Relative Rates of Single-Copy DNA Evolution in Cranes

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Data from DNA-DNA hybridization studies provide a means by which to estimate variation in molecular evolutionary rates within and among taxonomic groups. Statistical analyses (ANOVA and F-ratio tests) of such data for the 14 species of cranes (Aves: Gruidae) suggest that rates of single-copy DNA evolution vary significantly between members of the two crane subfamilies, with crowned cranes (Balearicinae: Balearica) showing a relative acceleration of 1.3–1.6 times over the other 13 species (Gruinae). No available evidence suggests that this disparity correlates with variable age-at-first-breeding, though a more general generation-time effect may exist. The fossil record for Gruiformes provides two approximate points of calibration for the molecular clock in cranes, corresponding to the divergence of cranes and limpkins (Aramidae) and to the divergence of the two gruid subfamilies. Fossil time calibration indicates that the average genomic rate of DNA evolution in cranes is close to Sibley and Ahlquist’s general estimate for birds with delayed breeding.

Introduction

Since the earliest application of genetic distance data in phylogenetic reconstruction, there has been much debate over the uniformity or nonuniformity of molecular evolutionary rates within and among lineages (Fitch 1976; Wilson et al. 1977; Avise and Aquadro 1982). Various molecular clocks have been proposed for electrophoretic (e.g., see Nei 1975; Sarich 1977), immunological (e.g., see Prager and Wilson 1975), and DNA hybridization (Sibley and Ahlquist 1981) data sets. Although DNA hybridization data were once thought to demonstrate a uniform average rate of single-copy DNA evolution, recent statistical analyses of avian and mammalian data sets demonstrate that rates are uniform in some taxa (Bledsoe 1987) but not in others (Catzeflis et al. 1987; Sheldon 1987; Sibley et al. 1987; Springer and Kirsch 1989). Britten (1986) documented even more widespread molecular rate variation within and among other animal groups.

Statistical techniques such as those proposed by Felsenstein (1984) and Houde (1987) have enhanced the ability to detect rate variation on the basis of DNA hybridization data. In the present study I employ DNA hybridization to detect variation in average genomic rates of single-copy DNA evolution among the 14 species of cranes (Aves: Gruidae).

Material and Methods
DNA Hybridization

The biochemical protocol for DNA hybridization employed here is essentially that described by Sibley and Ahlquist (1981); detailed descriptions have been given...
DNA was recovered from erythrocytes by using standard methods of phenol/chloroform extraction, proteinase and RNase treatment, and ethanol precipitation (Maniatis et al. 1982). Native DNA was fragmented into short strands (100–2,000 bp) by using high-frequency sound waves. Fragment size distributions were monitored for each sample by agarose gel electrophoresis and comparison with commercial size markers. Samples outside the range given above were not employed as tracers in hybridization experiments.

Single-copy sequences were recovered from each species by using reassociation-kinetic and hydroxyapatite chromatography methods (Sibley and Ahlquist 1981). Single-copy sequences were defined as those remaining single-stranded after incubation to Cot 200 (Cot = initial molar DNA concentration × seconds of incubation time in 0.48 M phosphate buffer).

Tracer DNA was prepared from single-copy samples according to the iodination method of Sibley and Ahlquist (1981), with modifications described by Krajewski (accepted). DNA hybrids consisted of a 1:500 mixture of tracer and driver (sheared native) DNA, boiled and incubated at 60°C to a Cot ≥ 5,600. Thermal elution of hybrids was performed in an automated thermal elution device similar to that described by Sibley and Ahlquist (1981).

Two tracer preparations were employed for every crane species, with replicate interspecies hybrids arranged in experimental sets of 25. Each experimental set was defined by one or two reference (homoduplex) hybrids (i.e., tracer and driver DNAs from the same extraction of the same individual bird), to which all interspecies hybrids were compared. Three to 10 replicate hybrids were examined for each pairwise combination of species (including reciprocals). Because normalized percent hybridization (NPH) values among cranes were essentially 100% (Krajewski, accepted), $T_m$ (the median melting point of all sequences that have hybridized in a particular experiment) was employed as the measure of hybrid thermal stability. $T_m$ is the temperature at which 50% of total counts above 60°C have eluted ($T_m$ values between specific elution temperatures were estimated by linear interpolation between the two adjacent temperatures).

Genetic distance measurements were calculated as delta $T_m$ values between homoduplex and interspecies hybrids within the same experimental set. Final distance estimates were taken as the average of all replicate delta $T_m$'s for each pairwise comparison (reciprocals were treated separately). In three cases, a single, anomalously large, value was trimmed from the sample of replicate measurements, according to the method described by Krajewski (accepted), to obtain a more robust estimate of actual distance. No further corrections of the data were employed.

Outgroup comparisons were provided by DNA hybrids between the 14 cranes and the limpkin (Aramus guarauna, Aramidae). Reciprocal comparisons involving Aramus were not performed because DNA from the limpkin did not produce adequate tracer preparations.

Tree Construction

Estimates of phylogenetic branching order were made using the FITCH routine of Felsenstein's PHYLIP software package (version 2.8), by using a least-squares criterion of fit ($P = 0.0$). Two negative average delta $T_m$'s were set equal to 0.01 for the PHYLIP input matrices. To increase the likelihood of globally optimum results, six alternative input orders of taxa were employed, and the solution of choice was taken as that with the lowest sum-of-squares value.

Since Aramus was not labeled, the distance matrix was folded (i.e., reciprocal
samples were pooled and averaged) to position the root of the crane tree. With Aramus specified as the outgroup, this root occurred as expected between the two traditional subfamilies. All subsequent analyses were performed on the square matrix (lacking Aramus) with Balearica designated as the outgroup to other cranes.

Rate Tests

The statistical formulation of Sarich and Wilson's (1967) relative-rate test is essentially a one-way-analysis-of-variance (ANOVA) problem. ANOVAs were performed on samples of replicate measurements from each crane species to the outgroup limpkin and on pooled reciprocal samples of replicate measurements from each gruine species to the designated outgroup Balearica. Pairwise tests (Scheffe's and Tukey-Kramer tests; Sokal and Rohlf 1981) were performed whenever significant differences among means were detected.

The F-ratio test of Felsenstein (1984) was employed as an alternative approach for detecting rate variation (for applications to DNA hybridization data, see Bledsoe 1987; Sheldon 1987; Springer and Kirsch 1989). This test assesses the statistical significance of differences in sum-of-squares values for trees generated under assumptions of rate uniformity and rate variability. These constraints correspond to the KITSCH and FITCH algorithms, respectively, of PHYLIP.

The F-ratio test is predicated on the fact that the alternative rate assumptions imply different df values (numbers of independent branch lengths) in fitting distances to a specified topology. In general, the df for a tree derived from a square matrix is:

$$\text{df} = (\text{no. of observations} - (\text{no. of branches}).$$

KITSCH and FITCH trees for n taxa have df values given by the following equations [modified for a square matrix from Sheldon (1987)]:

$$\text{df(KITSCH)} = (n^2-n) - (n-1),$$

$$\text{df(FITCH)} = (n^2-n) - (2n-3).$$

Calculation of the F-ratio and df for a corresponding F distribution follows the method of Sheldon (1987). I compared best-fit trees obtained by FITCH and KITSCH algorithms for the matrix of distances which did not include Aramus (since F-ratio tests do not require rooted topologies, an outgroup is unnecessary).

Results

Phylogeny Estimate

The complete data base of ~1,200 hybridization comparisons has been presented by Krajewski (accepted). Table 1 shows the matrix of genetic distances (average delta Tm's) among cranes and limpkin. The best-fit tree based on analyses of folded and square matrices is shown in figure 1; nodes of low confidence detected by Lanyon's (1985) jackknife method are also indicated. DNA hybridization supports the distinction of crane subfamilies Balearicinae and Gruinae, the former including only Balearica and the latter including species of Anthropoides, Bugeranus, and Grus. Among gruines, G. leucogeranus appears as the earliest branch of the tree, while the remaining 12 species cluster into four groups (fig. 1). Branching order among these four groups is not resolved.

ANOVA

Parameters for an ANOVA among samples of crane-to-limpkin delta Tm's are shown in table 2. The results imply that significant heterogeneity exists among mean
Table 1
Matrix of Average Delta-\(T_m\) Values among Cranes

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
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<tbody>
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<td>Aramus guarauna</td>
<td>7.4 (3)</td>
<td>6.8 (4)</td>
<td>6.4 (4)</td>
<td>6.0 (5)</td>
<td>7.0 (4)</td>
<td>7.3 (4)</td>
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<td>6.5 (3)</td>
<td>6.4 (4)</td>
<td>7.1 (4)</td>
<td>6.7</td>
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<td>R. regulorum</td>
<td>3.9 (7)</td>
<td>3.6 (4)</td>
<td>3.0 (4)</td>
<td>3.6 (4)</td>
<td>3.9 (5)</td>
<td>4.0 (5)</td>
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<tr>
<td>G. leucogeranus</td>
<td>3.2 (8)</td>
<td>1.0 (6)</td>
<td>1.5 (6)</td>
<td>1.3 (8)</td>
<td>1.4 (7)</td>
<td>1.6 (8)</td>
<td>1.6 (8)</td>
<td>1.6 (8)</td>
<td>1.5 (8)</td>
<td>2.0 (7)</td>
<td>1.3</td>
<td></td>
</tr>
<tr>
<td>G. antigone</td>
<td>0.5 (1)</td>
<td>0.2 (7)</td>
<td>0.2 (6)</td>
<td>0.4 (4)</td>
<td>0.4 (6)</td>
<td>0.6 (6)</td>
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<td>0.8 (8)</td>
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<tr>
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<td>1.1 (8)</td>
<td>1.4 (8)</td>
<td>2.0 (8)</td>
<td>1.4 (7)</td>
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<td>1.6 (8)</td>
<td>1.4 (7)</td>
<td>1.4</td>
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<td>G. rubicundus</td>
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<td>1.2 (8)</td>
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<td>Bu. carunculatus</td>
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<td>1.4 (6)</td>
<td>0.7 (6)</td>
<td>1.3 (8)</td>
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<td>1.7 (4)</td>
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<td>0.2 (2)</td>
<td>0.8 (7)</td>
<td>0.3 (2)</td>
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<td>1.3 (6)</td>
<td>0.7 (6)</td>
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<td>1.3 (8)</td>
<td>1.0 (8)</td>
<td>1.4 (8)</td>
<td>1.7 (5)</td>
<td>0.7 (8)</td>
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<tr>
<td>G. grus</td>
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<td>0.5 (7)</td>
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<td>0.3 (2)</td>
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<td>0.5 (4)</td>
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<tr>
<td>G. monachus</td>
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<td>0.8 (5)</td>
<td>1.2 (5)</td>
<td>1.2 (6)</td>
<td>1.0 (4)</td>
<td>1.0 (6)</td>
<td>1.1 (4)</td>
<td>0.4 (6)</td>
<td>0.5 (4)</td>
<td></td>
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<tr>
<td>G. americana</td>
<td>3.9 (4)</td>
<td>1.6 (6)</td>
<td>1.8 (5)</td>
<td>0.7 (5)</td>
<td>1.3 (5)</td>
<td>1.4 (6)</td>
<td>1.5 (6)</td>
<td>1.0 (5)</td>
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<td>0.6 (6)</td>
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<td>G. americana</td>
<td>3.8 (1)</td>
<td>1.6 (4)</td>
<td>1.9 (4)</td>
<td>1.0 (5)</td>
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<td>1.3 (5)</td>
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<td>1.4 (5)</td>
<td>0.8 (5)</td>
<td>0.8 (5)</td>
<td>0.1</td>
</tr>
</tbody>
</table>

NOTE.—Numbers in parentheses are number of observations; numbers in brackets are SD.
Rates of DNA Evolution in Cranes

**Fig. 1.**—Best-fit tree for a complete square matrix of average delta-$T_m$ values among crane species, constructed by the FITCH algorithm of PHYLIP (version 2.8; $P = 0.0$, sum-of-squares = 11.604, 360 trees were examined). *Aramus* and the root of the crane tree have been positioned on the basis of a folded-matrix analysis; *Aramus* was not included in the square input matrix. This tree displayed the lowest sum-of-squares value among trees generated from six shuffled input matrices. Values in parentheses indicate fitted path lengths from the gruid root to tips of the tree. Values on nodes indicate the frequency with which each implied clade occurred in Lanyon’s (1985) jackknife procedure (14 pseudo-replicates; nodes with frequency 1.0 are unlabeled). The branch to *Aramus* is broken at its midpoint. Genus abbreviations are as follows: *G.* = *Grus*; *A.* = *Anthropoides.*

...distances for these comparisons ($P < .05$). ANOVA does not suggest significant variation among gruines when *Balearica* is designated as an outgroup.

**F-Ratio Test**

The best-fit tree found by KITSCH (sum-of-squares = 13.689) differs from the FITCH topology only in that the positions of *G. grus* and *G. monachus* are interchanged. An F-ratio test on the topology in figure 1 indicates significant rate variation among cranes [df(FITCH) = 157; df(KITSCH) = 169; sums-of-squares 11.604 (FITCH) and 13.711 (KITSCH); $F = 2.38; P < .01$].

**Which Rates Are Different?**

Tests for paired contrasts (Sheffe’s and Tukey-Kramer tests) failed to pinpoint fast and slow lineages (the latter test is probably the most powerful, though both are

**Table 2**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Cranes vs. Limpkin</th>
<th>Gruines vs. <em>Balearica</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>$\sigma^2$</td>
<td></td>
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</tr>
<tr>
<td>Between</td>
<td>0.67</td>
<td>0.40</td>
</tr>
<tr>
<td>Within</td>
<td>0.32</td>
<td>0.26</td>
</tr>
<tr>
<td>$F$</td>
<td>2.09</td>
<td>1.53</td>
</tr>
<tr>
<td>$D_X$</td>
<td>13</td>
<td>12</td>
</tr>
<tr>
<td>$D_Y$</td>
<td>41</td>
<td>123</td>
</tr>
<tr>
<td>$F_{sd}(D_X, D_Y)$</td>
<td>1.975</td>
<td>1.83</td>
</tr>
</tbody>
</table>
weakened by small sample sizes). Some perspective on rate disparity, however, may be obtained from the FITCH tree. Since fitted distances in figure 1 have proportions of nucleotide substitutions as their expectations, one should be able to identify as rapidly evolving those lineages with the longest root-to-tip path lengths. Balearica stands out clearly in this regard. The root-to-tip distance for Balearica (2.20) is 1.3–1.6 times that for gruines. Since ANOVA could not detect significant rate variation among gruines, the magnitude of this range probably reflects experimental imprecision. Rate variation in cranes appears to occur only between the two subfamilies.

Discussion

Statistical Caveats

ANOVA and F-ratio tests assume that populations are normally distributed, have the same variance, and are sampled independently. When precision alone is considered, replicate DNA hybrids appear to have a symmetric and unimodal error distribution (Felsenstein 1987). Sibley et al. (1987) demonstrated that, for sample sizes \( >5 \), the mean and SD of replicate distances are not correlated with one another and that the SD stabilizes at \( \approx 0.5 \). These conclusions have been confirmed for the crane data (Krajewski, accepted) [Springer (1988) found a similar pattern in marsupials].

The most crucial caveat in using these tests is that any inaccuracy (bias toward incorrectly large or small distances) in the data could mimic rate variation and be misleading. Covariance patterns in a matrix of delta \( T_m \)'s may indeed occur, since sets of distances are derived from single reference (homoduplex) hybrids.

Biological and experimental factors have been identified which might produce inaccurate measurements (Caccone and Powell 1987; Springer and Krajewski 1989), though only the "compression effect" (on distances derived from low-melting-point tracers) appears to be present in the crane data (Krajewski, accepted). However, compression is not observed in distances derived from tracers of Balearica or Grus leucogeranus, species showing extremes of root-to-tip path lengths. Compression is so slight that reciprocity correction (Springer and Kirsch 1989) does not substantially improve the average percent nonreciprocity of the crane matrix and worsens the fit of least-squares trees derived from it. Finally, one would expect that major compression bias among gruines would mislead both ANOVAs. Opposite results for crane-versus-limpkin (significant variation) and gruine-versus-balearicine (insignificant variation) analyses suggest that compression had little effect on their outcomes.

Generation Time and Rate Variation

Perhaps the earliest and most often advanced explanation of variable molecular evolutionary rates among taxa relates to differences in generation length (Laird et al. 1969; Kohne 1970). The generation-time hypothesis states that the rate of nucleotide substitution should be proportional to the number of generations produced by members of a given species in a given interval of time. Species with longer generation times will have rates of substitution slower than those of species with shorter generation times.

Sibley et al. (1987) argued that there is a significant correlation between age at first breeding and average genomic rates of evolution: birds that breed early in life (most passerines) evolve more rapidly than those that have delayed maturity (many nonpasserines). Sibley et al. (1987) cite cranes as an example of long-generation-time birds with slow rates of change. But can either age at first breeding or generation time explain rate variation within the Gruidae?

Sibley et al.'s (1987) hypothesis predicts that crowned cranes (Balearica) should
breed earlier in life than gruines. Data on reproductive biology of cranes are spotty, but there does not appear to be a substantial age-at-first-breeding difference between *Balearica* and other species. Pomeroy (1987) estimates that crowned cranes breed at 4–6 years of age. This value is comparable to estimates for *G. americana* (5–6 years; Kuyt and Goosen 1987) and *G. canadensis* (4–5 years; Nesbitt and Wenner 1987) and to anecdotal reports for other gruines (Johnsgard 1983).

In another component of generation time, however, crowned cranes differ substantially from gruines. Crowned cranes have the largest average clutch sizes of any crane (2.5 eggs/clutch, compared to ~1.9 eggs/clutch for most gruines; Pomeroy 1980; Johnsgard 1983). If larger clutch size translates into higher net reproductive rate, then (other things being equal) population-replacement time and generation time will be shorter for *Balearica* than for gruines (Pianka 1974).

While the crane data do not provide definitive evidence for a relationship between generation time and rates of molecular evolution, they do provide a counterexample to Sibley et al.’s (1987) claim that age at first breeding is sufficient to explain patterns of rate disparity. Other counterexamples are found in the work of Sheldon (1987) and Springer and Kirsch (1989).

Approximate Calibration of the Molecular Clock

Because the crane tree is not fully resolved, only two cladogenic events can serve as temporal calibration points—the origin of limpkins from primitive gruoid stock and the origin of gruines from balearicine-like ancestors (*G. leucogeranus* has no Tertiary fossil record). The oldest cranes are from the Eurasian Eocene, and the oldest limpkins are from the Oligocene of Argentina (Cracraft 1973). Cracraft (1973) postulated that gruids and aramids diverged in the late Paleocene, so I will use its upper boundary [53.6 Myr ago (Mya)] as an approximate date. Gruines appear in the late Miocene of Europe (Grigorescu and Kessler 1977), but since a diverse North American gruine fauna existed in the early Pliocene (Brodkorb 1967), ancestral forms probably had originated by the earliest Miocene (23 Mya).

The average distance from *Balearica* to *Aramus* is 9.4 [corrected for NPH and multiple substitutions according to the formulas of Catzeflis et al. (1987) and Jukes and Cantor (1969), respectively]; that between gruines and *Aramus* is 8.4. If cranes and limpkins diverged ~53.6 Mya, the rate for *Balearica* is 5.7 Myr/unit distance, and that for gruines is 6.4 Myr/unit distance. The average distance from *Balearica* to gruines is 3.8 (corrected for multiple hits), giving a rate of 6.1 Myr/unit distance. These ratios are similar to the nonpasserine rate estimate of Sibley and Ahlquist (6 Myr/unit distance; J. E. Ahlquist, personal communication).

Because evidence for the divergence dates above is limited, the distance/time calibration suggested here is only a rough approximation. DNA hybridization may provide stronger estimates of average genomic rates in birds when quantitative stratigraphic methods can be applied to the poor fossil record of most groups.

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