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SHORT COMMUNICATIONS

Genetic variation in the Common Yellowthroat and some allies.—Considerable effort has been expended to document the nature of genetic variation at protein-coding loci within and among natural populations (Avise and Aquadro 1982, Lewontin 1985). Knowledge of intraspecific genetic variation can elucidate microevolutionary patterns and processes (Barrowclough 1983) and historical patterns of population fragmentation (Felsenstein 1982). Such genetic data also provide a perspective on the extent and organization of genetic variation among species. Relatively few studies of birds describe the geography of intraspecific genetic variation (Corbin 1983, Zink 1986, Zink et al. 1987, Johnson and Martin 1988) and genetic differentiation between species (Avise and Aquadro 1982). In this paper, we describe genetic variation within and among four populations of the Common Yellowthroat (*Geothlypis trichas*) and some congeners. Most of the taxa in the genus (with the exception of *G. poliocephala*) are essentially allopatric; hence, the species in the genus, excluding *G. poliocephala,* might constitute a group of allospecies. Our samples represent various geographic scales: "local scale"—populations of *G. trichas* representing three subspecies within Texas; "continental scale"—the samples from Texas plus Minnesota (*G. t. brachidactylus*) and Baja California (Mexico; *G. beldingi*); and "inter-continental scale"—congeners from Ecuador (*G. semiflava*) and Peru (*G. aequinoctialis*). The populations in south Texas inhabit areas that seem subject to periodic habitat extinctions (Klicka pers. obs.), which might lead to greater differentiation by founder events. Also, some or all of the south Texas samples and that of *G. beldingi* are from presumably resident populations, whereas the Minnesota population is migratory. Most studies of avian intraspecific genetic variation have included only migratory populations, and one might predict greater genetic differentiation among sedentary populations. Two taxa (*G. semiflava* and *G. aequinoctialis*) are considered full species, permitting comparison of within and between-species differentiation. In sum, our samples permit us to estimate the extent of genetic diversity at various levels within a genus distributed over two continents.

Methods.—We obtained tissue samples from 27 individuals in the Common Yellowthroat complex (Table 1); two specimens of *Oporornis* (MacGillivray's Warbler [*O. tolmei*] and Mourning Warbler [*O. philadelphicus*]) were used to estimate the genetic distance between the two genera. Within one hour of death, tissue samples from each specimen were placed on dry ice in the field, and upon return to the laboratory they were maintained at −70°C. Methods for preparation of tissue extracts and protein electrophoresis are documented elsewhere (Johnson et al. 1984, Zink 1986). Samples of tissue are retained in the Frozen Tissue Collection of the Museum of Natural Science, Louisiana State Univ. The computer program BIOSYS-1 (Swofford and Selander 1981) was used to compute allelic frequencies, Nei's (1978) and Rogers' (1972) genetic distances, and to construct a UPGMA phenogram and a distance-Wagner network. A computer program written by G. Barrowclough was used to compute F_{st}-values following Wright (1978); F_{st} is a measure of the amount of genetic variance partitioned among geographic samples.

Results.—Of the 30 loci surveyed, 12 were monomorphic and fixed for the same allele in all taxa: *SOD-1,2* (Enzyme Commission 1.15.1.1), *CK-2* (2.7.3.2), *αGPD* (1.1.1.8), *SDH* (1.1.1.14), *LDH-1,2* (1.1.1.27), *GPI* (5.3.1.9), *MDH-1,2* (1.1.1.37), *LAP* (3.4.11), and a general protein. The remaining 18 loci were variable, either within one of the samples (heterozygote) or between two or more taxa (Table 2). Heterozygosity (Table 1) averaged across taxa is 0.06 (excluding Mourning and MacGillivray's warblers). The percentage of loci that were polymorphic averaged 20.6%. Our samples are too small to test for departures from Hardy-Weinberg equilibrium expectations for genotypic proportions. Nei's (1978)

TABLE 1

TAXA EXAMINED, LOCALITY OF SPECIMENS, SAMPLE SIZE, AVERAGE DIRECT COUNT HETEROZYGOSITY (H), AND PERCENTAGE OF LOCI POLYMORPHIC[a]

Taxon	Locality	N	H	Percent of polymorphic loci
1. *Geothlypis trichas brachidactylus*	Minnesota: Scott Co.	5	0.10	33.3
2. *G. t. chryseola*	Texas: Val Verde Co.	5	0.05	16.7
3. *G. t. insperata*	Texas: Cameron Co.	5	0.10	26.7
4. *G. t. trichas*	Texas: Aransas Co.	6	0.06	20.0
5. *G. beldingi*	Mexico: Baja California Sur	3	0.03	6.7
6. *G. aequinoctialis auricularis*	Peru: Dpto. Lambaueque	2	0.10	20.0

[a] Values for the single individuals of *G. semiflava* (sample 7, from Ecuador: Prov. Pichincha), *Oporornis tolmei* (sample 8, Louisiana: Cameron Par.), and *O. philadelphia* (sample 9, Louisiana: Cameron Par.) are not reported.

genetic distance (not shown; available from authors or can be computed from the data in Table 2) averaged 0.006 among the three Texas samples, 0.009 for Texas plus Minnesota samples, 0.034 for the North American samples, and 0.070 ± 0.04 (SD) for the North and South American samples. Values of F_{st} followed a similar pattern: 0.04, 0.04, 0.14, and 0.21 for these levels of comparison, respectively. Adding *G. beldingi* to the comparisons substantially increased the level of genetic differentiation, as does adding the South American taxa. To examine the relationship between geographic and genetic distance among samples, we computed a rank-order correlation coefficient between the two sets of values, in essence an examination of the isolation-by-distance effect. The correlation coefficient of 0.66 ($P \leq 0.05$) indicates a significant positive relationship between geographic distance and genetic differentiation. We included samples of *G. semiflava* and *G. aequinoctialis* on the hypothesis that the entire complex constitutes a recently evolved group of allospecies; otherwise, considering genetic differentiation among sympatric congeners has no necessary significance in relation to geography. The average genetic distance from the two *Oporornis* species to the yellowthroats was 0.109.

The two branching diagrams (not shown, available from authors) based on Rogers' (1972) genetic distance revealed the following: the Texas samples cluster together and are most similar to the Minnesota sample, and the remaining taxa are rather distinct from the aforementioned group and each other; we lack confidence in the pattern of relationships among the species.

Discussion.—Levels of genetic variation (Table 1) within our population samples are consistent with those observed for other birds (Corbin 1983). Of interest are the values of F_{st}. For most bird species, F_{st} is less than 0.05 (Barrowclough 1983). This value was obtained from relatively few studies of migratory temperate passerine birds, many of which did not span the entire range of the species. Our value of 0.04 for North American *Geothlypis* (excluding *G. beldingi*) exceeds that found by Zink (1986) in a survey of the highly phenotypically differentiated Fox Sparrow (*Passerella iliaca*) over a similar geographic extent and is similar to that found by Johnson and Zink (1983) for the sapsucker superspecies *Sphyrapicus varius* (which also includes *S. ruber* and *S. nuchalis*). Hence, the partitioning by taxonomists of phenotypic variation in *G. trichas* into 12 subspecies (Lowery and Monroe

TABLE 2

ALLELIC FREQUENCIES FOR VARIABLE LOCI[a]

Locus (E.C. No.)	Sample 1	2	3	4	5	6	7	8	9
EST-D	A	A	A	A	A	A (0.75) B (0.25)	A	A	A
NP	A	A	A	A (0.92) B (0.08)	A	A (0.5) C (0.5)	A	A	A
LA1	A (0.8) B (0.2)	A	A	A	A	C (0.75) D (0.25)	A	A	A
LA2	A (0.7) B (0.1) C (0.2)	A (0.7) C (0.3)	A	A	A	A (0.75) D (0.25)	A	A	A
LGG	A (0.9) B (0.1)	A	A	A	A	A	A	A	A
EAP	A	A	A (0.9) B (0.1)	A	A	A	A	A	A
GSR	A (0.6) B (0.4)	A (0.9) B (0.1)	A (0.9) C (0.1)	A	A	A	A	A	A
MPI	A (0.5) B (0.5)	A	A (0.7) B (0.2) C (0.1)	A (0.42) B (0.58)	A	A	B	A	A (0.5) B (0.5)

TABLE 2
CONTINUED

Locus (E.C. No.)	Sample 1	2	3	4	5	6	7	8	9
ADA	A (0.8) B (0.2)	A	A (0.7) C (0.3)	A	A (0.17) D (0.83)	A (0.25) D (0.5) E (0.25)	A	A	A
CK2	A	A	A (0.9) B (0.1)	A (0.92) C (0.08)	A	A	A	A	A
CGOT	A (0.9) B (0.1)	A	A	A	A	A	A	A	A
MGOT	A	A	A	A	A	A (0.75) B (0.25)	A	A	A
PGM	A	A (0.5) B (0.5)	A (0.7) B (0.3)	A (0.67) B (0.33)	A	A	A	A	A
GPD	A	A	A (0.9) B (0.1)	A	A	A	A	A	A
ICD	A (0.9) B (0.1)	A	A	A	A	A	A	A	A
FUM	A	A	A	A	B	C	C	C	A
ACON	A (0.7) B (0.1) C (0.2)	A (0.9) C (0.1)	A	A (0.92) B (0.08)	A	A	A	C	C
PPRO	A (0.7) B (0.2) C (0.1)	A (0.7) C (0.3)	A (0.6) B (0.1) C (0.3)	A (0.6) B (0.1) C (0.3)	A (0.67) D (0.33)	C	E	A	F

[a] Numbers in parentheses are frequencies; samples are identified in Table 1; locus nomenclature follows Gerwin and Zink (1989).

1968) seems consistent with a relatively high degree of genetic differentiation, but study of other subspecies is necessary. Our genetic data are equivocal with respect to the influence of bottlenecks in south Texas and the migratory status of populations. For example, the average genetic distance among the three Texas samples, 0.006, is very low and is 50% of the average between the Texas and Minnesota samples, 0.012. Thus, geographic distance among demes (even when one, e.g., Minnesota, is migratory) seems more important than bottlenecking in promoting genetic differentiation in yellowthroats. However, the F_{st} of 0.04 among the samples from Texas and Minnesota is relatively high, and comparison of other migratory populations the same distance apart as our resident Texas populations is needed to distinguish between geographic distance and migratory tendency as influences on genetic differentiation (the three Texas samples could be part of a larger lineage that went through a bottleneck). In general, our data indicate that genetic surveys of nonmigratory avian species are needed to further our understanding of avian genetic population structure.

The taxonomic status of *G. beldingi* is uncertain, and has been considered a subspecies of *G. trichas* (Mayr and Short 1970) rather than a distinct species. The F_{st} value for the group including *G. beldingi,* 0.14, is higher than found for most avian intraspecific comparisons, suggesting that the group is: (1) simply older than most species surveyed electrophoretically, (2) monophyletic but containing two species, or (3) paraphyletic. In terms of F_{st} and genetic distance (0.07 from samples of *G. trichas*), *G. beldingi* is differentiated at a level consistent with most avian species, although genetic distance cannot be the sole arbiter of species limits (Johnson and Zink 1983).

Our F_{st} estimate of 0.21 calculated over the species of *Geothlypis* surveyed indicates considerable differentiation. Because *G. aequinoctialis* and *G. semiflava* are considered specifically distinct from *G. trichas,* our computation of F_{st} reflects a category such as allospecies, rather than the typical intraspecific meaning of this value. Genetic differentiation in the genus seems, based on our limited comparisons, to be consistent with other well differentiated avian genera. Others (e.g., Capparella 1988, Gerwin and Zink 1989) have documented considerable genetic differentiation within neotropical avian lineages relative to temperate lineages. However, the genetic distance from *G. semiflava* and *G. aequinoctialis* to the other taxa averages 0.10, which is within the range of values detected among temperate congeners. Thus, our data are consistent with the possibility that the species in *Geothylpis* are relatively recently evolved.

Our data set is limited in number of loci and in the sampling of taxa (and individuals) present in the genus. Hence, we are cautious in interpreting our data in a phylogenetic sense. The two *Oporornis* species are differentiated from *Geothlypis* at an average genetic distance (Nei 1978) of 0.11, a value exceeding that reported by others (Barrowclough and Corbin 1978, Avise et al. 1980); however, the same loci and species were not surveyed in these studies. The value of 0.11 is somewhat low for avian intergeneric comparisons, and future workers should evaluate the possibility of combining *Oporornis* and *Geothlypis,* as they are in some checklists. The main conclusion we draw is that the North American samples of *G. trichas* excluding *G. beldingi* seem genetically cohesive, and they may be a sister taxon to *G. beldingi. Geothlypis beldingi* is genetically closer to North American samples (D = 0.07) than to *G. aequinoctialis* (D = 0.097) or *G. semiflava* (D = 0.122). However, further interpretation awaits phylogenetic resolution of all *Geothlypis,* which is currently under study (P. Escalante P. pers. comm.).

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Growth of Monk Parakeets.—Growth characteristics of nestlings vary considerably among bird species. These may result from the diverse selective pressures these species experience. For example, species with open nests are more prone to predation and may have evolved comparatively high growth rates in order to reduce the time in the nest (Lack 1968). Also intra-specific variations in growth parameters among years or in relation to hatching order indicate that the ability of growth processes to respond to different conditions may have adaptive value (Ricklefs 1968, 1976).

Parrots offer interesting material for analysis in this respect, due to their extreme altriciality, slow growth, and completely asynchronous hatching. Unfortunately, data for the group are scarce. Growth curves are known for only seven species, and for most the data come from captive birds (Caccamise and Alexandro 1976; Caccamise 1980; Saunders 1982, 1986; Bucher 1983; Stamps et al. 1985). Unique among the Psittaciformes, the Monk Parakeet (*Myiopsitta monachus*) is not a true cavity-nester since it builds large enclosed communal nests made of sticks where several pairs breed independently (Forshaw 1973; Martella 1985).

In this work, we present the parameters that describe the growth curve of nestlings of *Myiopsitta monachus catita* in a wild population and examine their variation among years and in relation to the hatching order within a brood.

Study area and methods.—The study was carried out in an area of 600 ha, situated near Jesús María, Córdoba, Argentina (31°05'S, 64°11'W).

From the pre-laying period to fledging time (November to March) in 1985–1986, 1986–1987 and 1987–1988, all the parakeet nests situated below 7 m height were checked. In order to minimize disturbance caused by the observers, visits were spaced nine days on average (range 7–12).

The eggs were measured to the nearest 0.1 mm (length and breadth), weighed to the nearest 0.1 g, and individually marked with indelible ink. After hatching, the nestlings were initially identified by toenail clipping. Later they were banded with numbered aluminum bands. On each visit, the nestlings were weighed to the nearest 0.1 and 1 g, for the weights under and over 10 g, respectively.

All the nestlings found dead in the nest, as well as those that disappeared before the minimum fledging age (estimated as 35 days), were excluded in our calculations. Seven successful nestlings that showed signs of malnutrition or weight recession at an early age were not included. Also, and due to the fact that in this species there is a recession of weight at fledging, we truncated the data of each successful nestling at the maximum mass value observed up to 36 days after the first visit.

Logistic curves were fitted by following the trial-and-error least-squares method proposed by Brown (1979), which is based on testing the goodness of fit of a series of logistic growth curves generated by varying stepwise the parameters A, K, and W_0 (see definitions below) in all combinations over a reasonable range for each one of them. This method adapts better