between lineages at different taxonomic levels is assessed.

METHODS

GENERAL BACKGROUND

Most of the chromosomes of nearly all avian species are microchromosomes (see Glossary at end of article), which are difficult to count accurately. Consequently, it is difficult to determine whether differences in the total microchromosome number reported by authors

are real or are artifacts of preparation and analysis. This problem can be resolved only when large numbers of karyotypes per individual and meiotic analyses are included in a research plan. Such detailed studies are uncommon in current research on avian chromosomes, and most comparative studies emphasize variation in macrochromosomes.

Moreover, since differential banding analyses have been performed on only a few avian species, chromosomal variability is most commonly scored only in classically, nondifferentially stained material. Consequently, only rearrangements that change the diploid or fundamental numbers of chromosomes, or alter the position of the centromere in an obvious way, are scored.

Females are the heterogametic sex in birds and most of them possess a minute W sex chromosome that is comparable in size to most microchromosomes. Thus, in classically stained material the W chromosome is very difficult to identify; some authors either make a tentative identification or ignore it completely. Other chromosome markers such as nucleolar organizer regions, which have been characterized extensively in vertebrates other than birds, are not obvious in conventionally stained avian material.

I alleviated these difficulties to some extent by limiting my analyses to species for which a pictorial representation of the entire karyotype and relative chromosome lengths and arm ratios were available. All data for this review are from my laboratory or the published literature. The karyotypes that were studied in my laboratory were prepared from cultured kidney cells that were harvested and stained

in the usual way with carbol fuchsin (Shields 1973). Several individuals of each sex were usually karyotyped, and diploid and fundamental numbers were determined from at least ten nuclei of each individual. Sample sizes were much larger for species that were studied in other contexts (e.g., species of juncos and the White-throated Sparrow). The additional published and unpublished material that I use in this review were obtained essentially in the same way as those from my own laboratory.

Much of the early avian cytogenetic literature was based on methodology now recognized as inappropriate for detailed analyses; consequently I have not included pre-1966 literature in this review. I assessed chromosomal variability in birds through separate comparisons within species, between species of the same genus, and within orders. Of the nearly 300 species studied, approximately one-fourth were analyzed in my laboratory.

INTRASPECIFIC ANALYSIS

I examined the karyotypes (chromosomes homologously paired and arranged in decreasing order of size) of individual birds of each species for variations in the size of each pair of homologous chromosomes, and the location of the centromere. Intraspecific chromosomal variability was assumed to exist if either one or both members of a pair of homologous chromosomes of an individual bird differed in an obvious way from the same pair of chromosomes in other individuals of the same species. For individuals that showed variation, the suspected mechanism of chromosome change is given in Table 1.

INTERSPECIFIC ANALYSIS

In the present study, I also examined congeneric species for interspecific differences in karyotype. I excluded genera for which the karyotype of only one species was available. My analyses consist of comparisons of diploid and fundamental numbers and the locations of the centromeres on each chromosome.

In all, I examined the chromosomes of 136 species representing 46 genera (Table 2). All possible pairwise comparisons within a genus were made. I refer to a pair of species as "identical" if their karyotypes appeared to be the same. In cases where pairs differed, I present a brief description of the variation in the table.

ORDINAL COMPARISONS

Differences between unbanded, classically stained chromosomes from species in different genera are difficult to interpret because the cumulative changes in chromosomes that were once homologous may now be so numerous

as to obscure the homologies. Nonetheless, an assessment of the extent of chromosomal variability within orders may indicate the cytogenetic mechanisms that operate at higher taxonomic levels in birds. I include in this analysis all orders for which more than one species has been studied. It is possible, therefore, for a single species to appear in this analysis, although it was excluded from the interspecific analysis for lack of a comparative partner. In the present study, I compare variations in the range of diploid numbers among orders of birds (Fig. 1).

RESULTS AND DISCUSSION

INTRASPECIFIC CHROMOSOME VARIABILITY

Of the nearly 300 species analyzed, only 16 show intraspecific chromosomal variability (Table 1). This should only be considered a first approximation of the true variability present within any avian species since no complete cytogenetic analysis of a *population* of any wild avian species has yet been undertaken. Only the White-throated Sparrow (n = 397, Thorneycroft 1976), the Dark-eyed Junco (n = 219, Shields 1973), and the Great Horned Owl (*Bubo virginianus*; n = 40, Biederman et al. 1979) have been studied in detail, and only in restricted portions of their breeding ranges. Hence, at present we know very little about the extent of chromosomal variability in any wild avian species.

Despite these limitations, the summary of intraspecific chromosomal variation in Table 1 reveals several interesting trends. For example, inversion polymorphisms of chromosomes 2 and 5 are widespread among juncos. Indeed, they were found in all nominal taxa that have been studied extensively. While the potential for transfer of polymorphic chromosomes between some taxa of juncos (e.g., *J. h. hyemalis* and *J. h. oreganus*) exists, lineages such as *J. hyemalis* and *J. phaeonotus* are morphologically distinct, reproductively isolated, and considered to be good species, even though they share polymorphisms for both of these chromosomes. Clearly, the chromosomal rearrangements in this genus had little or nothing to do with speciation within the group. At present we do not know what mechanisms maintain the polymorphisms in this taxon in the face of the meiotic incompatibilities that must exist in heterozygotes (Shields 1976). Rising and Shields (1980) have correlated the various forms of chromosomes (*morphs*) in the genus *Junco* with several phenotypic features that apparently are associated with habitat partitioning, particularly in winter when food may be limiting, but this associa-

TABLE 1. Intraspecific chromosomal variation in birds.

Order and species	English name	Chromosomal variation[a]	Reference
Passeriformes			
Junco hyemalis	Dark-eyed Junco	Floating pericentric inversions in chromosomes 2 and 5	Shields 1973
J. caniceps	Gray-headed Junco	Floating pericentric inversions in chromosomes 2 and 5	Shields 1973
J. phaeonotus	Yellow-eyed Junco	Floating pericentric inversions in chromosomes 2 and 5	Shields 1973
Zonotrichia albicollis	White-throated Sparrow	Floating pericentric inversions in chromosomes 2 and 3	Thorneycroft 1976
Spizella arborea	Tree Sparrow	Centric dimorphism in chromosome 6	Troy and Shields, unpubl.
Cardinalis cardinalis	Cardinal	Centric dimorphism in chromosome 5	Bass 1979
Carduelis chloris	Greenfinch	Centric dimorphism in chromosome 1	Hammar and Herlin 1975
Oriolus xanthornus	Black-headed Oriole	Translocation in chromosome 3 and a microchromosome	Ansari and Kaul 1979b
Bombycilla cedrorum	Cedar Waxwing	Centric dimorphism in chromosome 2	Thorneycroft 1968
Lonchura striata	White-rumped Munia	Centric dimorphism in chromosome 8	Ray-Chaudhuri 1976
L. malabarica	White-throated Munia	Centric dimorphism in chromosome 8	Ray-Chaudhuri 1976
L. punctulata	Spotted Munia	Translocation in chromosome 4 and a microchromosome	Ansari and Kaul 1978
Falconiformes			
Accipiter gentilis	Goshawk	Centric dimorphism in chromosome 1	de Boer 1976
Charadriiformes			
Vanellus vanellus	Lapwing	Centric dimorphism in chromosome 1	Hammar 1970
Columbiformes			
Treron phoenicoptera	Yellow-legged Green Pigeon	Centric dimorphism in chromosomes 1 and 2	Ansari and Kaul 1979a
Piciformes			
Megalaima zeylanica	Oriental Green Barbet	Translocation in chromosome 1 and a microchromosome	Kaul and Ansari 1979

[a] See glossary for definitions of terms.

tion has not been examined in wild populations.

If the rearrangement of chromosomes in juncos were associated with reproductive isolation, then I might have found populations in which specific chromosomal morphs were fixed. Indeed, I found none: inversions were floating in all populations that I analyzed. Evidently, the chromosome rearrangements in the genus *Junco* are maintained either by balanced polymorphism or frequency dependent selection, the mechanism of which is presently obscure, or by niche preference (Mayr 1954).

The White-throated Sparrow is polymorphic in plumage (Lowther 1961), behavior (Lowther 1962), and karyotype (Thorneycroft 1966, 1976). Lowther (1961) found that adult White-throated Sparrows in alternate (nuptial)

plumage could be divided into two distinct phenotypes; no sex linkage was evident. He used the color of the median crown stripe (white or tan) to describe the morphs. White-striped birds of either sex were more responsive to the playback of recorded song than were their tan-striped counterparts and mate selection was associated with plumage and behavioral polymorphisms: white-striped birds of either sex mated with tan-striped birds of the opposite sex. Tan-striped × tan-striped matings were rare and no white-striped × white-striped matings were noted (Lowther 1962).

Thorneycroft (1976) also described chromosomal polymorphism in two pairs of autosomes of the White-throated Sparrow (Table 1). Phenotype was correlated with karyotype: all white-striped birds in alternate plumage

TABLE 2. Chromosomal variation within 47 genera of birds.

Taxa	English name	2n[a]	f.n.[a]	Description[b]	Reference
Podicipediformes					
Podiceps grisegena	Red-necked Grebe	80	104		Shields, unpubl.
P. auritus	Horned Grebe	80	104	Identical	Shields, unpubl.
P. cristatus	Great-crested Grebe	78	104	Centric rearrangement in chromosome 12	Hammar 1970
Anseriformes					
Anser albifrons	White-fronted Goose	80	90		Hammar 1966
A. anser	Graylag Goose	80	90	Identical	Hammar 1966
A. cygnoides	Swan Goose	80	90	Identical	Hammar 1966
A. rossii	Ross's Goose	82	90		Chromosome Atlas 1975
A. caerulescens	Snow/Blue Goose	82	90	Identical	Chromosome Atlas 1975
Aythya americana	Redhead	80	84		Chromosome Atlas 1973
A. valisineria	Canvasback	80	84	Identical	Chromosome Atlas 1973
A. fuligula	Tufted Duck	80	84	Identical	Hammar 1966
A. ferina	European Pochard	80	84	Identical	Hammar 1970
A. affinis	Lesser Scaup	80	84	Identical	Shields, unpubl.
Aix galericulata	Mandarin Duck	84	84		Shoffner 1974
A. sponsa	Wood Duck	80	84	Centric fission-fusion in chromosomes 1 and 2	Chromosome Atlas 1973
Mergus merganser	Common Merganser	82	88		Hammar 1970
M. cucullatus	Hooded Merganser	82	88	Identical	Chromosome Atlas 1975
Anas platyrhynchos	Mallard	80	86		Chromosome Atlas 1973
A. strepera	Gadwall	80	86	Identical	Chromosome Atlas 1973
A. discors	Blue-winged Teal	80	86	Identical	Chromosome Atlas 1973
A. acuta	Pintail	80	86	Identical	Chromosome Atlas 1973
A. clypeata	Northern Shoveler	80	84	Centric rearrangement in chromosome Z	Chromosome Atlas 1973
Falconiformes					
Buteo jamaicensis	Red-tailed Hawk	68	110		Shoffner 1974
B. buteo	Common Buzzard	68	110	Identical	de Boer 1976
B. lagopus	Rough-legged Hawk	68	108	Centric rearrangement in chromosome 13	Bulatova 1977
Falco sparverius	American Kestrel	50	52		Shoffner 1974
F. tinnunculus	Common Kestrel	52	52	Centric fission-fusion in chromosome 1	Bulatova 1977
F. biarmicus	Lanner Falcon	52	54	Centric rearrangement in chromosome 7	de Boer 1976
F. chicquera	Red-headed Falcon	52	54	Identical	Jensen, pers. comm.
Gyps coprotheres	Cape Vulture	66	98		de Boer 1976
G. fulvus	Griffon Vulture	66	98	Identical	de Boer 1976
Haliaeetus vocifer	African Fish Eagle	66	112		de Boer 1976
H. albicilla	White-tailed Sea Eagle	66	106	Centric fission-fusion in chromosomes 7, 8, and 9	de Boer 1976
H. leucocephalus	Bald Eagle	66	106	Identical	Au and Soukup 1974
Galliformes					
Lophortyx gambelii	Gambel's Quail	80	84		Shoffner 1974
L. californicus	California Quail	80	84	Identical	Shoffner 1974
Gallus domesticus	Domestic Fowl	78	86		Chromosome Atlas 1971
G. gallus	Red Jungle Fowl	78	86	Identical	Chromosome Atlas 1971

TABLE 2.   Continued.

Taxa	English name	2n[a]	f.n.[a]	Description[b]	Reference
Gruiformes					
Anthropoides virgo	Demoiselle Crane	80	94		Takagi and Sasaki 1974
A. paradisea	Paradise Crane	80	94	Identical	Takagi and Sasaki 1974
Grus canadensis	Sandhill Crane	80	94		Takagi and Sasaki 1974
G. grus	Common Crane	80	94	Identical	Takagi and Sasaki 1974
G. japonenesis	Japanese Crane	80	94	Identical	Takagi and Sasaki 1974
G. vipio	White-naped Crane	80	94	Identical	Takagi and Sasaki 1974
G. antigone	Sarus Crane	80	94	Centric rearrangement in chromosome W	Takagi and Sasaki 1974
Charadriiformes					
Charadrius hiaticula	Ringed Plover	76	94		Hammar 1970
C. semipalmatus	Semipalmated Plover	76	90	Centric rearrangement in chromosomes 8 and 9	Shields, unpubl.
C. vociferus	Killdeer	76	88	Centric rearrangement in chromosomes 1 and 3	Chromosome Atlas 1973
Tringa totanus	Redshank	88	100		Hammar 1970
T. flavipes	Lesser Yellowlegs	88	96	Centric rearrangement in chromosomes 3 and 4	Shields, unpubl.
Larus canus	Mew Gull	70	88		Hammar 1966
L. ridibundus	Black-headed Gull	70	88	Identical	Hammar 1966
L. fuscus	Lesser Black-backed Gull	70	88	Identical	Hammar 1966
L. argentatus	Herring Gull	70	88	Identical	Itoh et al. 1969
L. marinus	Great Black-backed Gull	70	88	Identical	Ryttman et al. 1979
Sterna hirundo	Common Tern	68	88		Hammar 1970
S. paradisaea	Arctic Tern	70	88	Fission-fusion in chromosome 12	Hammar 1970
Columbiformes					
Columba livia	Rock Dove	80	92		Chromosome Atlas 1971
C. palumbus	Wood Pigeon	78	90	Reduction of two microchromosomes	Hammar 1966
C. cayennensis	Rufous Pigeon	76	92	Fusion to form chromosome 8	de Lucca and de Aguiar 1976
C. picazuro	Picazuro Pigeon	76	92	Identical	de Lucca and de Aguiar 1976
C. speciosa	Scaled Pigeon	76	92	Identical	de Lucca and de Aguiar 1976
Columbina talpacoti	Ruddy Ground-Dove	76	90		de Lucca and de Aguiar 1978
C. passerina	Common Ground-Dove	76	92	Fission-fusion in chromosome 8	de Lucca and de Aguiar 1978
C. minuta	Plain-breasted Ground-Dove	76	90	Fission-fusion in chromosome 7	de Lucca and de Aguiar 1978
C. picui	Picui Ground-Dove	76	80	Fission-fusion in chromosomes 2, 3, Z, 5, and 8	de Lucca and de Aguiar 1978
Leptotila rufaxilla	Gray-fronted Dove	76	90		de Lucca and de Aguiar 1976
L. verreauxi	White-fronted Dove	76	96	Centric rearrangement in chromosome 7; fusion to form chromosome 9; increase of two microchromosomes	de Lucca and de Aguiar 1976

TABLE 2.   Continued.

Taxa	English name	2n[a]	f.n.[a]	Description[b]	Reference
Psittaciformes					
Psittacula krameri	Rose-ringed Parakeet	68	80		Ray-Chaudhuri et al. 1969
P. alexandri	Moustached Parakeet	68	80	Identical	Ray-Chaudhuri et al. 1969
P. cyanocephala	Plum-headed Parakeet	66	80	Fission-fusion in chromosome 2	Ray-Chaudhuri et al. 1969
Strigiformes					
Strix nebulosa	Great Gray Owl	80	92		Biederman, pers. comm.
S. aluco	Tawny Owl	80	92	Identical	Hammar 1970
S. uralensis	Ural Owl	80	92	Identical	Takagi and Sasaki 1974
Asio otus	Long-eared Owl	82	90		Biederman, pers. comm.
A. flammeus	Short-eared Owl	82	90	Identical	Biederman, pers. comm.
Piciformes					
Picoides pubescens	Downy Woodpecker	92	96		Shields, unpubl.
P. villosus	Hairy Woodpecker	92	96	Fission-fusion in chromosomes 2 and 4	Shields, unpubl.
P. major	Great Spotted Woodpecker	108	112		Shields, unpubl.
P. minor	Lesser Spotted Woodpecker	108	112	Identical	Shields, unpubl.
Coraciiformes					
Coracias garrulus	Eurasian Roller	90	104		Bulatova 1977
C. benghalensis	Indian Roller	78	82	Homologies cannot be determined	Misra and Srivastava 1975
Passeriformes					
Tyrannidae					
Empidonax traillii	Willow Flycatcher	82	98		Shields, unpubl.
E. alnorum	Alder Flycatcher	82	98	Identical	Shields, unpubl.
E. flaviventris	Yellow-bellied Flycatcher	82	96	Centric rearrangement in chromosome 7	Shields, unpubl.
E. minimus	Least Flycatcher	82	100	Centric rearrangement in chromosomes 1, 3, 8, and 12	Shields, unpubl.
Corvidae					
Corvus corax	Common Raven	78	88		Chromosome Atlas 1973
C. brachyrhynchos	Common Crow	80	92	Centric rearrangement in chromosome Z; increase of two microchromosomes	Jovanovic and Atkins 1969
Paridae					
Parus major	Great Tit	78	92		Hammar 1970
P. palustris	Marsh Tit	78	92	Identical	Hammar 1970
Turdidae					
Turdus migratorius	American Robin	80	94		Jovanovic and Atkins 1969
T. merula	Blackbird	80	94	Centric rearrangement in chromosomes 8 and 9	Hammar 1970
T. pilaris	Fieldfare	80	88	Identical	Bulatova et al. 1971
T. iliacus	Redwing	80	92	Centric rearrangement in chromosomes 3 and 4	Bulatova et al. 1971
T. amaurochalinus	Creamy-bellied Thrush	80	88	Identical to *T. pilaris* and *Zoothera sibirica*	de Lucca 1974

TABLE 2.   Continued.

Taxa	English name	2n[a]	f.n.[a]	Description[b]	Reference
T. philomelos	Song Thrush	80	96	Fission-fusion in chromosomes 2, 3, and 4; centric rearrangement in chromosome 3	Bulatova et al. 1971
Zoothera sibirica	Siberian Ground Thrush	80	88	Centric rearrangement in chromosome 6	Itoh et al. 1969
Muscicapidae					
Erithacus calliope	Siberian Rubythroat	82	92		Ray-Chaudhuri 1976
E. svecicus	Bluethroat	82	92	Fission-fusion in chromosome 1	Ray-Chaudhuri 1976
Oenanthe oenanthe	Common Wheatear	82	94		Bulatova et al. 1971
O. isabellina	Isabelline Wheatear	82	94	Identical	Bulatova et al. 1971
Motacillidae					
Motacilla flava	Yellow Wagtail	78	94		Hammar 1970
M. alba	White Wagtail	82	94	Centric rearrangement in chromosomes 6, 7, and 8	Hammar and Herlin 1975
M. maderaspatensis	Large Pied Wagtail	80	96	Increase of two microchromosomes	Ray-Chaudhuri 1976
Anthus trivialis	Tree Pipit	82	100		Hammar and Herlin 1975
A. novaeseelandiae	Richard's Pipit	78	90	Centric rearrangement in chromosomes 3, Z, W, 7, 8, and 9	Ray-Chaudhuri 1976
Laniidae					
Lanius minor	Lesser Gray Shrike	76	90		Bulatova et al. 1971
L. schach	Black-headed Shrike	76	90	Identical	Bulatova et al. 1971
L. collurio	Red-backed Shrike	76	90	Identical	Bulatova et al. 1971
L. cristatus	Brown Shrike	77	88	Centric rearrangement in chromosomes 3 and 5; fission-fusion in chromosome 7	Ray-Chaudhuri 1976
Vireonidae					
Vireo olivaceus	Red-eyed Vireo	80	96		Shields, unpubl.
V. solitarius	Solitary Vireo	80	96	Identical	Shields, unpubl.
V. flavifrons	Yellow-throated Vireo	80	96	Identical	Shields, unpubl.
V. gilvus	Warbling Vireo	80	100	Centric rearrangement in chromosomes 8, 9, and 10	Shields, unpubl.
Ploceidae					
Passer domesticus	House Sparrow	76	94		Bulatova et al. 1973
P. hispaniolensis	Spanish Sparrow	76	90	Fission-fusion in chromosomes 7 and W	Bulatova et al. 1973
P. montanus	European Tree Sparrow	78	94	Fission-fusion in chromosomes 5, 6, and W	Castroviejo et al. 1969
Lonchura striata	White-rumped Munia	78	90		Ray-Chaudhuri 1976
L. punctulata	Spotted Munia	78	94	Centric rearrangement in chromosomes 6 and 7	Ansari and Kaul 1978
L. malacca	Chestnut Munia	80	94	Fission-fusion in chromosome 6	Ray-Chaudhuri 1976
L. malabarica	White-throated Munia	80	94	Identical	Ray-Chaudhuri 1976
Pycnonotidae					
Pycnonotus cafer	Red-vented Bulbul	80	90		Ray-Chaudhuri 1976
P. jocosus	Red-whiskered Bulbul	82	94	Centric rearrangement in chromosome 6; increase of two microchromosomes	Ray-Chaudhuri 1976

TABLE 2. Continued.

Taxa	English name	2n[a]	f.n.[a]	Description[b]	Reference
Emberizidae					
Emberiza citrinella	Yellowhammer	80	94		Bulatova et al. 1973
E. leucocephala	Pine Bunting	80	94	Identical	Bulatova et al. 1973
E. flaviventris	Golden-breasted Bunting	80	92	Centric rearrangement in chromosome 3	Bulatova et al. 1973
E. hortulana	Ortolan Bunting	80	92	Identical	Bulatova et al. 1973
Junco hyemalis	Dark-eyed Junco	82	96		Shields 1973
J. phaeonotus	Yellow-eyed Junco	82	96	Standard karyotypes identical	Shields 1973
J. vulcani	Volcano Junco	82	96	Standard karyotypes identical	Shields 1973
Zonotrichia albicollis	White-throated Sparrow	82	104		Thorneycroft 1976
Z. leucophrys	White-crowned Sparrow	82	102	Centric rearrangement in chromosomes 3, 5, and 12	Shields, unpubl.
Fringillidae					
Carpodacus mexicanus	House Finch	80	96		Shields, unpubl.
C. erythrinus	Common Rosefinch	80	94	Centric rearrangement in chromosome 9	Bulatova 1973
Carduelis chloris	Greenfinch	80	94		Hammar and Herlin 1975
C. canabina	Eurasian Linnet	82	94	Centric rearrangement in chromosome 2; fission-fusion in chromosome 7	Bulatova 1973
C. spinus	Eurasian Siskin	80	86	Centric rearrangement in chromosome 3	Bulatova 1973
C. flammea	Common Redpoll	78	100	Centric rearrangement in chromosomes 8, 9, 10 and 11	Shields, unpubl.
Rhodopechys mongolica	Mongolian Trumpeter Finch	80	94		Bulatova 1973
R. githaginea	Trumpeter Finch	78	92	Fission-fusion in chromosome 4	Bulatova 1973

[a] 2n = diploid number; f.n. = fundamental number.
[b] Identical = no difference in the number or morphology of chromosomes of this species and the first species of the same genus listed in the table; standard karyotype = karyotype to which all others are compared. See the glossary for definitions of other terms.

possessed a single 2^m chromosome; tan-striped birds in alternate plumage lacked this autosome. This correlation was absolute and karyotype could be predicted from the color of the coronal stripe.

Morph types for chromosomes 2 and 3 in the White-throated Sparrow appear to be maintained as balanced polymorphisms. Plumage and behavioral polymorphisms based on chromosomal polymorphism promote selective breeding and maintain heterozygosity. However, chromosomal rearrangements in this species do not promote reproductive isolation and speciation.

The presence of identical polymorphisms of chromosome 8 in species of munia (*Lonchura* spp.; Table 1) may reflect a situation similar to that in juncos, but again no detailed population studies exist. Similarly, all Greenfinches are heterozygous for the dimorphic forms of chromosome 1 (Hammar and Herlin 1975). The presence of only heterozygotes in the population suggests that some form of heterosis or hybrid vigor is operating, but the differential survival of individual Greenfinches has not yet been studied to determine if this is the case.

As illustrated by Table 1, intraspecific chromosomal variability appears to be widespread among birds and the general contention that all avian karyotypes are extremely conservative in a phylogenetic sense (Takagi and Sasaki 1974) may be an overstatement. This is particulary apparent when we realize that most descriptions of avian karyotypes are based on only one or a few individuals and that analysis
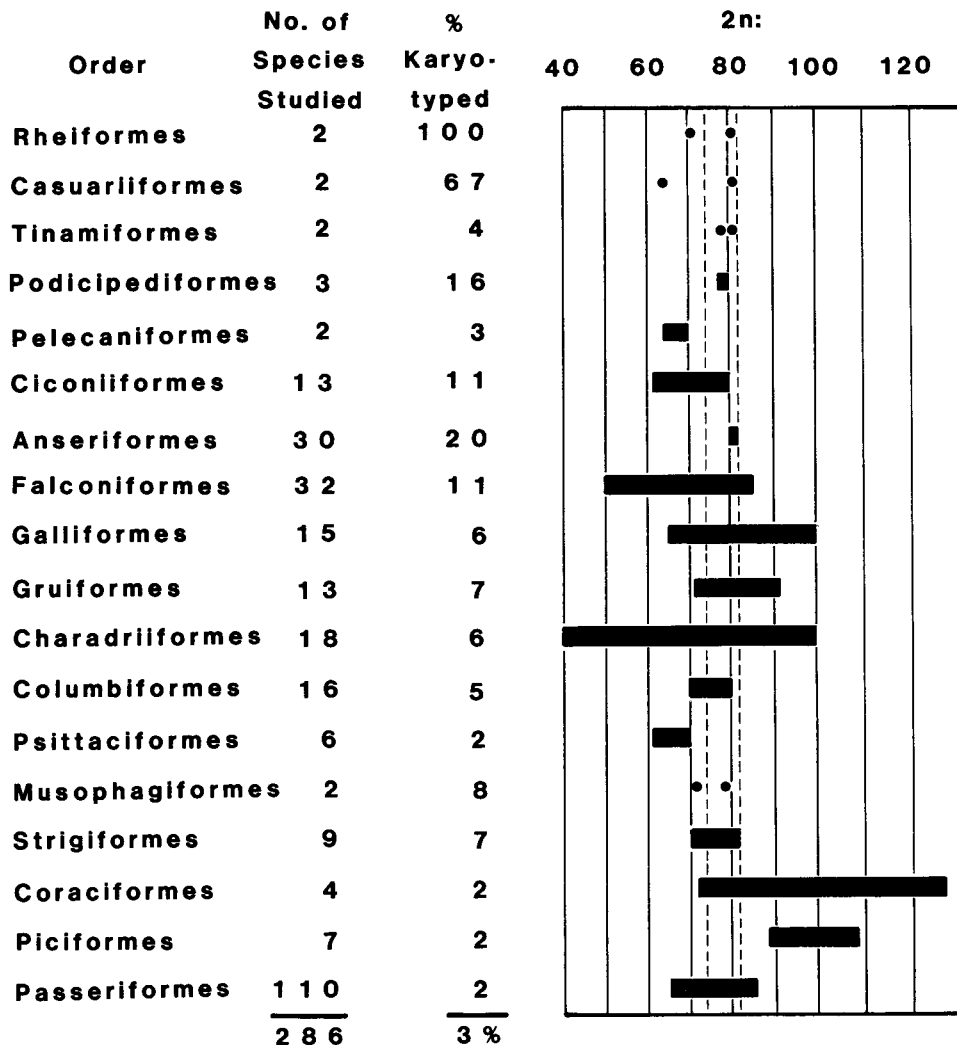
Order	No. of Species Studied	% Karyo- typed	2n:				
			40	60	80	100	120
Rheiformes	2	100					
Casuariiformes	2	67					
Tinamiformes	2	4					
Podicipediformes	3	16					
Pelecaniformes	2	3					
Ciconiiformes	13	11					
Anseriformes	30	20					
Falconiformes	32	11					
Galliformes	15	6					
Gruiformes	13	7					
Charadriiformes	18	6					
Columbiformes	16	5					
Psittaciformes	6	2					
Musophagiformes	2	8					
Strigiformes	9	7					
Coraciformes	4	2					
Piciformes	7	2					
Passeriformes	110	2					
	286	3%					

FIGURE 1.   Range of variation in the chromosome number among avian orders. About 60% of all species that have been studied possess chromosome numbers between 78 and 82 (hatched vertical lines). % karyotyped = percent of the species in each order that have been karyotyped.

of variation is restricted generally to the macrochromosomes. Moreoever, several lineages exhibit multiple chromosomal polymorphisms (*Junco, Zonotrichia,* and *Treron*). Furthermore no polymorphism for any chromosome has been found in the fixed condition in any population of an avian species. The data currently available give no evidence that intraspecific chromosomal variability leads to reproductive isolation and subsequent speciation.

Some avian lineages, however, do not exhibit multiple chromosomal polymorphisms. Biederman (pers. comm.) has carefully analyzed Giemsa (G) and centromeric (C) bands on the chromosomes of 40 Great Horned Owl chicks from 25 nests: he has found no chromosomal variability of any kind.

INTERSPECIFIC CHROMOSOME VARIABILITY

Seventy-eight of the possible 177 species in pairs in Table 2 have identical karyotypes. From these data alone, one might argue that chromosomal change does not accompany avian speciation, since so many good biological species of birds possess identical karyotypes. This is probably true, and in cases where chromosomal variation between species is present, it may have developed after the reproductive isolation of the lineages rather than in the speciation process. It is clear, however, that many avian genera contain species with identical karyotypes, e.g., *Aythya, Grus, Larus, Strix,* and *Asio*. In a recent study of the G and C bands on chromosomes, Ryttman et al. (1979) found that the karyotypes of the Lesser

and Greater Black-backed gulls, Herring Gulls, and Mew Gulls were identical.

Biederman (pers. comm.) has also recently shown that the G-bands on the chromosomes of the Great Horned Owl, the Snowy Owl (*Nyctea scandiaca*), and the Long- and Short-eared owls are identical. In other words, species within *different avian genera* also appear to possess identical banding sequences. Chromosomal rearrangement has apparently played little or no role in the speciation of these groups.

Most interspecific chromosomal variability among birds is minor when compared to the rather bizarre variability found in some mammals. The Assam muntjac deer (*Muntiacus muntjak vaginalis*), for example, has a diploid number of 6 (♀) or 7 (♂) whereas the Chinese muntjac (*M. reevesi*) has a diploid number of 46 (Wurster and Benirschke 1970). In contrast, the greatest interspecific variation between karyotypes in the present study is between the Eurasian Roller, in which the diploid number is 90, and the Indian Roller, whose diploid number is 78. These differences presumably involve changes in the number of microchromosomes. However, the validity of these diploid numbers is suspect, particularly since they were determined by different authors. Interspecific chromosomal variation nevertheless does not appear to be extensive among birds.

ORDINAL COMPARISONS

My ordinal comparisons are summarized in Figure 1. The most noteworthy information in this figure concerns the waterfowl (Anseriformes), which are characterized by extreme karyotypic conservatism. Among the 30 species studied, diploid numbers range from 80 to 84. (Extreme chromosomal conservatism within this group was detected at all levels of analysis.) No other reasonably well studied avian lineage exhibits such marked karyotypic conservatism. The propensity of waterfowl to hybridize naturally may be based in part upon the extreme similarity of their karyotypes. Interestingly, ducks of the genus *Aix* apparently do not form natural hybrids. Not surprisingly, those for which karyotypes are known have two macrochromosomal characteristics not found in other ducks.

The other orders in Figure 1 that appear to exhibit karyotypic conservatism have not been well studied and I am reticent to speculate on trends in their chromosomal evolution based on the fragmentary data currently available.

De Boer (1976) summarized evolutionary trends in the karyotypes of Falconiformes. Species of *Falco* are characterized by extremely low diploid numbers (50–52) and by low fundamental numbers (52–54); only chromosome 1 is biarmed. On the other hand, 14 genera of the family Accipitridae have moderately high diploid numbers (60–80) and very high fundamental numbers (98–128). Accipiters appear to be atypical among birds in that most of their chromosomes are biarmed. Such extreme dissimilarity in the karyotypes of two families within the same order is found in no other avian lineage, and its significance is unclear. However, it may bear on the question of whether the Falconiformes are monophyletic or polyphyletic. If karyotypes were the sole criterion (upon which determinations of phylogenies were based) one might justifiably split Falconiformes into two orders, as suggested by Voous (1972) on anatomical grounds.

The order Charadriiformes is considered extremely diverse on morphological grounds, and karyotypes within the order show similar diversity (Table 2). For example, the diploid number of the Stone Curlew (*Burhinus oedicnemus*) is 40 (Bulatova et al. 1971), while that of the Common Snipe (*Gallinago gallinago*) is 98 (Hammar 1970). The range of diploid numbers (40–98) within this order is unparalleled.

The order Coraciiformes is also considered a diverse lineage. Unfortunately, the karyotypes of only four species from three of the nine families are known. Species of the genus *Coracias* possess moderately high diploid numbers, but that of the Hoopoe (*Upupa epops*) is 126 (Misra and Srivastava 1975), the highest diploid number reported for any bird.

The karyotypic variability shown by species of Passeriformes at the specific and generic levels (Tables 1 and 2) is not present at familial and ordinal levels, even though more than one-third of the avian species that have been karyotyped are passerines.

PHYLOGENETIC IMPORTANCE OF CHROMOSOMAL CHANGES

Chromosomal rearrangements are of two types: those that increase the fitness of the heterozygote above that of both homozygotes (a situation apparently present in juncos and White-throated Sparrows) and those that lead to a decrease in the fitness of the heterozygote, but to a high degree of fitness in each homozygote (White 1978). Rearrangements of the latter type may be divisive agents in natural populations, and may lead to a speciation event. However, in view of currently accepted theory, it is difficult to see how such rearrangements could survive, since initially, at least, only heterozygotes would be formed and they would be selected against (see Mayr 1970:311–319). The severity of selection

against newly arisen chromosomal heterozygotes is currently being questioned (White 1978, Baker 1979, Baker and Bickham 1980, Bengtsson 1980, and Bickham and Baker 1980) and the innumerable cases of chromosome differences between closely related vertebrate species should be grounds enough for us to seriously consider the suggestion that chromosomal rearrangements can undergo fixation, to the homozygous state, in association with a speciation event.

The data presented here do not indicate that chromosomal change plays a major role in the speciation process of birds. Rather, chromosomal variability within local populations appears to be associated with mechanisms that promote either balanced polymorphism or frequency-dependent selection. Karyotypic differences among species of the same genus do not appear widespread in birds, and large numbers of congeneric species frequently have identical karyotypes (Table 2). Moreover, it is not known whether karyotypic variability between species was an integral factor promoting the initial reproductive isolation that preceded speciation or whether it developed after the speciation event. More detailed studies may indicate that chromosomal change is important in avian speciation, but the evidence accumulated to date does not suggest this. That the speciation process is not always accompanied by major chromosomal change is supported by recent work on bats (Baker and Bickham 1980). Thirty-four of 54 congeneric species showed no chromosomal rearrangements when subjected to detailed analyses of G and C banding. These studies merely postdate similar evidence from homosequential species of *Drosophila* (Carson et al. 1970), which cannot be distinguished on the basis of the detailed natural banding of their polytene interphase chromosomes, but are often strikingly different in phenotype. Their close relationship would never have come to light had their chromosomes not been studied.

In a series of studies, Wilson et al. (1974, 1975) and Bush et al. (1977) assessed rates of chromosome change in vertebrate lineages other than birds. They computed a nearly 100-fold difference in the rate of chromosomal change between the rapidly evolving horses, genus *Equus,* and several genera of salamanders that appeared to be conservative in their rate of karyotypic change. Further, they suggested that genetic drift may function in the rapid fixation of novel chromosomal rearrangements, particularly in lineages that have well developed social organizations and breed within small demes. Unfortunately, we cannot test this hypothesis with birds because we lack both detailed data on effective deme sizes and an accurate fossil record with which to date various lineages, particularly those of recent origin (e.g., Passeriformes).

An alternative hypothesis (Bickham and Baker 1979) suggests that the karyotype is important phylogenetically, that there is an optimal karyotype for each adaptive zone, and that it can evolve through chromosomal rearrangements. Consequently, when an organism invades a new adaptive zone there will be a period of karyotypic change that continues until the optimum or near optimum karyotype develops. Thereafter, change will be primarily by genic and morphological mechanisms, not chromosomal rearrangements. Implicit in this "canalization model" for chromosomal evolution is the postulate that the taxonomic level at which chromosomal variation occurs is a function of the evolutionary time that a lineage has occupied an adaptive zone. Further, the model suggests that most chromosomal evolution is phyletic or anagenic, and that a chromosomal mutation can become characteristic of a lineage without necessarily producing sister species. That is, the model is not primarily concerned with the role of chromosomal change as an isolating mechanism in the speciation process. It emphasizes the adaptive nature of the karyotype, whereas previous models have placed emphasis on chance events that permit chromosomal evolution.

Avian chromosomal data are consistent with the canalization model. Karyotypic conservatism (no obvious chromosomal variation) characterizes groups that are believed to be phylogenetically old (e.g., owls, cranes, falcons, accipiters, and waterfowl). Conversely, taxa that are currently undergoing adaptive radiation and are believed to be phylogenetically young (e.g., the passerines) are karyotypically variable, particularly at lower taxonomic (genus and species) levels. However, ages of avian lineages are difficult to determine and the number of avian species that has been karyotyped is still small.

Analyses of banding patterns on the chromosomes of turtles (Bickham 1981) indicate that such chromosomal rearrangements as centric fusions, pericentric inversions and interchanges develop during the diversification of families. In contrast, the types of rearrangements that accompany speciation are mostly heterochromatic additions. Thus, in turtles, not only do the rates of karyotypic evolution differ, but the kinds of chromosomal rearrangements also differ with the evolution of various taxonomic divisions. More detailed banding studies in birds will help to determine if similar trends are also present in this class.

Bengtsson (1980) used the standard deviation of the chromosome numbers within a mammalian genus as an estimate of the rate of karyotypic evolution. He concluded that the rate of karyotypic evolution was greater in small mammals than in larger ones, and in the genera with many taxa in contrast to genera with fewer taxa. He argued that the disadvantageous effects of chromosomal mutation must be strongest in animals that can mate only periodically (e.g., once a year) and produce only one or a few offspring at a time. However, body size and reproductive potential (i.e., age at first breeding and brood size) are most certainly interrelated and it is difficult to separate the effects of each.

Nonetheless, the present study also indicates that avian taxa of large body size and small brood size tend to be karyotypically conservative (e.g., cranes, hawks). However, the avian data do not support Bengtsson's contention that large brood size is associated with karyotypic variability. For example, most species of Anseriformes and Galliformes have large broods, yet these lineages are characterized by extreme karyotypic conservatism.

Karyotypic descriptions are available for only about 3% of all extant avian species (Fig. 1). I am aware of no data concerning 114 of the 174 avian families. Clearly, there is much work to be done. I hope that this synthesis of available data will encourage greater activity in this long-neglected field of avian biology.

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GLOSSARY

arm ratio—ratio of the length of the short arm of a chromosome to the long arm of the same chromosome.

autosome—a chromosome that is not involved with sex determination.

balanced polymorphism—an equilibrium mixture of homozygotes and heterozygotes maintained by separate and opposing forces of natural selection.

banding of chromosomes—any of a variety of procedures (generally in common use since 1968) that produce characteristic and reproducible lateral bands along the length of chromosomes.

centric dimorphism—homologous chromosomes whose centromeres are in different locations.

centric fission—breakage of a chromosome through the centromere resulting in an increase of chromosome number by one.

centric fusion—the joining of the centromeres of two nonhomologous chromosomes resulting in a decrease of chromosome number by one.

centric rearrangement (or *shift*)—insertion of the centromere region of a chromosome into a noncentromeric region of the same chromosome. Three chromosome breaks are required to produce such a rearrangement.

centromere—the region of a chromosome to which spindle fibers attach.

centromeric (*C*) *bands*—regions of a chromosome that contain constitutive heterochromatin.

constitutive heterochromatin—that type of deoxyribonucleic acid (DNA) which is in a constant state of inactivation.

diploid number—the normal double set (2n) of chromosomes in an individual derived from a fertilized egg.

floating rearrangement—condition in which ancestral homozygotes, derived homozygotes and heterozygotes for a chromosome change are present in a population.

fixed rearrangement—condition in which only ancestral and derived homozygotes for a chromosome change are present in a population. No heterozygotes are present.

fundamental number—the total number of chromosome arms in a diploid nucleus.

Giemsa (*G*) *bands*—regions of a chromosome revealed by exposing it to trypsin followed by Giemsa stain.

heterozygote—an individual whose homologous chromosomes have different alleles for a genetic trait or differ from one another morphologically.

homosequential species—species whose polytene chromosomes have identical banding patterns.

homozygote—an individual whose homologous chromosomes have the same alleles for a genetic trait.

interchange—a chromosome rearrangement involving separate breaks in two nonhomologous chromosome arms with reciprocal restitution.

inversion—a chromosome rearrangement involving two breaks with 180° rotation and restitution.

karyotype—a characterization of an entire set of chromosomes of an individual with regard to their number, size and shape.

macrochromosomes—those chromosomes of birds that are consistently recognizable. They are generally from 2–10 μm in absolute length.

microchromosomes—those chromosomes of birds that are not consistently recognizable. They are generally less than 2 μm in absolute length.

nucleolar organizer region—the area of the chromosome that codes for transcripts of ribosomal ribonucleic acid (rRNA).

pericentric inversion—inversion of a chromosome which includes the centromere.

polytene chromosomes—those chromosomes of certain dipteran insects which are multiply replicated, and hence at interphase exhibit a natural differential banding pattern along their length.

translocation—same as "interchange."

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RECENT PUBLICATIONS

Polynyas in the Canadian Arctic.—Edited by Ian Stirling and Holly Cleator. 1981. Occasional Paper No. 45, Canadian Wildlife Service. 70 p. Paper cover. Source: Minister of Supply and Services [Ottawa, Canada]. Polynyas are areas of open water surrounded by ice, some of which appear in the same locations each year. This volume contains five reviews of subjects pertaining to the biological importance of polynyas in the Canadian Arctic. The first three concern their distribution, physical causes, and their use by marine mammals. There follow articles on the significance of polynyas to arctic colonial seabirds (by R. G. B. Brown and David N. Nettleship) and to sea ducks (by R. W. Prach, H. Boyd, and F. G. Cooch). They are valuable for bringing together currently available information, pointing out gaps in our knowledge, and calling attention to the potential threats posed by recent human activities in the arctic. Illustrations, lists of references.

New Studies of Tropical American Birds.—Alexander F. Skutch. 1981. Publications of the Nuttall Ornithological Club, No. 19. Cambridge, MA. 281 p. $29.50. Source: N. O. C., c/o Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138. This book contains 27 life histories of birds ranging from doves to tanagers. Five of them are wholly new and the rest are updated from accounts that Skutch published years ago. The studies concentrate on describing nesting habits and nestlings, yet variously treat food, voice, behavior, and other aspects, according to the author's experience with each species. They take their place with his many earlier reports in providing a mine of sound information on the biology of birds in Central America. Collectively, they are unmatched in the literature of any other tropical avifauna. This book is illustrated with several nice wash drawings by Dana Gardner, unfortunately in monochrome rather than color. List of references, index.