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HALDANE'S RULE AND SEX BIASED GENE FLOW BETWEEN TWO  
HYBRIDIZING FLYCATCHER SPECIES (*FICEDULA ALBICOLLIS* AND  
*F. HYPOLEUCA*, AVES: MUSCICAPIDAE)

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**Abstract.**—The collared flycatcher (*Ficedula albicollis*) and the pied flycatcher (*F. hypoleuca*) hybridize where their geographic ranges overlap. Restriction fragment comparison of 5% of the mitochondrial genome showed a sequence divergence of 10% between these flycatcher species. This degree of sequence divergence between a closely related pair of bird species is unusually high and contrasts with the low level of divergence between *F. albicollis* and *F. hypoleuca* in nuclear genes (Nei's  $D = 0.0006$ ) revealed by enzyme electrophoresis. The low nuclear differentiation is explained by sex biased gene flow and introgression in nuclear genes (via fertile male hybrids), while the high mitochondrial DNA sequence divergence is preserved by sterility of female hybrids, which prevents mitochondrial introgression. This pattern is in accordance with Haldane's rule and is supported by field data on hybrid fertility. The high mtDNA differentiation could be explained by transfer of mitochondrial DNA from a third species during a past period of hybridization.

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Birds generally exhibit less genetic divergence than do other vertebrate taxa at comparable taxonomic levels (see e.g., Avise and Aquadro, 1982; Sibley and Ahlquist, 1984; Britten, 1986; Shields and Helm-Bychowski, 1988). In addition to the existing information on variation in proteins and nuclear DNA, data are now being accumulated on the extent of mitochondrial DNA (mtDNA) restriction site polymorphisms and mtDNA genetic distances in birds. Kessler and Avise (1984, 1985) compared mtDNA genetic distances between avian species (representing five different genera) with those of two non-avian vertebrate genera and found a lower degree of mtDNA sequence divergence for the avian congeners. Avise (1983) suggested two alternative hypotheses to explain the low levels of molecular divergence in birds: (1) the rate of molecular evolution is slower than that in other animal groups; or (2) avian taxa on average share a more recent common ancestry relative to non-avian vertebrates.

There is no evidence suggesting that the rate of mitochondrial DNA evolution in birds is decelerated compared to that of other vertebrates. Shields and Wilson (1987b) estimated a rate of sequence divergence in mtDNA of 2% per million years in geese, which is similar to the rate found among mammals (Brown et al., 1979, 1982; George, 1982; George et al., 1983; Ferris et al., 1983a, 1983b; George and Ryder, 1986;

Higuchi et al., 1987; Tanhauser, 1985), frogs (Carr et al., 1987) and fishes (Gyllensten and Wilson, 1987).

Small genetic distances between avian taxa could result from more recent origin compared to other vertebrate taxa, a tendency for avian systematists to oversplit avian taxonomy, or avian speciation occurring without extensive genetic changes (e.g., "genetic revolution" of Mayr, 1954). To evaluate the extent of genetic differentiation during speciation, we still lack empirical data on genetic differentiation between newly formed avian species.

The aim of this study is to investigate genetic differentiation of mitochondrial genotypes in two hybridizing, presumably recently evolved avian species, the collared flycatcher (*Ficedula albicollis*) and the pied flycatcher (*F. hypoleuca*), in relation to genetic differentiation of nuclear genes detected by protein electrophoresis.

## MATERIALS AND METHODS

Genetic variation in mitochondrial DNA was investigated in seven *Ficedula albicollis* and 19 *F. hypoleuca* individuals from two and three Swedish localities, respectively. In addition, four *F. albicollis* and two *F. hypoleuca* individuals were collected from Poland for comparison with Swedish specimens (Fig. 1). Birds were collected as adults by live trapping at their nest boxes.

Mitochondria were isolated from fresh

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Haldane's Rule and Sex Biased Gene Flow between Two Hybridizing Flycatcher Species (*Ficedula albicollis* and *F. hypoleuca*, Aves: Muscicapidae), by Hakan Tegelstrom and Hans P. Gelter © 1990 Society for the Study of Evolution.

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The collared flycatcher (*Ficedula albicollis*) and the pied flycatcher (*F. hypoleuca*) hybridize where their geographic ranges overlap. Restriction fragment comparison of 5% of the mitochondrial genome showed a sequence divergence of 10% between these flycatcher species. This degree of sequence divergence between a closely related pair of bird species is unusually high and contrasts with the low level of divergence between *F. albicollis* and *F. hypoleuca* in nuclear genes (Nei's  $D = 0.0006$ ) revealed by enzyme electrophoresis. The low nuclear differentiation is explained by sex biased gene flow and introgression in nuclear genes (via fertile male hybrids), while the high mitochondrial DNA sequence divergence is preserved by sterility of female hybrids, which prevents mitochondrial introgression. This pattern is in accordance with Haldane's rule and is supported by field data on hybrid fertility. The high

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