

Review Article

Variation of Multilocus Minisatellite DNA Fingerprints in Avian Populations

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ABSTRACT

Alexander Papangelou, Michael Ham and Michael M. Miyamoto (1998) Variation of multilocus minisatellite DNA fingerprints in avian populations. *Zoological Studies* 37(3):161-168. In recent years, multilocus minisatellite DNA fingerprinting has remained a primary genetic technique for the quantification of nuclear DNA variation in avian populations. After surveying the literature for use of this technique in birds, frequency distributions of average band-sharing differences among individuals were generated for outbreeding populations across species. In these populations, unrelated individuals differed by about 75% of their bands, whereas 1st-order relatives varied by approximately 40%. The latter value approximated those for populations of other species with known or suspected histories of strong inbreeding and/or genetic drift. Our frequency distributions for unrelated and related individuals of outbreeding species from many different orders establish a baseline against which the band-sharing counts of other avian populations can be evaluated for the potential effects of inbreeding and drift.

Key words: DNA fingerprinting, Multilocus minisatellite variation, Birds, Population structure.

INTRODUCTION

Multilocus minisatellite DNA fingerprinting has become a common technique for studying avian populations, since the discovery of hypervariable probes by Jeffreys et al. (1985). The technique is straight-forward, using probes to identify fragments from different regions of the genome which can vary in their numbers of tandem repeats. Subsequent band matching and analysis of these frag-

ments across different loci allow for the determination of the proportional genetic differences between pairs of individuals (D). This dissimilarity coefficient can then be averaged for all pairs of individuals in a sample, thereby providing a useful measure of mean nuclear DNA (nDNA) variation within the population (average proportional difference [APD]).

Multilocus minisatellite fingerprint probes were initially used to study nDNA variation in humans

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(Jeffreys et al. 1985). Soon after, this approach was applied to the study of dogs and cats (Jeffreys and Morton 1987) and bird populations (Burke and Bruford 1987, Wetton et al. 1987). These initial investigations of birds heralded a plethora of studies that enhanced the utility and popularity of minisatellite DNA fingerprinting as a tool in evaluations of natural avian populations. As a result, a large body of studies about multilocus minisatellite DNA variation in bird populations has accumulated since the introduction of this approach to avian biology in 1987.

In interpreting their results, many authors of previous bird studies (as for other vertebrate groups [Gilbert et al. 1990]) have made the significant assumption that APDs for unrelated individuals in "normal" outbreeding populations are 70% or greater. Thus, APD scores that are significantly less (i.e., about 40% to 50% or lower) have been taken as evidence that the bird populations under study have experienced the effects of strong inbreeding and/or genetic drift, quite often as the consequence of small or reduced population sizes. However, the value of 70% is usually based on just a few studies that are cited as representative. Thus, what is needed is a thorough review of multilocus minisatellite variation in outbreeding populations of birds from species of different orders to establish more firmly cutoffs of fingerprint dissimilarity scores for outbreeding populations versus those that have experienced extensive inbreeding and/or drift. The establishment of such cutoffs will greatly increase the importance of minisatellite data in the evaluation of population structure in birds.

This study reviews the literature on multilocus minisatellite DNA variation in natural populations of birds since Burke and Bruford (1987) and Wetton et al. (1987) to early 1996. APD scores from outbreeding populations of birds from different orders are summarized as separate frequency distributions for unrelated individuals versus 1st-order relatives. In the process, frequency distributions of APD scores for outbreeding populations are more firmly established with empirical data, thereby enhancing their value as baselines for the interpretation of minisatellite scores for other species where strong inbreeding and/or genetic drift are suspected.

MATERIALS AND METHODS

A thorough review of the literature was conducted by searching the databases Biological Ab-

stracts; Zoological Records; Biological Abstracts/ Reports, Reviews, Meetings; and Life Sciences Collection. These databases were searched from 1987 (i.e., from the date of Burke and Bruford [1987] and Wetton et al. [1987]) to early September 1996 (the closing date of our search). The thoroughness of our review was verified by L. Badger, Head Research Librarian at the Marston Science Library, University of Florida. Although our search was regarded by her as "extensive", we must acknowledge that some oversights are still inevitable. Relevant articles not incorporated in our study included those whose journals were lost, stolen, or unavailable from the library even after requests from interlibrary loan. We relied on the keyword searches "DNA fingerprint*" and "bird*," a strategy recommended to us by L. Badger. However, some articles may still have been missed if these keywords or their derivatives were missing from the titles and abstracts of the papers. After obtaining citations, their abstracts were screened to decide which articles would be pursued further. Thus, papers with different foci could have been missed even though they contained relevant information about minisatellite variation in natural bird populations. Despite these limitations, our search of the literature may be regarded as thorough as circumstances allowed. The few papers that were inevitably missed are unlikely to have had a major effect on the robust patterns that are described below.

APD scores for natural avian populations were obtained from the collected papers from our searches of the literature databases. Proportional difference (D) was defined as:

$$D = N_{AB} / (N_A + N_B), \quad (1)$$

where N_{AB} equals the number of different fragments between individuals A and B, and $(N_A + N_B)$ refers to the total number of bands scored in these 2 individuals (Gilbert et al. 1990). APD is then the average of D for all pairs of individuals within a sample. Estimates of APD were directly taken as reported in an article or were calculated from the data given in a paper. Most frequently, these calculations required the conversion of an average band-sharing count (BSC) to APD by the equation:

$$\text{APD} = 1 - \text{BSC}. \quad (2)$$

In studies where multiple minisatellite probes were used, APDs were chosen for those probes that detected significantly more scorable bands than the others (Miyamoto et al. 1994). Here, "sig-

nificant” was defined as a probe that detected 3 or more scorable bands. If the average number of bands did not differ to this extent between probes, then a weighted average based on their mean fragment numbers was calculated to derive a final APD.

A population was considered to be a “normal” outbreeding one if no direct independent evidence existed to suggest otherwise. In contrast, a population was classified as inbred and/or the product of strong genetic drift (because of current small size or historical bottlenecking) only when a published study provided clear evidence of such, independent of its DNA fingerprint results. Thus, only populations whose presumed inbreeding and/or influence under genetic drift could be documented with external evidence of small size, incest, and/or bottlenecking, or founder’s effect were removed from the “normal” outbreeding category and placed into a separate class for inbred/drifted populations.

Many studies of both outbreeding and inbred/drifted populations distinguished between the D and APD scores of close relatives versus unrelated individuals within the same populations. Our study followed these distinctions by evaluating the results for 1st-order relatives separately from those for unrelated individuals for both classes of populations. Second-order relationships were distinguished as well, but these situations were rarely encountered in the different articles. APDs from multiple studies of the same species were averaged together to obtain a single final score.

Separate frequency histograms were generated from the APD estimates: (1) for unrelated individuals of outbreeding species; (2) for 1st-order relatives of outbreeding species; and (3) for unrelated individuals of species with small and/or inbred populations. Statistical differences among these distributions were tested with the Mann-Whitney U-test. Furthermore, for species with APD scores for both unrelated individuals and 1st-order relatives, the expected degree of proportional band sharing by 1st-order relations (S_{exp}) was calculated by the equation:

$$S_{exp} = (1 + q - q^2) / (2 - q), \quad (3)$$

where q equals the mean allele frequency in the population (Birkhead et al. 1990). In our study, q was estimated as:

$$q = 1 - APD^{0.5}, \quad (4)$$

where APD refers to the APD value for unrelated

individuals of a species (Jeffreys and Morton 1987). Estimates of S_{exp} were then converted into dissimilarity scores for 1st-order relatives of these species (APD_{exp}) by the equation:

$$APD_{exp} = 1 - S_{exp}. \quad (5)$$

The discrepancies between the expected and observed APDs for 1st-order relatives in species with estimates for both this relationship and for unrelated individuals were evaluated against an expected difference of 0 by the Mann-Whitney U-test (Mendenhall and Beaver 1991).

RESULTS AND DISCUSSION

From 129 publications surveyed from literature databases for 1987 to September 1996, 69 were retained from which comparable data were compiled for use in our comparisons (Table 1). These articles covered 70 species from 9 of the 23 orders of living birds which are commonly recognized (Sibley and Monroe 1990). By far, the greatest number of studies focused on the order Passeriformes (songbirds) which is the most diverse group with its 5712 species from 1161 genera. Mean APD values for unrelated individuals and 1st-order relatives did not vary in any notable way from 1 order to another for outbreeding populations (Table 1). These scores ranged across orders from 0.68 to 0.83 for unrelated individuals and from 0.29 to 0.42 for 1st-order relatives. For inbred/small populations, the range in APDs varied from 0.37 to 0.60 for unrelated individuals and from 0.35 to 0.41 for 1st-order relatives.

The frequency distribution of APD scores for unrelated individuals of outbreeding populations was bell-shaped across species ($n = 54$) with a mean of 0.757 and standard deviation of 0.092 (Fig. 1). The frequency distribution for their 1st-order relatives was also bell-shaped ($n = 33$), but with a mean of 0.397 and standard deviation of 0.062. The 2 distributions did not overlap in their scores, except for that of unrelated individuals for the Galapagos Hawk *Buteo galapagoensis*. A Mann-Whitney U-test (2-tailed) confirmed that the APD distributions for unrelated individuals versus 1st-order relatives were significantly different ($z = 7.70$, $p < 0.00006$). Furthermore, this same test documented that the observed APDs for 1st-order relatives of these species agreed with those expected for them from equation (5) ($z = 0.82$, $p = 0.4094$).

Table 1. APD scores for bird orders that were represented in our literature survey of multilocus minisatellite fingerprinting in natural avian populations

Order Population class	Number of species represented	Mean APD (range) for unrelated individuals	Mean APD (range) for 1st-order relatives	References
Anseriformes				Meng et al. 1990, Triggs et al. 1992,
Outbred	5	0.72 (0.63 - 0.80)	0.38 (---)	Choudhury et al. 1993, Meng and Parkin
Inbred/small	4	0.41 (0.24 - 0.56)	---	1993, Rave et al. 1994, Rave 1995,
Ciconiiformes				Tegelstrom and Sjoberg 1995
Outbred	10	0.70 (0.38 - 0.85)	0.37 (0.20 - 0.45)	Graves et al. 1992 1993, Hunter et al.
Inbred/small	1	---	0.41 (---)	1992, Oring et al. 1992, Austin et al.
Columbiformes				1993, Decker et al. 1993, Heg et al. 1993,
Inbred/small	1	0.41 (---)	---	Millar et al. 1994, Signer et al. 1994,
Coraciiformes				Warkentin et al. 1994, Faaborg et al.
Outbred	1	0.80 (---)	0.38 (---)	1995, Owens et al. 1995, Parker et al.
Cuculiformes				1995
Outbred	1	0.73 (---)	---	Miyamoto et al. 1994
Galliformes				Jones et al. 1991
Outbred	3	0.77 (0.71 - 0.87)	0.41 (---)	Quinn et al. 1994
Inbred/small	2	0.56 (0.55 - 0.58)	---	Hanotte et al. 1992, Freeland et al. 1995
Gruiformes				Tokarskaya et al. 1990, Gibbs et al. 1994,
Outbred	2	0.68 (0.61 - 0.75)	0.29 (---)	Jamieson et al. 1994, Lambert et al. 1994
Inbred/small	2	0.37 (0.34 - 0.40)	---	Wetton et al. 1987 1991 1992, Burke et al.
Passeriformes				1989, Birkhead et al. 1990, Morton et al.
Outbred	32	0.78 (0.55 - 0.90)	0.42 (0.22 - 0.48)	1990, Rabenold et al. 1990, Smith et al.
Inbred/small	4	0.60 (0.33 - 0.85)	0.40 (0.40 - 0.40)	1990, Westneat 1990 1993, Gelter et al.
Psittaciformes				1991, Lifjeld et al. 1991 1993, Seutin et al.
Outbred	1	0.83 (---)	0.39 (---)	1991, Ashworth and Parkin 1992, Gelter
Inbred/small	1	0.56 (---)	0.35 (---)	and Tegelstrom 1992, Gullberg et al. 1992,
				Piper and Rabenold 1992, Reeve et al.
				1992, Yamagishi et al. 1992, Degnan
				1993, Dunn and Robertson 1993, Hartley
				et al. 1993 1995, Smith and von Schantz
				1993, Bensch et al. 1994, Dunn et al.
				1994a,b, Fleischer et al. 1994, Fornasari et
				al. 1994, Hill et al. 1994, Marin et al. 1994,
				Meek et al. 1994, Mulder et al. 1994, Otter
				et al. 1994, Parker et al. 1994, Pinxten et al.
				1994, Ritchison and Klatt 1994, Sheldon and
				Burke 1994, Stutchbury et al. 1994, Hahn
				and Fleischer 1995, Hasselquist et al. 1995,
				Riley et al. 1995, Yezerinac et al. 1995
				Brock and White 1992

This table relies on the Sibley and Monroe (1990) classification that is similar to the checklist of the American Ornithologists' Union (1983), except that the former combines Charadriiformes, Falconiformes, Pelecaniformes, and Procellariiformes into the single order Ciconiiformes. A summary of how these references were interpreted to generate this table and Figs. 1 and 2 is available from the 3rd author by request.

The frequency distribution of APDs for unrelated individuals in inbred/ small populations had a broader spread than those for outbreeding populations (Fig. 2). The mean and standard deviation for this distribution were 0.494 and 0.162, respectively. Thus, the mean APD for unrelated individuals from outbreeding populations (0.757) was nearly 50% greater than that for small/ inbred populations (Fig. 1). This difference was statistically significant as confirmed with the Mann-Whitney U-test (2-tailed, $z = 4.66$, $p < 0.00006$). In contrast, the average APD for 1st-order relatives of outbreeding populations was similar to that for unrelated individuals of small/inbred populations (0.397 versus 0.494, respectively) (Figs. 1, 2). Their difference in mean APD was not significant ($z = 1.86$, $p = 0.0628$).

The results of our study indicate that APD scores for unrelated individuals versus 1st-order relatives of outbreeding avian populations from

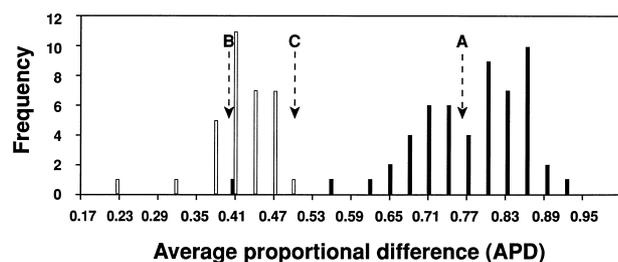


Fig. 1. Frequency histograms for unrelated individuals (solid bars, $n = 54$) versus known 1st-order relatives (open bars, $n = 33$) in outbreeding populations of birds. Arrows labeled A, B, and C refer to the mean APD scores for unrelated individuals in outbreeding populations, 1st-order relatives in outbreeding populations, and unrelated individuals in inbred/ small populations (Fig. 2), respectively.

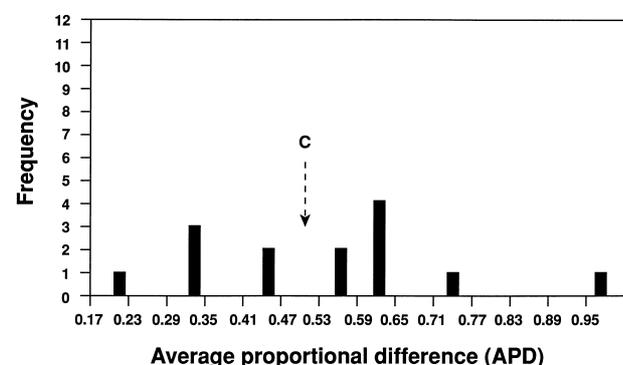


Fig. 2. Frequency histogram for unrelated individuals from small/inbred populations ($n = 14$). The arrow highlights the mean APD for these populations and is the same as that in Fig. 1 (C). First-order relatives of inbred/small populations were not considered in this study because of their small numbers ($n = 5$).

different species and orders are sufficiently distinct to allow for generalizations about them. In general, our results support the view that the background level of band differences is about 70% to 80% in outbreeding populations of birds. These levels are cut nearly in half for 1st-order relatives as predicted by equation (5). The relative constancy of these results provides a stronger empirical basis to evaluate the population structure of birds with multilocus minisatellite fingerprint data. APDs of 70% or greater would suggest that a population is largely an outbreeding one, whereas scores of 35% to 50% or less would indicate a genetically depauperate population. Populations like the latter would alert the investigator to the possibility of inbreeding, a recent bottleneck or founder's effect, and/or to the strong influences of genetic drift due to small population sizes. By placing these cutoffs on stronger empirical grounds, investigators will be able to interpret their DNA fingerprint results with greater confidence.

Despite the additional interpretive power and growing popularity of single-locus minisatellite and microsatellite techniques (Avise 1994), multilocus minisatellite approaches will remain important in studies of natural avian populations, because of their practical advantages in surveying many loci at the same time which vary among closely related individuals. Correspondingly, our findings of APDs of 70% to 80% for unrelated individuals versus APDs of 35% to 50% for 1st-order relatives in outbreeding populations is expected to assist investigators in the interpretation of their multilocus minisatellite fingerprint results. At the very least, our frequency distributions will allow others to develop initial hypotheses about the population/ breeding structures and histories of their bird species.

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鳥類多基因座小衛星 DNA 指紋之變異

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多基因座小衛星 DNA 指紋法在近幾年已成為定量鳥類族群的核-DNA 變異之基本遺傳技術。整理相關研究的文獻，可以得到鳥類族群平均個體間 DNA 條紋差異的頻度分布。在這些族群中，無親戚關係的個體間 DNA 條紋差異為 75%，而一等親個體間的差異約為 40%。後項數值和已知或推測具很強近親交配或遺傳浮動的物種之族群數值相近。我們由不同親緣關係的鳥類挑選許多非近親交配的種類。在這些種類中分析有親戚關係及無親戚關係的個體建立其頻度分布。其他鳥類族群受近親交配和遺傳浮動的影響可由其共有 DNA 條紋的數據和上述的基準比較加以評估。

關鍵詞： DNA 指紋法，多基因座小衛星 DNA 變異，鳥類，族群構造。

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