# On the Evolution of Genome Size of Birds

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**We measured genome size (nuclear DNA content) by fluorescence flow cytometry in 55 species of birds representing 12 different orders. Similar studies were performed in approximately 100 species by laboratories using absorption cytophotometry of Feulgen-stained nuclei. Although there have been apparent discrepancies in the assigned values for the species used as a reference, the values obtained in the different laboratories are generally in agreement. When the data are standardized in relation to a diploid (2C) value of 2.5 picograms (pg) of DNA for the domestic chicken (*Gallus gallus domesticus*), the mean for DNA content in 135 species representing 17 orders is 2.82 ± 0.33 (SD) pg with a range of 2.0–3.8 pg. Thus the genome size of birds is the most conservative of any vertebrate class and, all values considered, is smaller and more uniform in size than previous estimates would indicate. This could be explained by a previously unexplored hypothesis: that the genome of birds has evolved from a small ancestral genome that was reduced before emergence of the protoavian.**

Genome size has been called the DNA "C-value" (Cavalier-Smith 1985; Swift 1950) to reflect the relative constancy observed among individuals of a given species. Yet recent studies have demonstrated that genome size may vary considerably among conspecifics. Variation of 35% has been reported in pocket gophers of the genus *Thomomys*, for example (Sherwood and Patton 1982). These differences are small in comparison to the broad variation found among the vertebrates in general, in which DNA values range from about 1 to 280 picograms (pg) per diploid nucleus (Olmo et al. 1989).

Absorption cytophotometry of Feulgen-stained nuclei has been used for the estimation of DNA content in most organisms studied, including birds. Despite some apparent discrepancies in the data reported by different authors, the values obtained with this technique agree with those obtained with other methods, including flow cytometry (Rasch 1985). Biases in these values can occur because genome size is estimated in relation to the DNA content of cells from a standard, or reference, species. Cells from various tissues of different species have been used as standards in avian studies, and different values have been assigned to the same standard species by different researchers.

Genome size has been studied in some 100 species of birds since Mirsky and Ris (1951) presented the first broad survey on nuclear DNA mass in various animal species, including duck, goose, domestic fowl, and turkey. The bird most often studied is the domestic chicken, *Gallus gallus domesticus*, for which the genome sizes reported in 28 separate studies are summarized by Rasch et al. (1971).

We applied flow cytometry to the study of nuclear DNA content in 55 species of birds representing 12 orders. Our objectives were to survey genome size over a broad range of avian species and to standardize previously reported values, thereby enabling direct comparisons between the results of different studies. The data reveal that the genome size of birds is the most conservative of any vertebrate class and that, all values considered, it is smaller and more uniform in size than previous estimates would indicate. This permits development of an alternative hypothesis for the evolution of genome size in endothermic vertebrates.

## Materials and Methods

### Sample Preparation

The species surveyed are catalogued in Table 1. We collected blood samples in sodium citrate (Becton-Dickinson vacutainer #4606), then refrigerated and ana-

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**Table 1. Average diploid (2C) nuclear DNA content (in picograms) ± SD for 135 species of birds**

| Order | Species | Common name | Mean DNA content | | | |
|---|---|---|---|---|---|---|
| | | | Present study | Venturini et al. 1986[a] | Bachmann et al. 1972c[a] | Other studies |
| Casuariiformes | *Dromaius novaehollandiae* | Emu | 3.25 ± 0.02 (5) | | | 3.09 ± 0.07 (1)[b] |
| Sphenisciformes | *Spheniscus demersus* | Jackass penguin | 3.26 ± 0.08 (2) | | | |
| Podicipediformes | *Podiceps auritus* | Horned grebe | | | 3.03 ± 0.26 (1) | |
| Pelecaniformes | *Pelecanus onocrotalus* | Great white pelican | | 2.49 ± 0.10 | | |
| | *Pelecanus occidentalis* | Brown pelican | | | 2.80 ± 0.16 (2) | 2.76 —[c] |
| | *Phalacrocorax auritus* | Double-crested cormorant | | | 2.86 ± 0.03 (1) | |
| Ciconiiformes | *Ardea cinerea* | Gray heron | | 2.77 ± 0.09 | | |
| | *Ardea herodias* | Great blue heron | | | 2.93 ± 0.20 (1) | |
| | *Leptoptilos crumeniferus* | Marabou stork | | 2.68 ± 0.04 | | |
| | *Threskiornis aethiopicus* | Sacred ibis | | 2.49 ± 0.05 | | |
| | *Platalea leucorodia* | White spoonbill | | 2.49 ± 0.04 | | |
| Phoenicopteriformes | *Phoenicopterus ruber* | Greater flamingo | | 2.50 ± 0.04 | | |
| Anseriformes | *Dendrocygna viduata* | White-faced whistling duck | 2.74 ± 0.03 (2) | | | |
| | *Cygnus olor* | Mute swan | 2.96 ± 0.04 (3) | | | |
| | *Cygnus atratus* | Black swan | 2.89 ± 0.04 (3) | | | |
| | *Anser rossii* | Ross's goose | 2.76 ± 0.04 (2) | | | |
| | *Cereopsis novaehollandiae* | Cape barren goose | | 2.84 ± 0.06 | | |
| | *Cairina domestica* | Duck | | | | 2.68 —[c] |
| | *Anas castanea* | Chestnut-breasted teal | 2.71 ± 0.03 (4) | | | |
| | *Anas platyrhynchos* | Mallard | 2.88 ± 0.06 (2) | 2.54 ± 0.04 | | |
| | *Mergus cucullatus* | Hooded merganser | 2.56 ± 0.05 (2) | | | |
| Falconiformes | *Gymnogyps californianus* | California condor | | | | 3.02 — (1)[d] |
| | *Rostrhamus sociabilis* | Snail kite | | | | 2.82 — (8)[d] |
| | *Milvus milvus* | Red kite | | 2.99 ± 0.06 | | |
| | *Milvus migrans* | Black kite | | 3.26 ± 0.09 | | |
| | *Haliaeetus leucocephalus* | Bald eagle | 2.86 ± 0.02 (2) | | | |
| | *Accipter nisus* | Northern sparrowhawk | | 2.23 ± 0.06 | | |
| | *Buteo buteo* | Eurasian buzzard | | 2.61 ± 0.03 | | |
| | *Aguila chrysaetos* | Golden eagle | 2.96 ± 0.06 (2)[e] | 2.64 ± 0.06 | | |
| | *Falco sparverius* | American kestrel | 2.86 — (1)[f] | | | |
| | *Falco tinnunculus* | Eurasian kestrel | | 2.66 ± 0.04 | | |
| | *Falco eleonorae* | Eleonara's falcon | | 2.53 ± 0.05 | | |
| Galliformes | *Penelope* sp. | Guan | | 2.46 ± 0.04 | | |
| | *Coturnix japonica* | Japanese quail | 2.81 ± 0.02 (49) | 2.57 ± 0.04 | | |
| | *Gallus gallus domesticus* | Domestic chicken | 2.47 ± 0.04 (27)[g] | | 2.50 ± 0.13 (1) | 2.50 — (6)[d]<br>2.10 ± 0.21 (1)[a] |
| | *Phasianus colchicus* | Common pheasant | 2.51 ± 0.02 (2) | 2.53 ± 0.04 | | 2.45 —[c] |
| | *Chrysolophus pictus* | Golden pheasant | 2.41 ± 0.04 (20) | | | |
| | *Numida meleagris galeata* | Helmeted guineafowl | | 2.45 ± 0.03 | | |
| | *Guttera edouardi* | Crested guineafowl | 3.07 ± 0.03 (2) | | | |
| Gruiformes | *Grus grus* | Common crane | | | | 3.02 — (4)[d] |
| | *Grus canadensis* | Sandhill crane | | | | 3.08 — (6)[d] |
| | *Grus americana* | Whooping crane | | | | 3.18 — (6)[d] |
| | *Grus vipio* | Japanese white-naped crane | 3.25 ± 0.05 (4) | | | 3.04 — (4)[d] |
| | *Grus levcogeranus* | Siberian white crane | | | | 3.10 — (2)[d] |
| | *Anthropoides virgo* | Demoiselle crane | | 2.63 ± 0.06 | | |
| | *Balearica pavonina* | Black crowned crane | 3.04 ± 0.02 (4) | 2.81 ± 0.04 | | |
| | *Balearica regulorum* | Gray crowned crane | 3.02 ± 0.04 (3) | | | 2.90 —[h] |
| | *Rallus aquaticus* | Water rail | | 2.49 ± 0.06 | | |
| Charadriiformes | *Actitis hypoleucos* | Common sandpiper | | 2.84 ± 0.04 | | |
| | *Calidris alpina* | Dunlin | | 2.55 ± 0.04 | | |
| | *Larus argentatus cachinnans* | Herring gull | | 2.99 ± 0.03 | | |
| | *Larus atricilla* | Laughing gull | | | 2.89 ± 0.30 (1) | |
| | *Larus ridibundus* | Common black-headed gull | | | | 3.64 ± 0.35 (1)[i] |
| | *Sterna sandvicensis* | Sandwich tern | | | 2.80 ± 0.13 (1) | |
| Columbiformes | *Columba livia* | Rock dove | 2.92 ± 0.13 (2) | 2.65 ± 0.04 | | 2.99 ± 0.06 (1)[j]<br>2.88 —[c] |
| | *Streptopelia turtur* | Turtle dove | | 2.46 ± 0.03 | | |
| | *Ptilinopus pulchellus* | Crimson-capped fruit dove | 2.94 ± 0.02 (8) | | | |
| Psittaciformes | *Chalcopsitta* sp. | Lory | | 2.50 ± 0.21 | | |
| | *Trichoglossus haematodus* | Rainbow lorikeet | 2.65 ± 0.04 (2) | | | |
| | *Lorius garrulus* | Chattering lory | 2.71 ± 0.02 (2) | | | |
| | *Eolophus roseicapillus* | Galah | 2.86 ± 0.07 (10) | | | |
| | *Cacatua galerita* | Sulphur-crested cockatoo | 3.15 ± 0.10 (6) | 2.99 ± 0.04 | | |
| | *Cacatua moluccensis* | Salmon-crested cockatoo | 3.08 ± 0.05 (2) | | | |
| | *Cacatua sanguinea* | Little corella | 3.41 — (1) | | | |
| | *Nymphicus hollandicus* | Cockatiel | 2.92 ± 0.05 (2) | | | |
| | *Psittaculirostris edwardsii* | Edward's fig parrot | 3.04 ± 0.02 (4) | | | |
| | *Eclectus roratus* | Eclectus parrot | 3.34 ± 0.03 (2) | | | |
| | *Melopsittacus undulatus* | Budgerigar | | 2.04 ± 0.03 | 2.37 ± 0.16 (1) | 2.46 ± 0.02 (1)[j] |
| | *Psittacus erithacus* | Gray parrot | | 2.66 ± 0.05 | | |
| | *Agapornis roseicollis* | Peach-faced lovebird | 2.61 ± 0.08 (2) | | | |
| | *Agapornis personata* | Masked lovebird | 2.71 ± 0.05 (4) | | | |
| | *Psittacula krameri* | Ring-necked parakeet | 2.74 ± 0.02 (2) | | | |
| | *Anodorhynchus hyacinthinus* | Hyancinth macaw | 2.86 ± 0.15 (2) | | | |
| | *Ara ararauna* | Blue-&-yellow macaw | 2.95 ± 0.02 (2) | | | |
| | *Ara caninde* | Wagler's macaw | 3.03 ± 0.06 (2) | | | |
| | *Ara militaris* | Military macaw | 2.74 ± 0.06 (2)[f] | | | |
| | *Ara macao* | Scarlet macaw | 2.68 ± 0.06 (4)[f] | 2.86 ± 0.06 | | |

**Table 1. Continued**

| Order | Species | Common name | Mean DNA content | | | |
|---|---|---|---|---|---|---|
| | | | Present study | Venturini et al. 1986[a] | Bachmann et al. 1972c[a] | Other studies |
| Psittaciformes (*continued*) | *Ara chloptera* | Green-winged macaw | 2.96 — (1) | | | |
| | *Ara rubrogenys* | Red-fronted macaw | 2.83 ± 0.04 (5) | | | |
| | *Aratinga solstitialis* | Sun conure | 2.71 ± 0.05 (2) | | | |
| | *Amazona ventralis* | Hispaniolan Amazon | | | | 3.24 — (6)[d] |
| | *Amazona vittata* | Puerto Rican Amazon | | | | 3.16 — (4)[d] |
| | *Amazona ochrocephala* | Yellow-crowned Amazon | 3.79 — (1) | | | |
| | *Deroptyus accitrinus* | Hawk-headed parrot | 3.27 ± 0.02 (2) | | | |
| Strigiformes | *Tyto alba* | Common barn owl | | 3.05 ± 0.08 | | |
| | *Otus scops* | Eurasian scops owl | | 2.79 ± 0.04 | | |
| | *Otus asio* | Eastern screech owl | 2.93 ± 0.02 (3)[f] | | | |
| | *Pulsatrix perspicillata* | Spectacled owl | | 3.60 ± 0.04 | | |
| | *Bubo bubo* | Northern eagle owl | | 2.84 ± 0.04 | | |
| | *Bubo lacteus* | Verreaux's eagle owl | | 3.31 ± 0.04 | | |
| Coraciiformes | *Alcedo atthis* | River kingfisher | | | | 2.80 ± 0.07 (1)[i] |
| | *Bucorvus abyssinicus* | Abyssinian ground hornbill | 2.85 ± 0.06 (4) | | | |
| Piciformes | *Psilopogon pyrolophus* | Fire-tufted barbet | 3.38 ± 0.04 (2) | | | |
| | *Ramphastos toco* | Toco toucan | | 3.60 ± 0.05 | | |
| Passeriformes | *Sayornis phoebe* | Eastern phoebe | | | 2.89 ± 0.23 (1) | |
| | *Hirundo rupestris* | Crag margin | | 2.49 ± 0.05 | | |
| | *Troglodytes troglodytes* | Winter wren | | | | 2.59 ± 0.14 (1)[i] |
| | *Toxostoma rufum* | Brown thrasher | | | 2.53 — (1) | |
| | *Prunella modularis* | Dunnock | | | | 2.94 ± 0.14 (1)[i] |
| | *Erithacus rubecula* | European robin | | | | 3.64 ± 0.21 (1)[i] |
| | *Sialia sialis* | Eastern bluebird | | | 2.89 — (1) | |
| | *Hylocichla mustelina* | Wood thrush | 2.76 — (1) | | | |
| | *Turdus merula* | Blackbird | | 2.49 ± 0.04 | | 3.01 ± 0.42 (6)[i] |
| | *Turdus philomelos* | Song thrush | | 2.18 ± 0.04 | | 3.85 ± 0.21 (1)[i] |
| | *Polioptila caerulea* | Blue-gray gnatcatcher | | | 2.76 ± 0.46 (1) | |
| | *Phylloscopus collybita* | Chiffchaff | | | | 2.94 ± 0.21 (1)[i] |
| | *Sylvia atricapilla* | Blackcap | | | | 2.17 ± 0.14 (1)[i] |
| | *Regulus calendula* | Ruby-crowned kinglet | 2.62 — (1) | | 2.70 ± 0.46 (1) | |
| | *Parus atricapillus* | Black-capped chickadee | | | | 3.08 ± 0.14 (1)[i] |
| | *Parus carolinensis* | Carolina chickadee | | | 2.99 ± 0.30 (1) | |
| | *Parus ater* | Coal tit | | | | 3.15 ± 0.42 (1)[i] |
| | *Parus major* | Great tit | | | | 3.01 ± 0.17 (1)[i] |
| | *Parus caeruleus* | Blue tit | | | | 2.94 ± 0.14 (2)[i] |
| | *Zonotrichia albicollis* | White-throated sparrow | 2.73 — (1) | | | |
| | *Pipilo erythrophthalmus* | Rufous-sided towhee | 3.10 — (1) | | 2.63 ± 0.33 (1) | |
| | *Dendroica dominica* | Yellow-throated warbler | | | 2.80 ± 0.30 (1) | |
| | *Dendroica coronata* | Yellow-rumped warbler | | | 2.76 ± 0.39 (1) | |
| | *Dendroica palmarum* | Palm warbler | | | 3.16 ± 0.36 (1) | |
| | *Agelaius phoeniceus* | Red-winged blackbird | | | 2.66 ± 0.26 (1) | |
| | *Sturnella magna* | Eastern meadowlark | | | 2.96 ± 0.49 (2) | |
| | *Euphagus cyanocephalus* | Brewer's blackbird | 2.92 — (1) | | | |
| | *Fringilla coelebs* | Chaffinch | | | | 2.24 ± 0.35 (2)[i] |
| | *Serinus canaria* | Island canary | | | 2.96 ± 0.30 (1) | 3.22 ± 0.27 (1)[j]<br>3.08 ± 0.14 (1)[i]<br>3.15 ± 0.03 (1)[b] |
| | *Lonchura striata* | White-backed munia | 2.84 ± 0.03 (6) | | | |
| | *Amadina fasciata* | Cut-throat weaver | | 2.07 ± 0.04 | | |
| | *Passer domesticus* | House sparrow | 3.01 — (1) | 2.49 ± 0.05 | | 2.52 ± 0.28 (4)[i] |
| | *Passer montanus* | Eurasian tree sparrow | | | | 2.17 ± 0.14 (2)[i] |
| | *Sturnus vulgaris* | European starling | | | 2.60 ± 0.23 (1) | |
| | *Cyanocitta cristata* | Blue jay | 2.86 ± 0.04 (2) | | 2.63 ± 0.20 (3) | |
| | *Garrulus glandarius* | Eurasian jay | | 2.47 ± 0.03 | | |
| | *Pica pica* | Black-billed magpie | | 2.50 ± 0.03 | | |
| | *Corvus monedula* | Western jackdaw | | 2.49 ± 0.05 | | |
| | *Corvus brachyrhynchos* | American crow | | | | 2.50 — (5)[d] |
| | *Corvus corone* | Carrion crow | | 2.46 ± 0.04 | | |
| | *Corvus corax* | Common raven | | 2.42 ± 0.04 | | |

Sample size, where available, in parentheses. Values for 55 species were obtained by flow cytometry (present study), and literature values for 98 species were standardized to enable direct comparison (see text). Taxonomic sequence and nomenclature are based on Howard and Moore (1990).

[a] Values from Atkin et al. 1965; Bachmann et al. 1972c; Martin 1974; Venturini et al. 1986; and Wagenmann et al. 1981 were standardized to chicken = 2.5 pg DNA per diploid nucleus.

[b] From Martin 1974.

[c] From Wagenmann et al. 1981; no SD given.

[d] From Rasch 1985; no SD given.

[e] Stored at −20°C prior to analysis.

[f] Feather pulp used for analysis.

[g] Combined values of the four varieties of that species: SC White Leghorn 2.44 ± 0.04 (2)[e]; 500 New Hampshire 2.49 ± 0.04 (2)[e]; Rhode Island Red 2.44 ± 0.08 (5)[e]; Rhode Island Red × Barred Rock 2.48 ± 0.04 (18).

[h] From Rash 1976; no SD given.

[i] From De Smet 1981; values were standardized to human = 7.0 pg DNA per diploid nucleus.

[j] From Atkin et al. 1965.

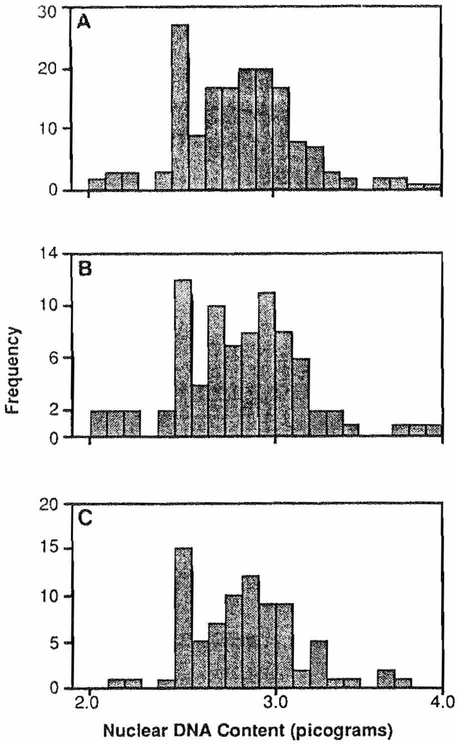

**Figure 1.** Distribution of DNA content values in birds. (A) Bimodal distribution of 165 values of 2C nuclear DNA content for 135 species of birds. (B) Similar distributions for 82 observations of DNA content in the Psittaciformes and Passeriformes. (C) Distributions for 83 values in 15 other orders.

**Table 2. Diploid (2C) values of nuclear DNA content in pg for 17 orders of birds**

| Order | *N* | DNA content (mean ± SD) | Range | Homogeneous groups |
|---|---|---|---|---|
| Phoenicopteriformes | 1 | 2.50 — | — | a |
| Galliformes | 13 | 2.53 ± 0.22 | 2.10–3.07 | ab |
| Ciconiiformes | 5 | 2.67 ± 0.19 | 2.49–2.93 | abc |
| Pelecaniformes | 4 | 2.73 ± 0.16 | 2.49–2.86 | acd |
| Anseriformes | 10 | 2.76 ± 0.14 | 2.54–2.96 | acde |
| Passeriformes | 51 | 2.76 ± 0.35 | 2.07–3.85 | acde |
| Falconiformes | 12 | 2.79 ± 0.27 | 2.23–3.26 | acdef |
| Columbiformes | 5 | 2.79 ± 0.23 | 2.46–2.99 | acdefg |
| Coraciiformes | 2 | 2.82 ± 0.04 | 2.80–2.85 | acdefgh |
| Psittaciformes | 31 | 2.88 ± 0.34 | 2.04–3.79 | dfgh |
| Charadriiformes | 6 | 2.95 ± 0.37 | 2.55–3.64 | ghi |
| Gruiformes | 12 | 2.96 ± 0.22 | 2.49–3.25 | hi |
| Podicipediformes | 1 | 3.03 — | — | defghi |
| Strigiformes | 6 | 3.09 ± 0.31 | 2.79–3.60 | i |
| Casuariiformes | 2 | 3.17 ± 0.11 | 3.09–3.25 | i |
| Sphenisciformes | 1 | 3.26 — | — | ij |
| Piciformes | 2 | 3.49 ± 0.16 | 3.38–3.60 | j |

Sample size (*N*) refers to the number of observations of species studied for each order; in some cases individual species were studied more than once. Homogeneous groupings were made by the least significant difference (LSD) multiple range test, 95% LSD intervals. Groups sharing a letter were not significantly different.

lyzed them in random order as described previously (Tiersch et al. 1989). In brief, blood cells (~1 μl of sample) of the species under study and blood cells of a species used as an internal reference, were suspended as a mixture in 0.5 ml of lysis-staining buffer containing 25 μl buffered RNase (1.0 mg/ml), 0.1% sodium citrate, 0.1% Triton ×100, and 25 μg propidium iodide.

### Flow Cytometry

We estimated the DNA content of the cells using the EPICS V flow cytometer (Coulter Electronics, Hialeah, Florida) with argon-ion laser operated at a wavelength of 488 nm at 500 mW in the light-stabilized mode. Filters included two 515 nm long passes, a 560 nm dichroic, and a 570 nm long pass in front of the photomultiplier tube. The fluorescence values of at least 40,000 stained nuclei were digitized individually and used to calculate DNA content in relation to a value of 7.0 pg DNA assigned for fresh human leukocytes analyzed previously in a mixture with cells of the internal reference. In each test the value of the internal reference (channel catfish, *Ictalurus punctatus, G. gallus,* or the domestic swine, *Sus scrofa*) was cancelled during the calculation of bird DNA content, according to the formula: nuclear DNA (pg) $= 7.0 \times B/R \times R/H$, where $B$, $R$, and $H$ are, respectively, the fluorescence values for the nuclei of bird, internal reference, and human.

### Normalization and the Analysis of Data

Venturini et al. (1986) reported the DNA content of 48 bird species calculated in relation to a standard value of 3.45 pg for *G. gallus.* This value was derived from an earlier study of 23 species (Bachmann et al. 1972c). Because most studies in *G. gallus,* including our own, have yielded estimates of about 2.5 pg (Rasch et al. 1971; Shapiro 1976; Tiersch and Chandler 1989), we adopted this value for the purpose of standardization. Accordingly, values from various studies could be compared by normalizing against a standard value of 2.5 pg DNA for *G. gallus* or a standard value of 7.0 pg for the human. Correction factors were derived for any given study by dividing the reported value for *G. gallus* or human by the standard value for these species. We then multiplied the other values within the given study by the correction factor to obtain normalized values. This treatment reduced the variation in genome size between species and, in general, resulted in lower values for DNA content. One-way analysis of variance and the least significant difference multiple comparison test were performed by use of STRATGRAPHICS computer software. This program corrects for unequal sample sizes.

## Results

Flow cytometry allows precise estimates of DNA content. We could routinely identify male–female differences due to sex-chromosome heteromorphism (Elias et al. 1988; Nakamura et al. 1990). The 55 species that we studied were distributed across 12 orders, including the most primitive and advanced orders that have been studied for DNA content.

The mean of 165 values of DNA content in 135 species of birds was 2.82 ± 0.33 pg (Table 1). Significant differences were present among orders (ANOVA, $P < .001$), yet there was no relation between DNA content and taxonomic position of the groups that were studied (Table 2). There was a mode at 2.9 pg DNA, and a second mode of tightly-grouped values at 2.5 pg (Figure 1). The pattern of bimodality was mirrored in the Passeriformes (51 observations in 41 species) and Psittaciformes (31 observations in 27 species) and in the 67 species in the other 15 orders (Figure 1).

## Discussion

With respect to genome size, birds have the smallest level of interspecific variation of any vertebrate class (Cavalier-Smith 1978; Sparrow et al. 1972). The less-than-two-fold intraclass variation reported here is smaller than the variation described previously. Despite their small and consistent genome size modern birds are speciose and ecologically diverse, although the nature of avian diversity can best be described as "variations on a theme" (Goin

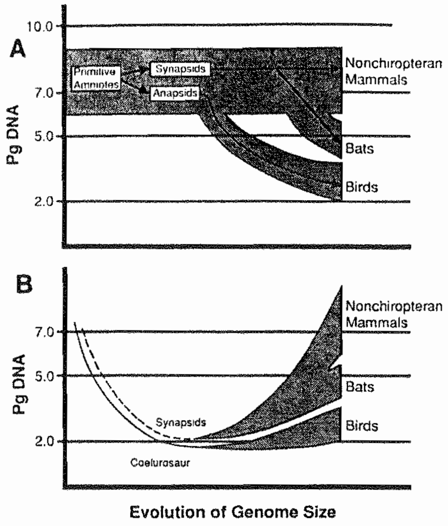

**Figure 2.** Models for the evolution of genome size in endotherms. (**A**) Conventional scheme (see Discussion) for evolution of small genome sizes in bats and birds from a larger genome (between 5 and 10 pg). (**B**) According to this model, genome size in bats and birds arose through the retention of a small ancestral genome, less than the 5 to 10 pg suggested for early amniotes (Thomson and Muraszko 1978). This signifies a convergent trend toward increased rather than decreased DNA content. Bats and birds—their genome size arrested by the metabolic constraints of flight—each represent an "evolutionary snapshot" in an ascending grade of genome sizes in the endotherms. This figure is not intended to convey actual time spans or evolutionary distances.

and Goin 1968). Intraspecific variation is also low, as indicated by our analysis of 49 Japanese quail (*Coturnix coturnix*) of both sexes, in which we found a mean of 2.81 ± 0.02 pg DNA and a range of 2.78 to 2.85 pg. The variation of 2.5% in quail was lower than the intraspecific value of 4.7% in 12 species of salmonids (Johnson et al. 1987) and the 6.0% in 20 species of cyprinids (Gold and Amemiya 1987). As noted above, intraspecific variation as high as 35% has been reported in pocket gophers.

Conservation of genome size in birds may reflect monophyletic origin or evolutionary constraint. Bats possess substantially less DNA than do other mammals (Burton et al. 1989), and birds possess less DNA than do their closest living relatives, the reptiles. These observations suggest that the metabolic demands of flight may place a constraint on genome size (Burton et al. 1989; Cavalier-Smith 1978). Cell size is related to genome size, and selection for a favorable cell-surface-to-volume ratio could thus influence the DNA content of the nucleus (Cavalier-Smith 1978; Szarski 1974). According to that scheme, reduced DNA content would be expected in small, vigorous birds such as hummingbirds of the family Trochilidae. Study of the DNA content in other taxa in which flight has evolved—e.g., fossil species such as pterosaurs—might provide useful information in that regard. In addition, it might be informative to estimate genome size in primitive birds by measuring cell size in fossil material.

Among extant reptiles, the Squamata possess about 3.5 to 3.9 pg of DNA, the Chelonia, about 4.6 to 4.9 pg, and the Crocodilia, about 5.6 to 6.0 pg (De Smet 1981; Goin and Goin 1968). In contrast, primitive fishes such as *Polypterus palmas* and the coelacanth, *Latimeria chalumnae*, possess larger genome sizes (11.7 and 7.22 pg DNA, respectively) (Bachmann et al. 1972b; Cimino and Bahr 1974). On the basis of these observations and given the measurement of cell sizes of fossil fishes and amphibians, it could be inferred that emerging amniotes possessed a DNA content of about 5 to 10 pg (Thomson and Muraszko 1978) at the time of the amphibian-to-amniote transition. This would suggest that the genome size of birds was reduced after their evolution from a reptilian precursor and possibly during their subsequent radiation (Figure 2) (Bachmann et al. 1972a; Goin and Goin 1968; Mirsky and Ris 1951).

Alternatively, birds *inherited* a reduced genome and retained this throughout their evolution. In other words, small genome size is not directly associated with flight per se. The long-period interspersion pattern of DNA sequences and the small percentage of repetitive DNA sequences in the avian genome are distinctive among the vertebrates (Olmo et al. 1989; Wagenmann et al. 1981). Based on the composition of their genome, the DNA values of birds could have been maintained through the minimization of repeat sequences. In fact, larger genome size in birds is associated with increases in single-copy DNA that are larger than the increases found in repetitive DNA (Olmo et al. 1989). An evolutionary decrease in genome size—i.e., from an ancestor with a large genome—could accordingly result in a loss of single-copy sequences (Schmidtke and Epplen 1980) at a faster rate than the loss of repetitive sequences. Regardless of the basic trend in DNA quantity, however, the avian DNA values are continuous and overlapping, and it appears that differential accumulation and loss of DNA has also occurred (Hinegardner 1976).

Given the broad range of genome sizes in extant animals and extinct groups (e.g., conodonts) (Morris and Harper 1988), it follows that similar diversity existed during the 150 million years of the reptilian era. There is compelling evidence for a monophyletic origin of birds, and a carnivorous dinosaur of about the size of a chicken would seem an excellent candidate for the precursor of the avian (Carroll 1988; Feduccia 1980). Small genome size associated with the active predatory lifestyle of the dinosaur ancestor would then serve as a critical adaptation for the development of flight and endothermy (Figure 2). Moreover, the earliest fossil bird, *Archeopteryx lithographica*, may well have been a homeothermic endotherm (Houck et al. 1990). The pronounced mode at 2.5 pg DNA reported here accordingly represents not the end result of an evolutionary reduction in DNA content, but, instead, a starting point for the avian genome.

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