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KARYOTYPIC UNIFORMITY IN THE RED-WINGED BLACKBIRD

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ABSTRACT.—Karyotypes of 52 Red-winged Blackbirds (*Agelaius phoeniceus*) from four widely separated populations were analyzed for possible regional differences in diploid numbers ($2n$) and in the sizes and shapes of the seven largest chromosomes. G-banded karyotypes for a subset of these individuals were compared to assess the banding homology between two of the populations. Results thus far indicate that Red-winged Blackbirds are karyotypically invariant across much of their geographic range and have an estimated $2n$ of 76.

The recent discoveries of intraspecific chromosome polymorphisms in several avian species (Thorneycroft 1966, 1976; Shields 1973, 1982; Ansari and Kaul 1979a, b; Bass 1979; Kaul and Ansari 1979) have generated considerable new interest in avian cytogenetics. Therefore, the once common notion that birds are karyotypically conservative organisms (Ohno et al. 1964, Takagi and Sasaki 1974) needs to be reevaluated, especially in relation to recent speculation on the role that chromosomal polymorphisms may play in speciation processes (White 1978, but see Shields 1982).

Intraspecific chromosomal variation may be more common in birds than is presently recognized. In order to detect such variation, one must sample the karyotypes of many individuals. Most avian karyotypes, however, have been determined from too few individuals to yield information about intraspecific variation. Consider a hypothetical example in which an avian species possesses a pair of chromosomes with two different morphologies because of a pericentric inversion. If the polymorphism exists in Hardy-Weinberg equilibrium with relative frequencies of $p = 0.8$ and $q = 0.2$ for the two morphs, then one may use a binomial distribution to calculate the probability of not detecting the lower- (or higher-) frequency morph at given sample sizes. In this example, most of the individuals (p^2 or 64%) are homozygous for the higher-frequency morph and thus yield no information about the presence or absence of any intraspecific polymorphism. The remaining 36% ($2pq$ or 32% + q^2 or 4%) exhibit the polymorphism in either the hetero- or homozygous condition. If repeated samples of five individuals were karyotyped in this species, then the chromosomal polymorphism would be undetected in slightly over 10% of the samples (the exact probability is $[0.64]^5 = 0.1074$). Because even five individuals are an unusually large sample in many avian cytogenetic studies, many of the 556 avian species so far karyotyped (de Boer 1983) may harbor undetected chromosomal polymorphisms.

In addition, banded chromosomes can show differences that are not evident in standard karyotypes (Mateescu et al. 1974, Pollock and Fechheimer 1981, Shields 1983). In a recent review of avian cytogenetics, Shields (1982) contended that karyotypic variability has not been satisfactorily assessed in any avian species studied to date, regardless of the number of individuals karyotyped. He argued that detailed C- and G-banded karyotypes are seldom used, and in no instance have current techniques been used to karyotype several individuals from different populations within the geographic range of a species.

We present here the results of an extensive karyological study of the mitotic chromosomes of the Red-winged Blackbird (*Agelaius phoeniceus*). Between 9 and 20 individual birds from each of four widely separated breeding populations were analyzed for differences in the sizes and shapes of the seven largest chromosomes (hereafter referred to as "macrochromosomes") and also for differences in diploid chromosome numbers ($2n$). A subset of these karyotypes was G-banded for comparisons of banding homologies between two populations. The Red-winged Blackbird has considerable morphological size and shape variation across its North American range (Power 1970, James 1983), with 14 subspecies recognized by the American Ornithologists' Union (1957). The extent to which this phenotypic variation covaries with genetic variation (either chromosomal or electromorphic) is unknown, but such information is crucial to understanding evolutionary processes in this species, as well as other avian species. Although chromosomal morphology is just one aspect of the total genetic constituency of any

organism, correlations of phenotypic characters with certain chromosomal morphs have been found in species shown to have intraspecific chromosome polymorphisms (Rising and Shields 1980). Chromosomal data are, therefore, a logical starting point for studying the covariation of genetic and morphological characters in the Red-winged Blackbird.

METHODS

Individual Red-winged Blackbirds from populations in Larimer Co., Colorado, Clearwater Co., Minnesota, and Dade and Leon counties, Florida, were collected with mist nets or as nestlings during the breeding seasons (April–July) of 1980–1982. The populations from Colorado and Dade Co., Florida, exhibit the extremes of adult morphological size and shape variation for this species within the contiguous United States (Power 1970, Mosimann and James 1979).

Spreads of somatic chromosomes were prepared by two in vivo methods: a modified version of Patton's (1967) bone-marrow technique and a feather-pulp technique developed by Shoffner et al. (1967). In the modified bone-marrow procedure, birds were injected intraperitoneally with a 0.05% colchicine solution (0.1 ml/15 g body weight). We killed them 1.5 h later and removed their femora and tibiotarsi, which we flushed with 0.8% sodium citrate preheated to 37°C. The resulting cell suspensions were incubated at 37°C for 27 min, centrifuged, and then fixed in a 3:1 (v/v) solution of methanol and acetic acid for 15 min. We changed the fixative twice before dropping the cell suspension onto slides and allowing them to air dry overnight. We then stained them with a 6% Giemsa solution (buffered with Sörensen phosphate buffer to pH 7.0) for 12 min. The feather-pulp method of Shoffner et al. (1967) was used without modification. Staining procedures were those described for the bone-marrow technique.

G-banded karyotypes were prepared using the trypsin method of Seabright (1971) as modified by Shoffner et al. (1979). Ten-day-old slides were immersed in 50 ml 0.9% NaCl solution containing trypsin for 2–3 min, then dipped in 0.9% NaCl solution lacking trypsin, flushed twice with distilled water, and stained as above.

Photomicrographs of the sets of chromosomes in two cells per individual were made using a Zeiss automatic microscope. Five additional cells per individual were used to estimate diploid numbers ($2n$). Karyotypes were prepared from one photomicrograph per individual, selected from the two available photomicrographs by coin toss. All of the photomicrographs were enlarged to a standard size beforehand. We then arranged the chromosomes in order of decreasing size.

To detect possible intraspecific differences among localities, we made statistical comparisons of the size and shape of the seven macrochromosomes, including the Z chromosome. One homolog, selected by coin toss, was used for the size measurement and the other for the shape measurement. In the heterogametic females, the single Z chromosome was used for both measures. The size of a chromosome was its proportion of the sum of the lengths of all seven chromosomes, calculated from measurements to the nearest 0.05 mm with dial calipers. This method was used by Shoffner et al. (1979) to detect subtle differences in chromosome lengths between congeneric species of geese. The shape of a chromosome was the same ratio of the arm lengths that is commonly used to standardize centromere terminology (Levan et al. 1964). Log transformations of these shape measurements (log long-arm length minus log short-arm length) were made for statistical tests of geographical differences in the morphology of the macrochromosomes (see appendix of Mosimann and James 1979). The karyotypes of individuals whose nestmates were also karyotyped were eliminated from the statistical analysis. Selection among siblings of the karyotype to be used in statistical tests was made randomly by coin toss or by a draw of numbers. We used this procedure so that estimates of regional chromosomal variation would not be biased by sibling relationships.

RESULTS

Fifty-two individuals (9–20 from each locality; see Table 1) were karyotyped, but eight were eliminated from statistical analyses because of sibship constraints. The standard female karyotype (Fig. 1) had a $2n$ of 76 and included a hypothetical W chromosome, which was indistinguishable from many of the microchromosomes. The karyotype may be described as follows using the centromeric terminology of Levan et al. (1964). The largest pair of autosomal chromosomes was submetacentric. The next four autosomal pairs were subtelocentric. Chromosome pair number 5 had an arm ratio of 0.09 (Table 2) with a standard deviation of 0.02. This pair was borderline between subtelocentric and telocentric according to the indices of Levan et al., by which chromosomes with arm ratios of 0.1 or less are considered telocentric. Hobart et al. (1982) and Makino and Baldwin (1954) considered this chromosome to be subtelocentric. The remaining autosomal complement appeared to be acrocentric with chromosomes varying in size. The Z

TABLE 1. Distribution of samples of Red-winged Blackbirds by site and sex. Numbers in parentheses represent the number of individuals eliminated in statistical analyses because of sibship (see Methods).

Site	Male	Female	Total
Larimer Co., CO	5	5	10 (1)
Leon Co., FL	12	8	20 (3)
Dade Co., FL	4	5	9 (2)
Clearwater Co., MN	6	7	13 (2)
Total	27	25	52 (8)

chromosome was subtelocentric and the fourth largest in size when compared to the autosomal chromosomes.

No geographical differences were apparent in the first seven macrochromosomes (Fig. 2). In fact, 14 analyses of variance (ANOVAs) indicated no statistically significant regional differences in either the size or the shape of these chromosomes (Table 2). The karyotypes of siblings that we excluded from the statistical comparisons appeared to be identical to those in Figure 2.

Almost half (47%) of the cells that we analyzed had 76 pairs of chromosomes. Only four cells had larger diploid numbers. One cell had a $2n$ of 68, but most estimates lower than 76 were between 72 and 75. There were no significant between- or within-locality variations in $2n$ (one-way ANOVA, $F_{3,40} = 0.87$; $P = 0.45$).

G-banded karyotypes for the largest six chromosomes were obtained from three individuals of Leon Co., Florida, and two individuals of Clearwater Co., Minnesota. As with the standard karyotypes, chromosomal banding patterns did not appear to differ among individuals from these areas (Fig. 3).

DISCUSSION

METHODOLOGY

The feather-pulp method first suggested by Sandes (1954) and refined by Shoffner et al. (1967) is a relatively quick and easy method of obtaining high-quality C-metaphase chromosome spreads for birds. Samples do not have to be centrifuged as they do in the bone-marrow and in vitro culture methods; consequently samples can be collected easily in field situations and birds can be released unharmed after sampling. The mitotic index for nestling birds just acquiring feathers is dramatically lower than that of adult birds, but the few C-metaphase cells present in nestling feathers may make this technique feasible for sex determination. However, the method requires that developing feathers be present. In adults, if no developing feathers are present they can be easily induced to form by removing a few fully grown feathers. In Red-winged Blackbirds, for example, developing feathers are at an appropriate stage for analysis as early as five to eight days after the removal of preformed feathers. Consequently, the procedure of Shoffner et al. (1967) may be used when aviary space is available or when individuals such as territorial males can be easily recaptured.

Unfortunately, the quality of G-band karyotypes differs in feather-pulp and bone-marrow spreads. At present, bands in feather-pulp preparation are less distinct than those in the bone-marrow spreads. Minor modifications of either the feather-pulp or G-banding methods may alleviate this problem.

One traditionally useful procedure that we did not use for chromosomes in this study was C-banding. This technique defines areas rich in constitutive heterochromatin (Brutlag 1980). Although C-bands may vary among Red-winged Blackbirds, we feel that intraspecific variation in the macrochromosomes is unlikely or has questionable evolutionary importance for three reasons. First, birds generally contain smaller amounts of the repetitive DNA associated with constitutive heterochromatin than do C-band-variable mammalian species (Comings and Maltoccia 1972). Consequently, C-band variation is less likely to exist. Second, mammalian species with intraspecifically variable C-bands usually also exhibit some corresponding variation in their

TABLE 2. Average size (proportional length) and shape (log long-arm length minus log short-arm length) of the seven largest chromosomes of Red-winged Blackbirds (sample size = 44) from breeding populations in Colorado, Minnesota, and Florida.

	Chromosome number						
	1	2	3	4	5	6	Z
Average proportional length	0.22	0.19	0.17	0.10	0.09	0.08	0.14
P-values*	0.64	0.54	0.38	0.45	0.76	0.32	0.55
Average arm ratio	0.64	0.23	0.20	0.37	0.09	0.02	0.27
P-values*	0.57	0.43	0.39	0.52	0.67	0.63	0.18

* The *P*-values indicate the lowest level of significance at which the hypothesis of no difference in chromosome size or shape can be rejected by an analysis of variance with 3,40 degrees of freedom. These *P*-values indicate that there are no statistically significant regional differences in the size or shape of these seven chromosomes.

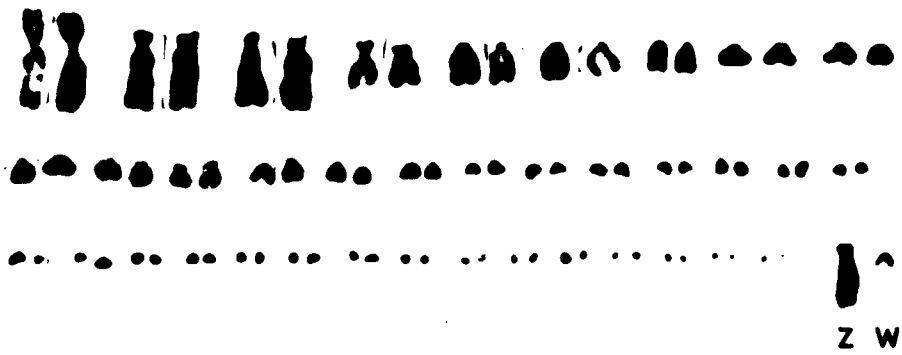

FIGURE 1. Standard karyotype of a female Red-winged Blackbird (*Agelaius phoeniceus*) collected in Leon Co., Florida. The estimated diploid chromosome number for this species is 76. The true W chromosome could be a different microchromosome from the one placed next to the Z chromosome.

standard karyotypes (Duffey 1972, Pathak et al. 1973), something that we did not find among Red-winged Blackbirds. Finally, the C-band variation described for *Gallus gallus*, var. *domesticus*—cytogenetically the best-studied avian "species"—is extremely variable (Pollock and Fechheimer 1981), even in the C-band patterns between different cells of single individuals. Thus, even if C-band variation were detected in Red-winged Blackbirds, it might not have an underlying genetic basis. The C-band procedure could, however, be used to identify the W chromosome of females (Wang and Shoffner 1974).

The estimates of chromosome size and shape used in this study are only approximations of karyotypic diversity. Nonetheless, they do provide a reasonable basis for determining the similarity between standard karyotypes of different individuals. We feel that for some cases of putative chromosomal similarity (and dissimilarity) the use of such quantifiable estimates of chromosomal shape must be interpreted carefully. One particularly disturbing quality of the ratio estimate used in this study is its potential violation of certain independence assumptions for error estimates. The correlation between the standard error of a ratio estimate for a particular chromosome and relative chromosome length is −0.57. This

FIGURE 2. Representative female karyotypes for the seven largest chromosomes of *A. phoeniceus* from four localities: *A*, Leon Co., Florida; *B*, Dade Co., Florida; *C*, Larimer Co., Colorado; and *D*, Clearwater Co., Minnesota.

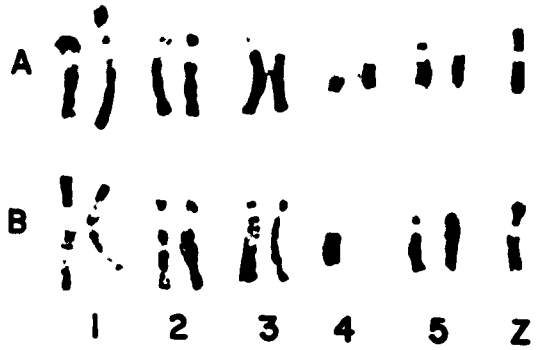

FIGURE 3. G-band karyotypes of *A. phoeniceus* from two localities: *A*, Leon Co., Florida; and *B*, Clearwater Co., Minnesota.

negative relationship indicates that variance increases with decreasing chromosome length. When seven similar-sized chromosomes from four different locales are compared (as in this study), this dependence does not present a problem if the variances for each size class of chromosome are independently and identically distributed, which they appear to be. However, were one to apply multivariate statistical tests of this characteristic of chromosomal shape to several chromosomes of different size, violations of the independence assumption might make the analyses less valid. A similar problem did not exist for the measure of chromosome size that we used, but to limit karyotypic comparison to this one characteristic would be of questionable value.

KARYOTYPIC INVARIABILITY

The macrochromosomal similarity that we found among four populations of Red-winged Blackbirds suggests that this species is karyotypically invariable across much of its North American range. Our results are identical to other published standard karyotypes of this species (Makino and Baldwin 1954, Hobart et al. 1982) for the largest macrochromosomes, but give slightly different estimates of diploid number. A combination of our regional samples with those from other published studies includes almost 60 individuals with indistinguishable macrochromosomes. Macrochromosomal variation would either have to occur at very low frequencies or be fairly localized to have been overlooked in these studies. If an undetected chromosomal polymorphism does exist in this species and exists in Hardy-Weinberg equilibrium (like that of the hypothetical species in our introduction), we can predict its frequency of occurrence using a certain level of confidence, say 95%, and the sample sizes we obtained. The relative frequency of some undetected morphological variant would have to be 0.04 or less to have gone undetected in our total sample of 52 individuals. Because of differences in sample sizes among our sites, however, local frequencies of a chromosomal morph that would have passed unnoticed range from 0.073 to 0.15.

Our estimate of $2n$ (76) was determined from more than 200 cells and approximately 100 photomicrographs. The $2n$ of this species was reported to be 80 by Hobart et al. (1982) using bone-marrow samples from an unspecified number of individuals and 76 by Makino and Baldwin (1954) based on mitotic gonad spreads from several embryos. Differences in these $2n$ estimates probably reflect not intraspecific variation, but rather the difficulty in estimating this characteristic for birds. Underestimations probably occur more often than overestimations because microchromosomes are often covered by larger chromosomes in C-metaphase spreads. On the other hand, either prolonged colchicine treatment, which causes chromosome arms to dissociate at the centromere and could therefore split a single microchromosome in two, or the presence of darkly stained non-chromatin materials in C-metaphase spreads might lead to overestimations of $2n$. Totally reliable $2n$ estimates for birds must await refinements either in somatic cell preparations or in the use of meiotic tissues, where diploid numbers are reduced by half.

G-band patterns in *A. phoeniceus* also appear to be well conserved, at least for a few individuals from Minnesota and Leon Co., Florida. Our sample size is much too small to make firm statements about G-band conservatism in this species, but other studies have shown G-band characteristics to be conservative even among congeners (Ryttman et al. 1979) and confamilials (Beiderman, as cited in Shields [1982]) when standard karyotypes are similar. On the other hand, a G-band polymorphism has been described in the domestic fowl (Pollock and Fechheimer 1981).

Elucidating relationships between genetic and phenotypic variation is critical to understanding evolutionary processes, but has been inadequately done for most avian species. Rising and Shields (1980) found phenotypic correlates of different intraspecific chromosome morphs in *Junco* and speculated that the phenotypic variation was related to a partitioning of winter food resources. Conversely, although substantial morphological (Power 1970, Mosimann and James 1979, James 1983), behavioral (Orians 1980), and electromorphic variation (Spendelow 1980) exists throughout the range of Red-winged Blackbirds, corresponding macrochromosomal variation is apparent-

ly absent. This situation is similar to that in certain well-studied mammalian species (Schnell and Selander 1981), for which there appears to be no concordance among several different phenotypic and genetic characteristics. Schnell and Selander (1981) suggested that much more information will be required before evolutionary processes can be reliably inferred for species of small mammals. In general, species (and genera) are less karyotypically diverse in birds than in mammals. This relative invariability of avian karyotypes has contributed to the belief that chromosomal rearrangements are of little significance in the evolution of birds (Hobart et al. 1982, Shields 1982).

Lande (1979) modeled the fixation of novel chromosome rearrangements in instances where there is selection against the heterozygous chromosomal condition. He proposed that much of the karyotypic diversity exhibited by mammals is the result of genetic drift operating in small populations. A possible explanation, then, for the invariability of most avian species (and Red-winged Blackbirds, in particular) is their large effective population sizes (see Barrowclough and Shields 1984). These would reduce the influence of genetic drift. It is of some interest that bats, which share with birds the characteristic of flight, show somewhat lower levels of chromosomal diversity than other small mammals (Baker and Bickham 1980). We hasten to point out, however, that extensive chromosomal studies of either avian or chiropteran species are rare.

Population studies of chromosomal variation in birds have provided important information about evolutionary relationships in those species where intraspecific variation exists. In the Red-winged Blackbird, however, we found no chromosomal variation in 52 individuals from four widely separated populations on which to base phylogenetic speculation.

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RECENT PUBLICATIONS

The Seaside Sparrow, its biology and management.—Edited by T. L. Quay, J. B. Funderburg, Jr., D. S. Lee, E. F. Potter, and C. S. Robbins. 1983. Occasional Papers of the North Carolina Biological Survey 1983–5. 174 p. Paper cover, $15.00. Source: North Carolina State Museum of Natural History, P.O. Box 27647, Raleigh, NC 27611; checks should be made payable to NCDA, Museum Extension Fund. The Seaside Sparrow (*Ammodramus maritimus*) inhabits coastal salt and brackish marshes from Massachusetts to Cape Sable, Florida, and thence westward around the Gulf of Mexico to southern Texas. Since the species is essentially restricted to that habitat, it is threatened by the loss of salt marshes through exploitation for human activities, particularly in Florida. A symposium to address the situation was held at Raleigh, NC in October 1981, and its Proceedings are published in this book. The nineteen papers are grouped into three sections: an overview of the bird and its habitat, aspects of the sparrow's biology, and protection and management. The two articles on vocalizations are furnished with a seven-inch phonodisc that gives examples, produced by J. W. Hardy. The frontispiece is a color painting by John Henry Dick illustrating the nine races of the sparrow. This volume represents a benchmark for future work on the species because it assembles most of our present knowledge, raises new questions, and broadens our perspective for considering management proposals.

Kirtland's Warbler: the natural history of an endangered species.—Lawrence H. Walkinshaw. 1983. Including Chapter 14, on nesting success, by Mark Bergland. Cranbrook Institute of Science, 500 Long Pine Road, Bloomfield Hills, Michigan. Bull. No. 58. 207 p. Paper cover. No price given. Data from fifty years of observations, specimens, banding records, and much more make up this thorough report on a large warbler that summers in a small part of lower Michigan and winters in the Bahamas. Walkinshaw presents a well-documented picture of the bird on its summer range. Taken together with Harold Mayfield's 1960 book of similar title, also from the Cranbrook Institute of Science (Bull. No. 40), it is evident that much is known about one-fourth of the annual cycle of this endangered species. The production of this book, however, is faulty; the editors could have done more to improve the layout and appearance of tables (e.g., Table 1 lacks important legend information), maps (e.g., Figure 1 is of poor quality); and the use of standard terminology (e.g., names of colors on p. 81). Forty-five black and white photographs and other figures, fifty-five tables, sonograms, summary, selected bibliography, index of plant and animal species, subject index. A valuable contribution to our knowledge of the Kirtland's Warbler.—J. Tate.