Regional dialects in the contact call of a parrot

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SUMMARY

This study describes a system of regional dialects in the contact call of a parrot, the yellow-naped amazon (*Amazona auropalliata*). Spectrographic cross-correlation analyses of calls from multiple adults at 16 roosts in Costa Rica reveal two distinct patterns of geographic variation in call structure: first, variation in the basic structure of the call by which roosts can be classified into three distinct dialects, and second, fine-scale variation of call structure among roosts within a dialect. Some birds at roosts bordering two dialects use the calls of both neighbouring dialects interchangeably. These results suggest that there are two distinct processes governing the diffusion of call types among roosts, with dialect borders acting as barriers to the spread of foreign calls. Such a dialect system could be maintained through either reduced dispersal of birds across dialect boundaries or alternatively, by reduced diffusion of call types. These two possibilities have different implications for the genetic isolation of populations and thus for both speciation and learning. This pattern is broadly similar to those seen in some songbirds and may be maintained in a similar manner.

1. INTRODUCTION

Scientists have studied the role played by avian vocal dialects in the process of speciation and the evolution of vocal learning for the past 50 years. Despite this attention, the interactions between learning, speciation and dialects remain far from clear (see reviews in Payne 1981; Baker & Cunningham 1985; Catchpole & Slater 1995). Geographic differences in vocalizations may be maintained by reduced gene flow between dialect populations that are ecologically adapted to certain areas; such differences could lead to reproductive isolation and speciation (Mayr 1942; Nottebohm 1969). Alternatively, dialects could be maintained by selection on dispersing birds to learn the calls of their new home areas to facilitate social interaction (Payne 1981; Feekes 1982; Rothstein & Fleischer 1987) and this same selective pressure might promote the evolution of vocal learning (Baker & Cunningham 1985). A further hypothesis suggests that dialects are simply a consequence of accumulated learning errors in local populations of species that have evolved vocal learning for purposes such as intrasexual competition (Wiens 1982). All these hypotheses have found support in separate studies, and no clear picture has emerged.

The vast majority of dialect research has been done in a single group of avian vocal learners, the oscine songbirds (Order Passeriformes). Relatively little attention has been paid to patterns of vocal variation in another taxa of well-known vocal learners, the parrots (Order Psittaciformes). Important differences exist between the two groups in the ontogeny of vocal learning, the composition of the vocal repertoire, and the typical social structure (Farabaugh & Dooling 1996). Do these behavioural differences create different patterns of vocal variation in the two groups?

Geographic variation in calls of parrots have been described for two species, an Australian cockatoo (Saunders 1983) and a neotropical parrot of the genus *Amazona* (Nottebohm 1970). Unfortunately, both descriptions provided sparse data on which to base comparisons with dialects in the songbirds. In this paper I provide a detailed description of regional dialects in the contact calls of another *Amazona* species, the yellow-naped amazon, which cover large geographic areas encompassing many traditional night roosts in Costa Rica.

2. MATERIALS AND METHODS

The contact call is the most frequently uttered component of the yellow-naped amazon's vocal repertoire. Although the communication function of this call is not fully understood in this species, similar calls in other parrots are used to initiate group activities and maintain contact between flock members and pair mates (Saunders 1983; Rowley 1990; Farabaugh & Dooling 1996). Some parrots also use contact calls to recognize family members or flockmates (Rowley 1990; Farabaugh *et al.* 1994). In the yellow-naped amazon, both sexes use these calls in a similar manner, although other portions of the vocal repertoire are sex-specific. Contact calls are most commonly uttered near nests and at night roosts. These roosts contain large numbers of birds (20–300) and are located in widely dispersed and highly traditional sites; one roost site in this study has been used for at least the past 30 years (H. Guadamuz, personal communication). Individually recognizable adults regularly attend the same roost over the course of months (T. Wright, unpublished data).

From March to June in 1994, I visited 20 night roosts of the yellow-naped amazon, representing most of the known roosts of this species in Costa Rica. I recorded contact calls from unmarked adults of both sexes perched near roosts in early morning and late afternoon using a TEAC DAT DAP-20 recorder with a Sennheiser MKH816 P48 directional microphone. Of these, three distinct variants of the contact

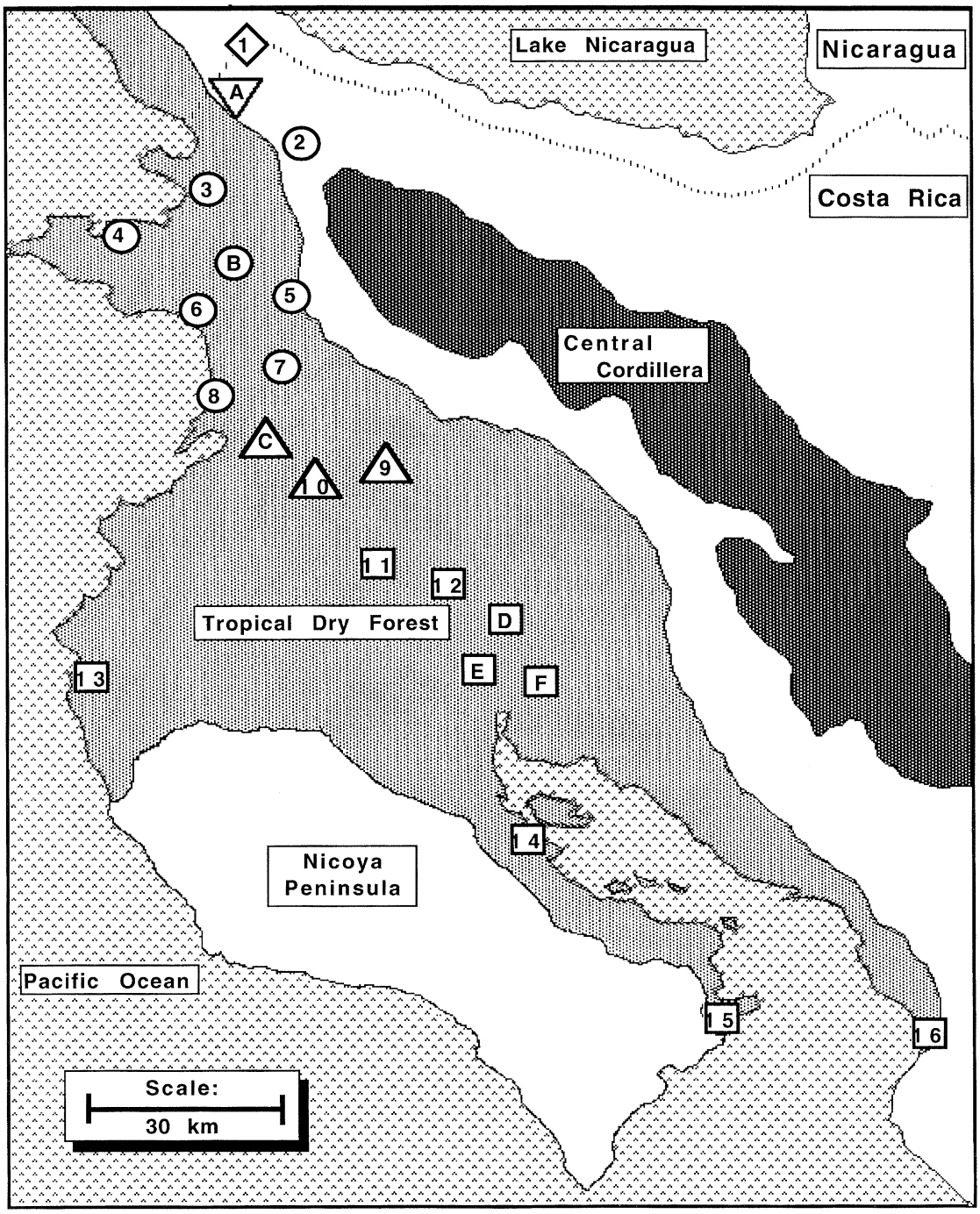

Figure 1. Map of northwestern Costa Rica showing the distribution of roosts and dialects. The circles indicate Northern dialect roosts, the squares Southern roosts, triangles Border roosts, and the diamond the single Nicaraguan dialect roost discovered. The 16 numbered roosts were used in the spectrogram correlation analysis: 1-Penas Blancas (four birds, 40 calls), 2-Hacienda Inocentes (four birds, 37 calls), 3-Playa Junquillal (four birds, 40 calls), 4-Bahia Santa Elena (three birds, 28 calls), 5-Pelon Altura (four birds, 40 calls), 6-Playa Naranjo (four birds, 34 calls), 7-Horizontes (four birds, 40 calls), 8-Playa Cabuyal (two birds, 13 calls), 9-Finca Gisa (three birds, 34 calls), 10-Hacienda San Jeronimo (two birds, 29 calls), 11-Finca Zapolita (four birds, 40 calls), 12-Pelon Bajura (four birds, 40 calls), 13-Playa Grande (three birds, 25 calls), 14-Puerto San Pablo (two birds, 20 calls), 15-Finca Curu (two birds, 20 calls), 16-Tarcoles (three birds, 24 calls). Lettered roosts were excluded because of insufficient high quality recordings at the time of analysis: A-Colinas del Norte, B-Parque Santa Rosa, C-Finca Las Trancas, D-Finca Llano Cortez, E-Parque Palo Verde, F-Hacienda Taboga. The grey shading indicates tropical lowland dry forest habitats, which largely delimits the range of the yellow-naped amazon in Costa Rica. The white areas are transitional tropical moist and rain forests and the dark shading represents high-altitude tropical rain forests.

call could be distinguished by ear, each used at a number of geographically contiguous roosts (see figure 1). These distinct note types were used to provisionally define three dialects (Southern, Northern, Nicaraguan) for subsequent analyses (see figure 2). At two roosts bordering the Northern and Southern dialects, some individuals used contact calls from

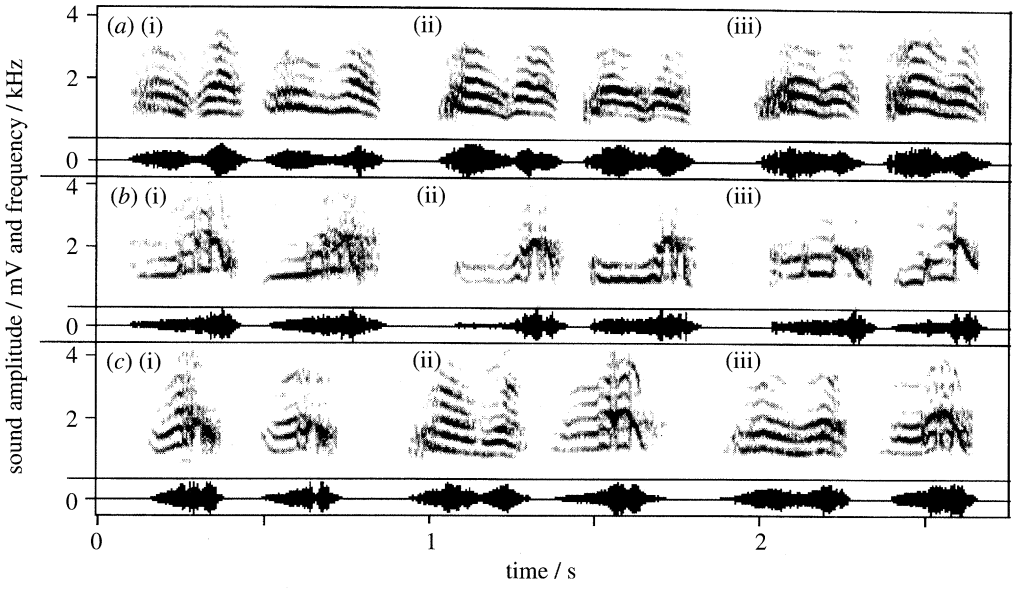

Figure 2. Spectrograms and waveforms of yellow-naped amazon contact calls. (*a*) Calls from two different birds at each of three separate Northern dialect roosts ((i) roost 2; (ii) roost 5; and (iii) roost 8). (*b*) Calls from two different birds at each of three Southern dialect roosts ((i) roost 12; (ii) roost 13; and (iii) roost 16). (*c*) Calls from: (i) two different birds at Nicaraguan dialect roost; and Northern and Southern dialect calls from (ii) a bird at Border roost 10 and a different individual at Border roost 9.

both neighbouring dialects; these roosts were classified as Border roosts and the individuals' calls classified as Northern or Southern as appropriate. In November 1995, I recorded bilingual birds at two additional locations, one between the Northern and Nicaraguan dialects, and the other between Northern and Southern.

For two to four individuals ($n = 54$; mean = 3.4; s.d = 0.8) from each roost I randomly selected three to ten high quality contact calls ($n = 504$; mean = 9.3; s.d = 1.6). At six roosts I failed to record sufficient numbers of high quality calls (see figure 1); these roost were excluded from subsequent analyses. Calls were pre-filtered with a RANE GE-30 filter set at band-pass 250 Hz to 8 kHz then digitized with a Macintosh Powerbook 180 internal 8-bit digitizer sampling at 22 kHz. I created spectrograms of each call using Canary™ software for the Macintosh (spectrogram analysis resolution of 352.94 Hz bandwidth, 11.5 ms frame length and grid resolution of 1.438 ms, 43.47 Hz, 87.5% overlap, FFT size 512 points, Hamming window and −130 dB clipping) (Charif *et al.* 1993). To compare the auditory structure of these spectrograms, I did normalized cross correlations between each call and all others (504 calls total) using the batch correlation routine in Canary™. This routine tabulates the peak correlation values of all possible comparisons in a symmetric correlation matrix with the autocorrelations of the value 1 along the main diagonal. Because of size limitations in subsequent analyses, this larger matrix was collapsed to an individual by individual matrix by averaging the set of correlation coefficients for each pair of birds and again setting values of the main diagonal to 1. I then did multidimensional scaling on this averaged matrix with SYSTAT version 5.2.1. and graphed the scaling values from the first two dimensions (Wilkinson *et al.* 1992).

To test whether the provisional dialects determined by ear were confirmed by the cross-correlation analysis, I compared the averaged correlation matrix with a second matrix coded with 1's for provisional within-dialect and 0's for provisional across-dialect comparisons using the Mantel test (Smouse *et al.* 1986; Gaunt *et al.* 1994). To examine effects among roosts within a dialect, I divided the full matrix into two sub-matrices representing individuals in the Northern dialect (27 individuals) and Southern dialect (23 individuals). Individuals from the border roosts that used both dialects appeared in both matrices as appropriate. The four individuals from the single Nicaraguan roost were excluded from these analyses. Mantel tests then compared each single-dialect matrix against each of two prediction matrices: (i) 1–0 matrices coded for shared roost membership of compared individuals to test for differences among roosts; and (ii) matrices filled with inter-roost distances to test the hypothesis that call similarity is dependent on distance. All Mantel tests were done using the 'R' statistical package (Legendre & Vaudor 1991).

3. RESULTS

There are three distinct structural variants of the contact call (figure 2), each used exclusively at a group of geographically contiguous roosts (figure 1). The Northern dialect consists of eight surveyed roosts covering an area of roughly 2200 km^2, while the Southern dialect contains nine surveyed roosts in an area of roughly 3200 km^2. Inter-roost distances are greater in the Southern dialect (mean 65.9 km, s.d. = 43.2) than in the Northern dialect (mean 27.3 km, s.d. = 13.2). The Nicaraguan dialect, while represented by only one roost in Costa Rica, almost certainly extends northward into Nicaraguan populations of the species. Between each of the dialects there exist Border roosts at which some birds use both neighbouring dialects by alternating calling bouts of each dialect. Bilingual birds were uncommon (5–10% of birds observed at each Border roost), and the remaining birds at these roosts all used the same dialect. Between the Northern and Southern dialects I observed a cline in the degree of dialect use, with most of the birds at roosts 9 and 10 (in figure 1) using the Southern dialect while at roost

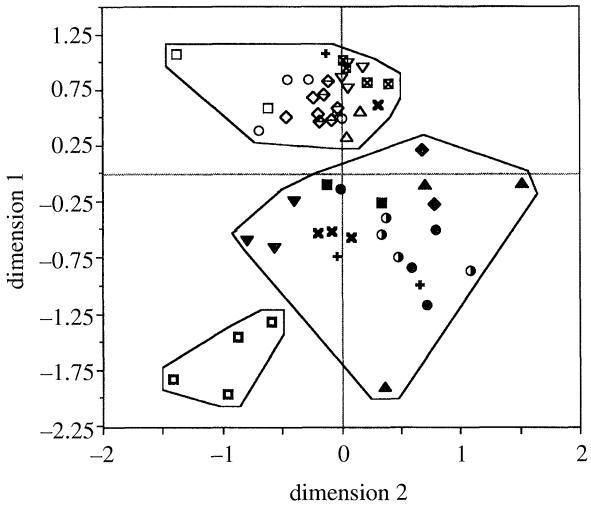

Figure 3. Multidimensional scaling of values from spectrogram cross-correlations of calls from sixteen roosts. Each point represents a single individual coded by roost; the proximity of points indicates the degree of similarity between individuals. Minimum-area convex polygons enclose individuals from roosts provisionally classified as Northern (roost 2-(▽), 3-(◇), 4-(□), 5-(⊠), 6-(○), 7-(⊕), 8-(△)), Southern (roost 11-(●), 12-(◑), 13-(▼), 14-(■), 15-(◆), 16-(▲)) and Nicaraguan (roost 1-(◘)). Border roosts 9-(✕) and 10-(✚) each have one individual that used both Northern and Southern calls and clusters with both dialect groups.

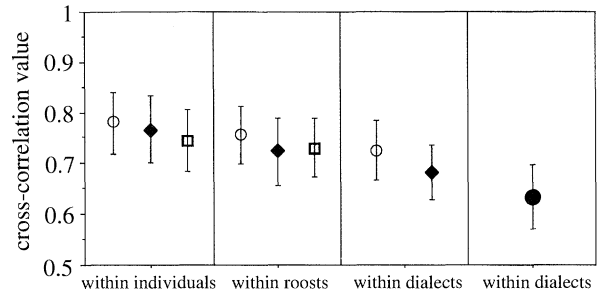

Figure 4. Means (±1 s.d.) of cross-correlation values from four different classes of call comparison for the Northern (○), Southern (◆), and Nicaraguan (◘), and for the Among Dialect comparisons, of all dialects combined (●). Calls from Border roosts were assigned to either Northern or Southern categories depending on dialect type.

C, closer to the Northern roosts, all non-bilingual birds use the Northern dialect.

The multidimensional scaling of the averaged cross-correlation matrix (see figure 3) shows distinct clumping of individuals by provisional dialect. The calls of bilingual individuals from Border roosts are not intermediate types, but clearly group with either the Northern or Southern dialects. The robustness of this pattern is confirmed by a Mantel test of the averaged cross-correlation matrix versus the 1–0 matrix coded for provisional dialect membership (array size = 54, 1000 permutations, $r = 0.65$, $p(r) < 0.001$).

Vocal variation within dialects is characterized by subtle changes in note frequency and time parameters rather than wholesale structural change (figure 2). Within both the Northern and Southern dialects there is variation among roosts in call structure. Mantel tests of averaged correlation values versus 1–0 matrices of roost membership were significant for both dialects (for Northern, array size = 27, $r = 0.24$, $p(r) < 0.001$; for Southern, array size = 23, $r = 0.32$, $p(r) < 0.001$). Inter-roost distance had a strong effect on call similarity in the Southern dialect and a less pronounced effect in Northern dialects (Mantel of correlation values versus inter-roost distances: For Southern, array size = 23, $r = -0.42$, $P(r) < 0.001$; for Northern, array size = 27, $r = -0.21$, $p(r) < 0.05$).

Within all three dialects the degree of variation among contact calls decreases monotonically with level of social organization (see figure 4). Cross-correlation values are on average lower for across-dialect comparisons than for within-dialect comparisons. Within each dialect, the mean values for comparisons among individuals from different roosts are lower than those among roostmates, which are in turn lower than within-individuals comparisons. As figure 4 illustrates, however, variation does exist even among calls from the same individual, as the mean values for within individual comparisons are considerably less than one. The Southern dialect shows a greater degree of variation among roosts, probably because of the greater distances between the sampled roosts there than in the Northern dialect. The non-independence of correlation values precludes statistical tests of these mean differences.

4. DISCUSSION

Patterns of variation in cultural traits such as learned vocalizations presumably reflect the underlying processes governing the transmission of these traits (Jenkins 1978; Boyd & Richerson 1985). There are two classes of variation in the contact calls of the yellow-naped amazon, which suggest two distinct processes affecting the diffusion of call types across roosts. The first class is fine-scale variation of the basic call structure within large regional dialects. Calls vary to an increasing degree within individuals, among roostmates, and among different roosts. At no level of social organization are contact calls invariant. This variability argues that, at least within dialects, contact calls do not function either as stereotyped 'signature calls' of individual identity or 'passwords' for roost membership as has been found in calls in of some parrots (Farabaugh *et al.* 1994; J. Bradbury, personal communication) and flocking songbirds (Mundinger 1970; Feekes 1982). Nonetheless, an individual's contact calls may have consistent structural features that permit recognition at the individual or roost level (Nelson 1989; Weary & Krebs 1992); such features could account for the relatively higher correlations at these levels (figure 4). Overall, this pattern suggests a conservative process of call diffusion, possibly through local copying of call types coupled with a low level of movement between roosts (Jenkins 1978).

The second class of variation is in the basic call structure itself, which is constant over large areas and then undergoes radical shifts at dialect borders. These

radical shifts in call structure suggest that dialect borders represent major barriers to the normal process of call diffusion, resulting in the highly differentiated call dialects. Such a pattern could be maintained by barriers to either diffusion of call types or dispersal of the birds themselves.

There is no evidence that there are physical barriers to dispersal of individual birds from one dialect area to another. Each dialect encompasses many different types of habitats (Savitsky *et al.* 1995) and the yellow-naped amazon commonly occurs in both natural and modified habitats. Radio-tracking data show that collared individuals will utilize several habitats in the course of a single day (T. Wright, unpublished data), suggesting that present habitat types are not barriers to dispersal. The variety of habitats within each dialect also discounts the importance of the 'acoustic adaptation' hypothesis, which suggests that dialects are the result of differential selection on acoustic features that maximize transmission properties in the habitats of different regions (Hansen 1979; Handford & Lougheed 1991).

Several other mechanisms have been proposed that would maintain dialects by limiting the dispersal of individual birds across dialect boundaries. One of the earliest hypotheses suggested that dialect groups represent populations that are genetically adapted to survive within a certain area (Marler & Tamura 1962; Nottebohm 1969). A conceptual variant of this hypothesis is that regional populations are culturally adapted for local survival; that is, they have survival techniques, such as food localization and processing or nest site selection, that are transmitted vertically by learning. In both hypotheses, geographic variations in vocalizations serve as markers of these genetic or cultural differences, with individuals that cross dialect boundaries suffering reduced fitness in terms of either survival or reproduction. These hypotheses share in common the prediction that dialect populations should show excess genetic differentiation above that predicted simply by the effect of distance.

It is unclear whether dialect populations of the yellow-naped amazon would be expected to show such excess genetic differentiation. This species is a member of the *Amazona ochracephala* superspecies that shows considerable geographic variation in plumage and voice characters throughout its range (Forshaw 1989). In captivity, however, hybridization within the *A. ochracephala* group and between these species and others in the genus is common (Bosch & Wedde 1984), suggesting that species recognition may be based on learned rather than innate characters. Studies of dialect populations in several songbird species have found only weak evidence of genetic subdivision along dialect lines (see review in Catchpole & Slater 1995). To my knowledge, however, there are no published studies of the genetic structure of any natural population of parrots upon which to base predictions for the yellow-naped amazon.

Dialects can only serve as dependable markers of population differences if birds are philopatric or if all vocal learning occurs before juvenile dispersal. Dispersal patterns in the yellow-naped amazon are poorly understood. Radio-collared juveniles join together in nomadic flocks that attend roosts irregularly, but I still have few data on how far such flocks travel and where juveniles eventually settle. On the other hand, it is clear that vocal learning in the yellow-naped amazon is unlikely to be restricted to a period before dispersal. While wild juveniles do use rough versions of their parent's contact calls within days after fledging (T. Wright, unpublished data), adult learning is common in captive birds. If adult learning is coupled with extensive dispersal in this species, then dialect boundaries would not limit the movement of birds but rather limit the diffusion of the cultural trait of contact call type.

If dispersal across dialect boundaries occurs, then dialect maintenance would depend on strong social selection on immigrants to learn local calls (Payne 1985; Rothstein & Fleischer 1987). Matching of local calls may be necessary for dispersing birds to gain access to feeding and roosting flocks (Mundinger 1970; Nowicki 1983) or to successfully pair and reproduce (O'Loghlen & Rothstein 1995). Such vocal convergence occurs rapidly in captive budgerigar flocks (Farabaugh *et al.* 1994). Bilingual yellow-naped amazons may maximize their acceptance among various local groups by learning and using both neighboring dialects. If contact call dialects are maintained by post-dispersal call matching, then no genetic differentiation of dialect populations is predicted.

This description of dialects in parrots underscores the value of comparisons between parrots and the two other avian taxa for which geographic variation in learned vocalizations has been described: the songbirds and the hummingbirds (Trochilidae) (Gaunt *et al.* 1994 and references therein). Dialects in the songbirds and hummingbirds occur in the adult male song, a complex call used primarily within a male's territory to attract mates and defend the territory. In contrast, yellow-naped amazon dialects occur in the contact call, which is a simple vocalization used by both sexes and all age groups in a number of social contexts. Learning appears to be more temporally restricted in songbirds than in parrots (Farabaugh & Dooling 1996), although this difference may be an artefact of past experimental designs (Catchpole & Slater 1995). Interspecific mimicry is rare among songbird species but commonplace in captive parrots, suggesting that there are different mechanisms governing the selection of models for learning in these two groups. Furthermore, recent work on budgerigars provides strong evidence that the neural pathways for vocal control evolved independently in parrots and songbirds (Striedter 1994). Less is known of either the ontogeny or neuroanatomy of learning in hummingbirds (but see Baptista & Schumann 1990), but it is clear that substantial differences exist among at least two, if not all, of the taxa of vocal learners. Despite these differences, the parrot dialects described here are similar in pattern, if not always in scale, to those seen in both songbirds and hummingbirds. Although further work remains to be done on the social behaviour and population genetics of this species, this initial de-

scription of dialects in a parrot does not suggest a novel mechanism for the maintenance of such geographic variation in vocalizations. Further studies contrasting these three avian taxa should provide much insight into the evolution of vocal learning.

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