

Population genetic structure and vocal dialects in an amazon parrot

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The relationship between cultural and genetic evolution was examined in the yellow-naped amazon *Amazona aurocollata*. This species has previously been shown to have regional dialects defined by large shifts in the acoustic structure of its learned contact call. Mitochondrial DNA sequence variation from a 680 base pair segment of the first domain of the control region was assayed in 41 samples collected from two neighbouring dialects in Costa Rica. The relationship of genetic variation to vocal variation was examined using haplotype analysis, genetic distance analysis, a maximum-likelihood estimator of migration rates and phylogenetic reconstructions. All analyses indicated a high degree of gene flow and, thus, individual dispersal across dialect boundaries. Calls sampled from sound libraries suggested that temporally stable contact call dialects occur throughout the range of the yellow-naped amazon, while the presence of similar dialects in the sister species *Amazona ochrocephala* suggests that the propensity to form dialects is ancestral in this clade. These results indicate that genes and culture are not closely associated in the yellow-naped amazon. Rather, they suggest that regional diversity in vocalizations is maintained by selective pressures that promote social learning and allow individual repertoires to conform to local call types.

Keywords: vocal dialects; population genetic structure; *Amazona*; parrot vocal communication; vocal learning

1. INTRODUCTION

The relationship between cultural and genetic evolution was identified by Wilson (1998) as one of the 'great remaining problems of the natural sciences' (p. 2049). Studies of the inheritance of learned communication signals have figured prominently in the effort to understand this relationship (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985; Kroodsma *et al.* 1985; Sokal *et al.* 1990; Catchpole & Slater 1995; Piazza *et al.* 1995; Cavalli-Sforza 1997; Wilson 1998). These studies have been largely restricted to either humans or songbirds. While both humans and songbirds are well known for their ability to learn complex communication signals, contrasting patterns have emerged regarding the relationship between genes and learned signals in these two groups. For traditional human societies there is mounting evidence that language variation is often highly correlated with variation in neutral genes, suggesting that transmission of language has been primarily vertical (i.e. from parents to offspring) (Sokal *et al.* 1990; Piazza *et al.* 1995; Cavalli-Sforza 1997) although some exceptions have been noted (Ward *et al.* 1993; Chu *et al.* 1998; Monsalve *et al.* 1999). Conversely, studies of male song in oscine songbirds have generally not found a strong association between vocal and genetic variation (Kroodsma *et al.* 1985; Fleischer & Rothstein 1988; Payne & Westneat 1988; Loughheed & Handford 1992; Catchpole & Slater 1995) suggesting that horizontal or oblique transmission (i.e. between unrelated individuals) is more common (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985). It remains uncertain whether these differences in transmission patterns are related to differences in the communicative functions of human language versus bird

song or are simply a by-product of differences in life-history traits such as the timing of dispersal relative to vocal learning. Expanding the scope of such studies to other taxa with vocal learning could offer insight into the origin of these differences.

The parrots (order Psittaciformes) are thought to have evolved their impressive vocal learning abilities independently of the songbirds (Nottebohm 1972; Striedter 1994) and, thus, represent an independent opportunity for examining the relationship between genes and culture. Here we examine the association between genes and culture in a parrot species, the yellow-naped amazon (*Amazona aurocollata*).

Yellow-naped amazons in Costa Rica exhibit large regional dialects that are characterized by large-scale shifts in acoustic structure for a given call type (Wright 1996). Although first described for the contact calls, the most common call class in this species' repertoire, dialects are now known to extend across multiple vocal classes (Wright 1997; Wright & Dorin 2001). All classes show shifts in acoustic structure at the same discrete boundaries (Wright 1997) as typically found in human languages. Dialects are comprised of eight to ten communal night roosts each comprising 50–200 birds. Most birds attending a roost within a dialect only use calls specific to that dialect; the rare exceptions are some birds at roosts bordering two dialects that produce the calls of both neighbouring dialects (Wright 1996). Many call classes are used by both sexes in similar contexts both within and outside of the mating season (Wright 1996, 1997). Playback experiments using one of these functional classes, the pair duet, revealed strong reactions by nesting pairs to duets from their own dialect but not those of neighbouring dialects, confirming that parrots attend to dialect differences (Wright & Dorin 2001). The multiclass nature of these parrot dialects and their occurrence in

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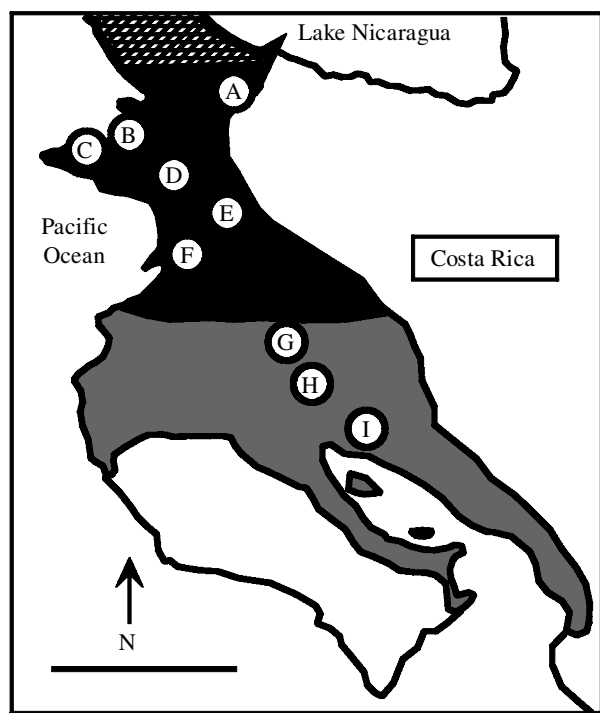


Figure 1. Genetic sampling locations from two dialects of the yellow-naped amazon in north-western Costa Rica. Sites with number of samples in parentheses for north dialect (black shading): A, Inocentes (two); B, Cuaniquil (three); C, Bahía Santa Elena (one); D, Santa Rosa (eight); E, Ahogados (seven); F, Playa Cabuyal (two). Sites with number of samples in parentheses for south dialect (grey shading): G, Pelon Bajura (nine); H, Llano Cortes (seven); I, Tamarindo (two). The hatched area indicates the southern extension of the Nicaragua dialect (Wright 1996), which was not sampled in this study. Scale bar, 50 km.

calls used by both sexes stand in sharp contrast to songbird dialects which primarily occur in a single class, the song of males (Marler & Tamura 1962; Nottebohm 1969; Catchpole & Slater 1995).

In this study we compared geographical variation in vocalizations to variation in the first domain of the mitochondrial control region. This region evolves very rapidly in birds (Quinn & Wilson 1993; Baker & Marshall 1997) and, thus, provides a highly sensitive assay for intra-specific genetic structure. We examined the distribution of genetic variation between two dialects using haplotype analysis, genetic distance analysis, a maximum-likelihood estimator of migration rates and phylogenetic reconstruction. We also used spectrographic analysis of archived calls from sound libraries for estimating the extent and temporal stability of dialects in the yellow-naped amazon and a related species.

2. MATERIAL AND METHODS

In order to determine whether dialect boundaries are associated with restricted gene flow we obtained genetic samples from 41 matrilineal (nesting females or a single nestling per nest) at nine sites spanning two adjacent dialects in Costa Rica (figure 1). We sampled one captive individual each from the yellow-headed amazon *Amazona oratrix* and the yellow-crowned amazon

Amazona ochrocephala, two species long considered to form a super-species with *A. aurophalliata* (Forshaw 1989), for outgroups. We extracted DNA from either feather tips or blood samples preserved in lysis buffer (Longmire *et al.* 1992) with QIamp tissue extraction kits (QIAGEN, Valencia, CA, USA). We amplified 680 base pairs of the first domain of the mitochondrial control region and the flanking region using a polymerase chain reaction (PCR) with the primer LThr (5'-TGGTCTTGTAAC-CAAAGA-3') (designed by T. Wright) located in tRNA^{Thr} and the primer CR522Rb (5'-TGGCCCTGACYTAGGAACCAG-3') (A. Cooper, personal communication) located in the conserved D-block of the control region (Quinn & Wilson 1993). Annealing temperatures of 50–55 °C were used. The single PCR product was visualized on ethidium bromide-stained 1% agarose gels. We sequenced both strands of the products with the amplifying primers using Big Dye cycle sequencing chemistry (PE Applied Biosystems, Foster City, CA, USA) and an ABI 310 genetic analyser. A portion of this segment is thought to undergo sporadic gene conversion events with a second duplicate control region in the mitochondria (J. Eberhard, T. Wright and E. Bermingham, unpublished data). Although there is the potential for such conversions to obscure phylogenetic signals our analyses did not show any major differences between separate trees constructed from converting and non-converting portions of this sequence. Thus, the entire segment was used in all analyses below.

Sequences were aligned using the Clustal routine in Mega-Align 1.1 (DNASTAR). The sequences are deposited in Genbank (accession numbers AF323131–AF323173). Haplotypes for the *A. aurophalliata* sequences were identified using Collapse 1.1 (D. Posada); we conservatively excluded seven ambiguous sites that apparently represent heteroplasmic polymorphisms (Wilkinson & Chapman 1991).

In order to determine whether genetic distances are correlated with dialect membership we calculated Tamura–Nei genetic distances (Tamura & Nei 1993) between all *A. aurophalliata* sequences. We then compared this matrix of pairwise genetic distances between individuals to a similarity matrix of dialect membership using the Mantel (1967) test for association between two distance matrices. We also constructed a matrix of geographical distances between sampling sites and employed a multiple correlation extension of the Mantel test (Smouse *et al.* 1986) in order to examine the partial correlation between Tamura–Nei genetic distances and dialects after removing the potentially confounding effect of geographical distance on genetic distance. We used the program Haplo2 v.2 (Lynch & Crease 1990) to calculate N_{st} , a measure of population subdivision at the nucleotide level.

We estimated the effective number of migrants per generation (N_{em}) between the two *A. aurophalliata* dialects using the program Migrate-n, a maximum-likelihood method based on coalescence theory (Beerli & Felsenstein 1999). We simultaneously estimated N_{em} , the product of the effective population size and migration rate and $N_{e\mu}$, the product of the effective population size and mutation rate, for ten replicate runs using our control region sequences. We used the default parameters for all runs with the exception of the number of trees sampled in each chain (20 000 for short chains and 200 000 for long chains) and the transition:transversion ratio (see below). These values generally provide adequate sampling of genealogies for obtaining accurate maximum-likelihood estimates of the migration and mutation parameters (Beerli & Felsenstein 1999).

We created maximum-parsimony and maximum-likelihood phylogenies with PAUP 4.0b2a (Swofford 1999). Optimal

Table 1. Pairwise Tamura–Nei genetic distances within and between dialects using mitochondrial control region sequences from two dialects of the yellow-naped amazon

pairwise comparison	minimum	maximum	mean
within-north dialect	0.0	0.056	0.030
within-south dialect	0.0	0.053	0.024
north versus south	0.0	0.054	0.027

parameters for maximum-likelihood searches were obtained using Modeltest 2.0 which identifies the most appropriate model of DNA substitution for a given data set from among 40 alternative models using hierarchical likelihood ratio tests (Posada & Crandall 1998). For our data these parameter values corresponded to the Hasegawa–Kishino–Yano model with a transition:transversion ratio of 12.7, invariable sites (proportion = 0.64), rate heterogeneity (gamma distribution shape parameter = 0.52) and no molecular clock enforced. For the maximum-parsimony searches we set all characters to be unordered and of equal weight with gaps treated as a fifth base and multistate taxa treated as polymorphisms. We obtained starting trees for both optimality criteria via stepwise addition and used a tree bisection–reconnection branch-swapping algorithm. We conducted a single heuristic search using the likelihood criteria and 500 bootstrap replicates of heuristic searches using parsimony criteria. We treated dialect membership as a single discrete character with three states (north, south and other) and compared the number of character state changes in our maximum-likelihood trees to the number of changes in randomly generated trees with the same taxa using MacClade 3.08a (Maddison & Maddison 1992).

We used recordings deposited in sound libraries for assaying the extent of geographical variation in the contact calls of *A. auropalliata* and its sister species *A. ochrocephala*. Contact calls were the most common call type in our initial studies documenting dialects in Costa Rican populations of the yellow-naped Amazon, representing 46% of the 19 449 calls recorded (Wright 1997). These calls exhibited only fine-scale variation among individuals and roosts within dialects when compared to the large differences in acoustic structure between dialects (Wright 1996). Although the holdings of the sound libraries were not extensive enough to permit the same degree of sampling used in those earlier studies, they did allow us to assess whether large-scale differences in acoustic structure consistent with the presence of dialects occur throughout the range of these two species. We made spectrograms of contact calls from *A. auropalliata* and *A. ochrocephala* from recordings by T. Wright, J. Gilardi and others deposited in the archives of the Cornell Library of Natural Sounds (accession numbers 8436, 8438, 37 282, 51 909, 57 785, 58 279 and 82 321) and the Florida Museum of Natural History (accession numbers 873-12, 143-21, 1133-13 and 1359-28) using Canary 1.2 (Cornell Laboratory of Ornithology). We selected a single example of the most common call used by a recorded individual as a representative contact call for a site with the exception of three cases where recordings from the same site in different years allowed additional temporal comparisons of calls presumably from different individuals. For 8 out of the 12 sites multiple recordings confirmed that the selected call represented the most common call type at that site. In order to test for acoustic differences between the two species we measured the frequency of peak energy, the total duration

Table 2. Results of Mantel tests comparing matrices of genetic distances, geographical distances and dialect membership for pairs of samples

matrices of pairwise comparisons	Mantel's r	P
genetic distance versus dialect membership	−0.02	0.25
genetic distance versus geographical distance	−0.07	0.09
genetic distance versus dialect membership after controlling for geographical distance	0.05	0.22

and the lowest and highest frequencies of the fundamental frequency using on-screen cursors in Canary 1.2. Insufficient recordings were available for *A. oratrix* to determine the extent of geographical variability in that species.

3. RESULTS

Four lines of evidence indicated that cultural boundaries do not restrict genetic exchange in yellow-naped amazons. First, mitochondrial DNA haplotypes showed no segregation by dialects. We found 19 haplotypes defined by 59 variable sites. Comparison of the haplotype frequencies revealed no difference between dialects (χ -perm test with 1000 permutations, $\chi^2 = 18.8$ and Monte Carlo, $P = 0.39$) (Hudson *et al.* 1992). The proportional base composition of the light strand (A = 0.27, C = 0.26, G = 0.17 and T = 0.29) and transition:transversion ratio (Tr:Tv = 12.7) were similar to those found in domain I of other avian control regions (Baker & Marshall 1997). There were no insertions or deletions among *A. auropalliata* sequences and only two insertions or deletions between *A. auropalliata* and the two outgroup sequences.

Second, genetic distances were no greater between dialects than within dialects. We found a high degree of genetic variation among samples, with an average pairwise Tamura–Nei distance among all samples of 0.028. Pairwise genetic distances between samples drawn from the same dialect were no smaller, on average, than those drawn from different dialects (table 1). Mantel tests revealed no effect of dialect membership on pairwise genetic differences either before or after controlling for geographical distance (table 2). $N_{st} = -0.003$ for the two dialect populations, a value that was not significantly different from zero, indicating no genetic structure related to dialect (Lynch & Crease 1990).

Third, the maximum-likelihood estimator of gene flow indicated substantial movement between dialects. Ten replicate runs gave a mean \pm s.e. of 8.4 ± 1.2 for $N_c m$ and of 0.046 ± 0.003 for $N_c \mu$, where N_c is the effective population size, m is the migration rate per generation and μ is the mutation rate per generation. This value is likely to underestimate the true rate of movement between dialects as it only includes females who both migrated and successfully reproduced in their new dialect.

Fourth, phylogenetic reconstructions provided no evidence of reciprocal monophyly between dialects. Coalescence theory predicts that individuals from the two

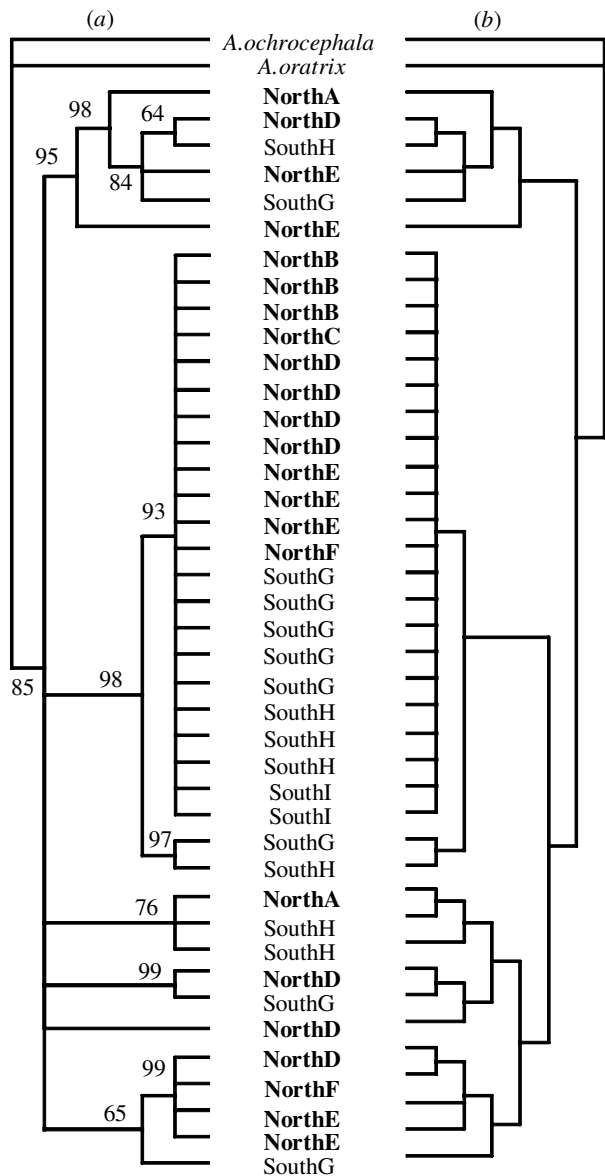


Figure 2. Two phylogenies of mitochondrial control region sequences; both show that variation between matriline is not structured by dialect. Instead, closely related individuals are commonly found at widely separated sites in both dialects. (a) The bootstrap consensus tree of 500 heuristic parsimony searches with bootstrap support values indicated by each node. (b) The strict consensus of the six equally likely trees obtained using maximum likelihood. Both phylogenies are rooted with sequences from the outgroup taxa *A. ochrocephala* and *A. oratrix*. Individual names correspond to the dialects and sites described in figure 1 and are coded by dialect of origin (italic, outgroups; bold, north; Roman, south).

dialects will form reciprocally monophyletic clades if no dispersal occurs between dialects for $4N_e$ generations, where N_e is the effective population size (Barton & Wilson 1996). In this case the distribution of dialects as character states on a phylogeny could be explained by one transition in dialect state. Alternatively, if dispersal is frequent among dialects, then individuals from both dialects should be distributed throughout the tree and the number of character state changes should not differ from those expected on randomly generated trees (Maddison

& Slatkin 1991). Tracing dialect character state changes onto the six best trees obtained from a heuristic search using maximum likelihood (figure 2) resulted in a mean of 14 steps required to explain the observed distribution of dialects as compared to a mean of 13.4 steps for 50 randomly generated trees with the same taxa (t -test, d.f. = 54, $t = -0.98$ and $p = 0.33$). The bootstrap consensus from 500 parsimony searches produced a tree that differed from the likelihood consensus tree only in the degree of resolution of one clade (figure 2). In both consensus trees most terminal clades contain individuals from both dialects, providing further evidence of extensive gene flow among dialects.

Recordings deposited in sound archives indicated that variation in the acoustic structure of contact calls consistent with the presence of dialects occurs throughout the range of the yellow-naped amazon (figure 3). Contact calls are short (0.2–0.4 s), overtone-rich notes throughout the range of this species with the bulk of spectral energy falling between 1 and 3 kHz. However, there was considerable variation between sites in the pattern of frequency modulation through a call (figure 3). In contrast to this geographical variability, there were two cases in which there was a high degree of structural similarity between calls recorded over a decade apart at the same site (figure 3). Sound recordings from the same sources revealed a similar pattern of geographical variability and temporal stability in the contact calls of *A. ochrocephala* (figure 3). Comparisons between the two species revealed no difference in the mean duration of the call and either the lowest or highest frequencies of the fundamental frequency, results indicative of the high degree of structural variability within each species. However, there was a significant difference between the species in the frequency of the peak energy of their calls (table 3) suggesting that this acoustic feature may be a conserved trait that is suitable for species recognition.

4. DISCUSSION

All the genetic measures examined here indicated high levels of gene flow across dialect boundaries. We conclude that the persistence of dialects in the yellow-naped amazon is best explained by dispersal of individuals across dialect boundaries followed by post-dispersal vocal matching of most classes of the vocal repertoire. This dispersal is sufficient to prevent any genetic divergence between dialects, contrary to predictions of the long-standing hypothesis that avian dialects contribute to reproductive isolation between populations (Mayr 1942; Marler & Tamura 1962; Nottebohm 1972). A similarly low degree of correspondence between population genetic structure and dialect boundaries has been found for a number of songbird species (Fleischer & Rothstein 1988; Payne & Westneat 1988; Loughheed & Handford 1992). The results have been less clear-cut in a few other species, with genetic discontinuities apparent at some but not all dialect boundaries (Kroodsma *et al.* 1985; Balaban 1988). In contrast, studies in humans have repeatedly found a strong correspondence between geographical variation in neutral genes and languages (Barbujani & Sokal 1990; Sokal *et al.* 1990; Chen *et al.* 1995; Piazza *et al.* 1995; Cavalli-Sforza 1997) although some exceptions to these

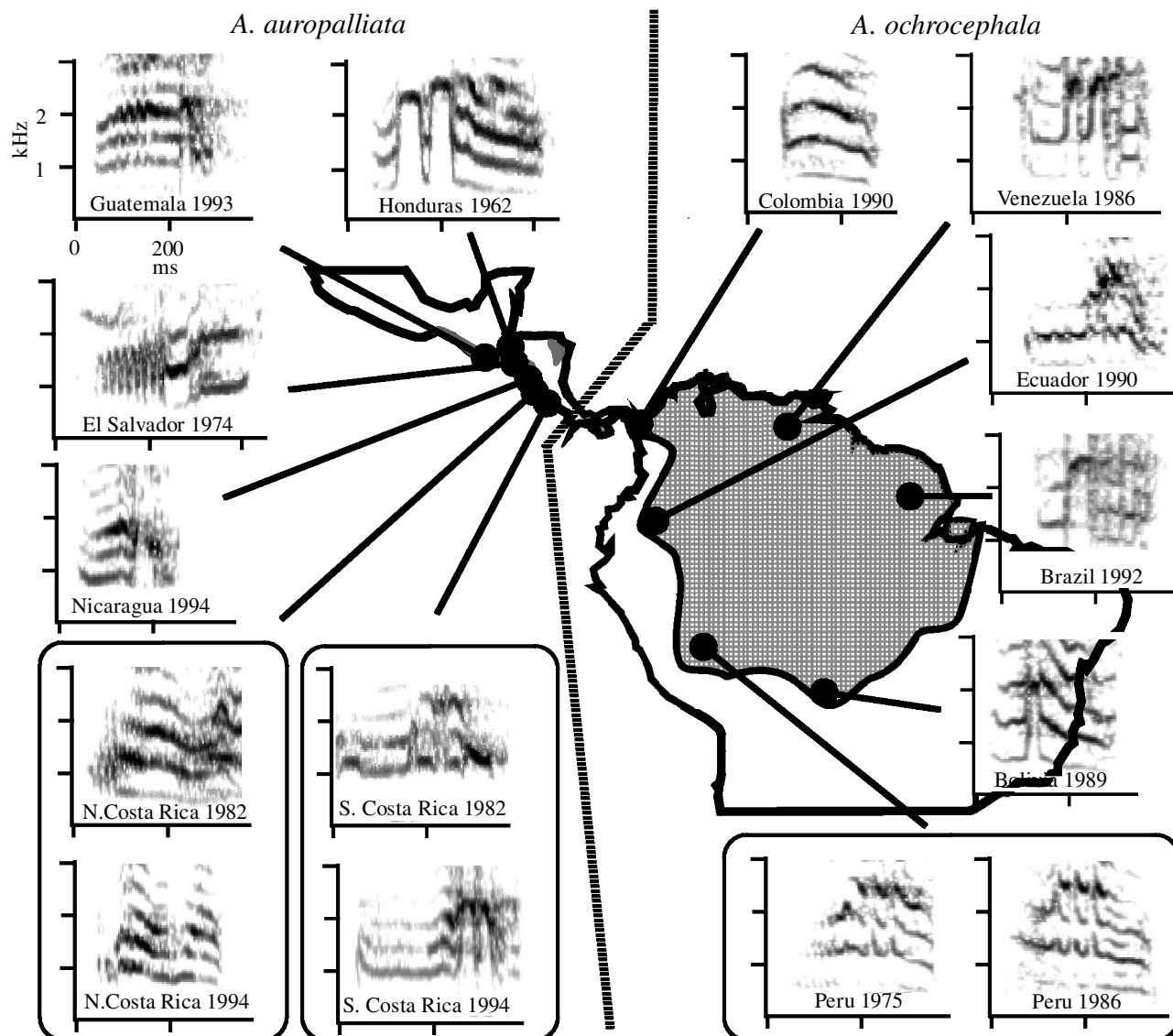


Figure 3. Dialect variation in amazon parrot contact calls. Spectrograms illustrate extensive variation in contact call structure consistent with the presence of vocal dialects throughout the range of the yellow-naped amazon (light shading) in Central America and the closely related yellow-crowned amazon (hatching) found in South America. Three locations (south Costa Rica, north Costa Rica and Peru) have spectrograms of calls from two different years.

patterns have been noted. These exceptions appear to correspond to either rare cases of language replacement or genetic admixture between two linguistically distinct populations (Cavalli-Sforza 1997; Chu *et al.* 1998) or cases in which the underlying classification of language variation remains uncertain (Ward *et al.* 1993; Monsalve *et al.* 1999). Thus, there appears to be a real difference between humans and birds in the degree of coevolution of genetic and cultural traits.

Why should patterns of coevolution between genes and learned communication signals differ so strongly between humans and birds? One possibility is that these differences reflect qualitative differences in the modes of cultural transmission that predominate in each group. Predominantly vertical transmission of human languages from parents to children could account for the strong correspondence between language variation and genetic variation. Conversely, the lack of such correspondence in both parrots and songbirds suggests that horizontal or

oblique transmission between unrelated individuals commonly occurs in these taxa. Both humans and songbirds are known to have temporally defined sensitive periods for vocal learning (Doupe & Kuhl 1999). In humans this period of maximal learning occurs between birth and puberty (Doupe & Kuhl 1999), a period during which children typically remain with their parents. In contrast, in white-crowned sparrows (*Zonotrichia leucophrys*), the songbird species for which the learning process is best understood, the critical period for song memorization extends through the time of juvenile dispersal (Nelson 1998). Furthermore, many parrot species are well known for their abilities to learn vocalizations as adults (Forshaw 1989; Farabaugh *et al.* 1994; Pepperberg 1994) suggesting that dependence on a sensitive period is reduced or perhaps entirely absent in parrots (but see Rowley & Chapman 1986). Thus, the presumed differences in transmission patterns could simply arise from differences in the timing of dispersal relative to the period of maximal

Table 3. Comparisons of acoustical measures of contact calls (means \pm s.e.) shown in figure 1 of the yellow-naped amazon (*A. auropalliata*) and the yellow-crowned amazon (*A. ochrocephala*)

(Only the most recently recorded call for each site was included in the analysis ($n = 6$ calls per species). The asterisk indicates a p -value for a t -test significant at $\alpha < 0.05$ after Bonferroni correction for multiple tests.)

acoustical parameter	<i>A. auropalliata</i>	<i>A. ochrocephala</i>	t	p
frequency of peak energy in call (Hz)	1737 \pm 152	2317 \pm 98	3.2	0.009*
lowest frequency of fundamental (Hz)	445 \pm 39	515 \pm 41	0.5	0.620
highest frequency of fundamental (Hz)	1902 \pm 284	1460 \pm 304	1.2	0.240
call duration (ms)	311 \pm 26	294 \pm 20	1.1	0.310

learning. However, this mechanistic explanation is incomplete because both the timing of dispersal and the extent and timing of critical periods for learning have presumably evolved in response to selection. The ultimate explanation for these differences between humans and birds probably lies in presumed differences in the communicative functions of human language and avian vocalizations.

In this study we assayed variation in the first domain of the control region, the most rapidly evolving portion of the mitochondrial genome (Quinn & Wilson 1993). The rapid accumulation of mutations in this region coupled with the smaller effective population size of the mitochondrial genome (Avice 1994) provides a more sensitive assay of population structure than the allozyme markers used in most previous studies of avian dialects. Indeed, we did record a high level of sequence variation among our yellow-naped amazon matriline. Nevertheless, our measure of N_{st} for parrot dialects was no greater than previous estimates of F_{st} from allozyme data for dialects in Nuttall's white-crowned sparrows (*Zonotrichia leucophrys nuttalli*) (Zink & Barrowclough 1984), rufous-crowned sparrows (*Zonotrichia capensis*) (Lougheed & Handford 1992) and indigo buntings (*Passerina cyanea*) (Payne & Westneat 1988). One limitation of mitochondrial DNA is that it only measures the gene flow of maternal lineages. Although previous studies in the rufous-crowned sparrow found few differences between the distribution of mitochondrial and allozymic variation across vocal dialects (Lougheed & Handford 1992, 1993), it remains possible that the high gene flow we report for the mitochondrial genome is representative of female movements only. Examination of nuclear markers such as microsatellites could reveal a different pattern in the yellow-naped amazon, as recently found for red grouse (*Lagopus lagopus scoticus*) (Piertney *et al.* 2000). Although the general pattern in temperate resident songbirds is one of male philopatry (Greenwood 1980), the extent of sex-biased dispersal in parrots is unknown. Nonetheless, our results clearly imply that at least one sex of yellow-naped amazons is capable of learning its vocal repertoire after dispersal.

It remains possible that current dialect boundaries do restrict dispersal, but dialect origins are too recent for sequence variation to have accumulated in the control region. Although it is difficult to exclude this hypothesis in the absence of direct observations of cross-dialect dispersal, available evidence suggests that the dialects examined here are not recent phenomena. We found acoustic variation consistent with the presence of dialects throughout the range of both *A. auropalliata* and *A. ochrocephala* and at some sites there has been no

obvious change in contact call structure over a decade. The third species in the clade, *A. oratrix*, is reported to have regional dialects that are stable over three decades (M. Schindlinger, personal communication). Thus, the presence of temporally stable dialects appears to be characteristic of all three species and the propensity to form such dialects can be inferred to have been present in the common ancestor of this clade.

The maintenance of stable dialects in the face of high dispersal requires social learning to match local vocal repertoires, a phenomenon that has been termed the 'conformist' transmission of cultural traits (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985) or 'social selection' (Nettle 1999). While rapid convergence of call structure has been observed in captive budgerigars (Farabaugh *et al.* 1994) and African grey parrots (Pepperberg 1994) our results are the first to indicate that such learning occurs in natural parrot populations. Gene-culture coevolution models predict that conformist transmission could evolve as a rule of thumb for identifying locally favoured cultural traits in spatially heterogeneous environments (Boyd & Richerson 1985). Other possible sources of selection for social learning include mating preferences for local repertoires, as has been demonstrated in some birds (Payne *et al.* 1988; O'Loughlen & Rothstein 1995) or benefits of group membership that can only be obtained through matching local repertoires (Feekes 1982). Such group membership benefits have recently been invoked as the driving force behind the evolution of linguistic diversity in humans, with languages defining networks of reciprocally cooperative aid (Nettle 1999). However, reciprocal altruism is thought to be rare among unrelated animals (Wilkinson 1984), and it remains to be seen whether such interactions are a viable explanation for avian dialects. Direct observation of the behaviour of dispersing individuals could help distinguish between these alternative sources of selection for cultural conformity by identifying the timing and context of vocal convergence. The existence of such convergence in natural populations does provide an evolutionary explanation for the well-known ability of captive parrots to mimic the speech of their human captors.

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