

KARYOTYPES OF FIVE SPECIES OF *EMPIDONAX* FLYCATCHERS

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ABSTRACT.—Conventional karyotypic techniques were applied to five species of tyrant flycatchers (*Empidonax*) of the family Tyrannidae in order to determine the extent of chromosome differentiation within the group. The karyotypes of the Alder Flycatcher (*E. alnorum*), the Willow Flycatcher (*E. traillii*), and the Hammond's Flycatcher (*E. hammondi*) appeared identical. The Yellow-bellied Flycatcher (*E. flaviventris*) and the Least Flycatcher (*E. minimus*) possess one and three unique chromosomes, respectively. These data suggest an alternative hypothesis for relationships within the group. Received 11 Aug. 1986, accepted 9 Dec. 1986.

Karyotypic comparisons of closely related bird species are uncommon (Shields 1982), yet specific trends in karyotypic evolution have now been identified for a variety of better understood nonavian lineages (see White 1978:45-106). Such comparisons might help to elucidate trends in avian chromosome evolution. Herein, we describe the chromosomes of five species of *Empidonax* flycatchers and discuss the taxonomic relationships within this group.

MATERIALS AND METHODS

All birds in this study were captured in mist nets during the breeding season. Specimens of the Alder Flycatcher (*Empidonax alnorum*) and the Willow Flycatcher (*E. traillii*) were all of known song type or mated to males of known song type. Karyotypes were obtained from primary cultures of kidney cells according to the procedures of Shields (1983). At least 10 chromosome spreads of high quality were analyzed for each species. Chromosomes were karyotyped using conventional photographic and measurement techniques. Skins and partial skeletons of birds collected in Ontario were deposited in the ornithology collection of the Royal Ontario Museum, Toronto, (specimens and identification numbers: *E. flaviventris* male, ROM#126751; *E. traillii*, 2 males, ROM#114105, ROM#114107; female, ROM#114106; *E. alnorum*, 2 males, ROM#114153, ROM#114155; *E. minimus*, 2 males, ROM#114188, ROM#115134.

RESULTS

Our culture procedures routinely produce excellent, well spread complements from which the chromosomes can be tentatively paired (Fig. 1). For the comparative studies we felt justified in homologously pairing the 12 largest chromosomes. These macrochromosomes, which are usually

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FIG. 1. Complete karyotype of the Alder Flycatcher (*E. alnorum*).

greater than 1μ in length, are shown in Fig. 2 for the five species of flycatchers.

Table 1 lists relative chromosome lengths and arm ratios for all species of this study. Of necessity, we arranged chromosomes in order of decreasing size. The karyotypes of conventionally stained chromosomes of *E. alnorum*, *E. hammondii*, and *E. traillii* appeared identical, with the exception that the *hammondii* sampled was female and thus had Z and W sex chromosomes. The small metacentric chromosome 11 served as a convenient marker. It must be stressed that this alpha level of analysis (White 1978) is only a first approximation of the variability within this group.

The karyotype of the Yellow-bellied Flycatcher (*E. flaviventris*) differs from those just described in that the arm ratio of its first set of chromosomes is clearly smaller (see Fig. 2 and Table 1).

The karyotype of the Least Flycatcher (*E. minimus*) clearly differs from those of the above described species in that chromosomes one, three, and eight possess a unique morphology. No other chromosomes in these respective size ranges among the other species possess such unique morphologies.

DISCUSSION

Our results do not fully support the conventional taxonomy of the group. The chromosomes suggest that *E. alnorum*, *E. traillii*, and *E.*

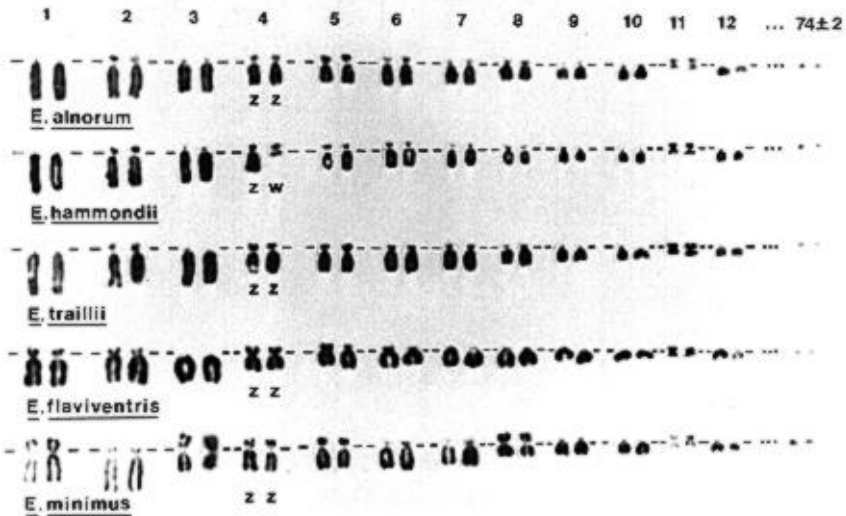


FIG. 2. Karyotypes of the 12 largest chromosomes of five species of flycatchers.

hammondii constitute one natural cluster. *E. flaviventris* differs with regard to the morphology of chromosome one. *E. minimus* appears to form yet a third category.

It is difficult to determine which of the three karyotypes described here is the most primitive. Similarity to some outgroup species would be indicative of common ancestry. Unfortunately, of the nearly 375 other species of tyrant flycatchers recognized worldwide only the Blue-bellied Black Tyrant (*Knipolegus cyanirostris*) has been karyotyped (Lucca and Chamma 1977). Its karyotype is most similar to that of *E. flaviventris*, but chromosome banding studies (Shields 1983) would have to be performed on all species under consideration in order to unequivocally determine the extents of chromosome homology.

Johnson (1980) concluded that *E. traillii* and *E. alnorum* have differentiated the most among several constellations of *Empidonax* flycatchers, but that *E. hammondii* and *E. minimus* are next to them in amount of differentiation. The latter are apparently in an earlier stage of differentiation in his view because they are vocally more similar than *E. traillii* and *E. alnorum*, but they are less similar in morphology and color to each other than they are vocally. Johnson (1980) felt that *E. traillii* and *E. alnorum* are more distinct both vocally and morphologically than *E. hammondii* and *E. minimus*.

TABLE I
RELATIVE LENGTHS AND ARM RATIOS OF THE TWELVE LARGEST CHROMOSOMES OF FIVE FLYCATCHERS

	Chromosome number												
	1	2	3	4	5	6	7	8	9	10	11	12	
Alder Flycatcher													
Relative length	0.138	0.138	0.108	0.101	0.086	0.084	0.079	0.065	0.057	0.050	0.043	0.036	
Arm ratio	1:18.0	1:5.3	1:14.0	1:3.6	1:2.0	1:5.5	1:4.5	1:6.5	1:7.0	1:6.0	1:1.0	1:4.0	
Willow Flycatcher													
Relative length	0.139	0.133	0.119	0.097	0.097	0.084	0.084	0.069	0.056	0.049	0.042	0.035	
Arm ratio	1:19.0	1:5.3	1:16.0	1:3.7	1:3.3	1:5.0	1:5.0	1:6.1	1:8.0	1:6.0	1:1.0	1:4.0	
Hammond's Flycatcher													
Relative length	0.147	0.139	0.124	0.101	0.085	0.085	0.078	0.062	0.054	0.046	0.039	0.039	
Arm ratio	1:18.0	1:5.1	1:17.0	1:3.3	1:3.9	1:4.5	1:5.1	1:7.0	1:6.0	1:5.0	1:1.0	1:4.0	
Yellow-bellied Flycatcher													
Relative length	0.152	0.144	0.110	0.093	0.093	0.085	0.076	0.068	0.051	0.042	0.042	0.042	
Arm ratio	1:2.6 ^a	1:4.7	1:19.1	1:2.8	1:2.7	1:4.0	1:3.5	1:7.0	1:6.1	1:8.1	1:1.0	1:4.8	
Least Flycatcher													
Relative length	0.138	0.131	0.117	0.096	0.096	0.083	0.083	0.076	0.055	0.041	0.041	0.041	
Arm ratio	1:1.9 ^a	1:5.3	1:4.2 ^a	1:2.5	1:2.5	1:5.0	1:3.0	1:1.4 ^a	1:7.0	1:5.0	1:1.1	1:3.0	

^a Indicates chromosomes of unique morphology.

The views of Johnson have now been supplemented and modified by electrophoretic data (Zink and Johnson 1984). These data do not support the hypothesis of a close relationship of *E. hammondii* and *E. minimus*. Indeed, *E. minimus* is moderately distinct from all 11 other congeners with which it was compared according to the protein evidence. Thus, the allozyme data are essentially in agreement with the distinctiveness of *E. minimus* as proposed here on the basis of chromosome morphology. The allozyme data, however, do not necessarily support a particularly close relationship of *E. hammondii*, *E. traillii*, and *E. alnorum*, although the latter two forms are close, as expected.

A solution to the dilemma of nonconvergence between suites of traits using a variety of methodological analyses may be realized when we appreciate that reproductive isolation can be accomplished by various processes, each of which may differ in overall effect and rate. Thus, Templeton (1980) stressed a novel nomenclature for the genetic processes by which reproductive isolation might take place. Such a nomenclature stresses mechanisms which are at the basis of the promotion of reproductive isolation rather than a geographic nomenclature which simply defines whether the incipient species are breeding in sympatry or in allopatry.

Templeton (1980) defines two types of processes that may lead to reproductive isolation but which are markedly different in the way in which the isolation takes place. A *genetic transilience* is defined as reproductive isolation that is accomplished by mutation in a small number of genes but with major effect: Chromosomal rearrangements that become rapidly fixed due to genetic drift are also defined as transiliences. Genetic divergence, as opposed to genetic transilience, occurs when reproductive isolation is accomplished gradually by the effect of mutation on a larger number of genes. Thus, in birds we might expect to see closely related species which are indeed phenotypically similar (e.g., *E. minimus* and *E. hammondii*) but chromosomally distinct. Alternatively, species pairs may be phenotypically divergent (e.g., *E. traillii* and *E. alnorum*), yet they may possess seemingly identical karyotypes.

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WESTERN RAPTOR MANAGEMENT SYMPOSIUM AND WORKSHOP

The Western Raptor Management Symposium and Workshop, coorganized by the National Wildlife Federation and the Idaho Chapter of The Wildlife Society, will be held 26-28 October 1987 in Boise, Idaho. The symposium will feature technical paper sessions on the status of western raptors and their habitats, land-use activities impacting raptors, as well as workshops and a poster session. For more information, contact the National Wildlife Federation, Institute for Wildlife Research, Department 162, 1412 Sixteenth Street, N.W., Washington, D.C. 20036-2266 or call (703) 790-4264.