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Vocal Communication in Wild Populations of the Yellow-naped Amazon

(Amazona auropalliata)

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People have long marveled at the striking mimicry abilities of parrots. Mimicry occurs when birds raised in captivity learn vocalizations and other sounds used by their human companions and incorporate these learned sounds into their large and varied communication repertoire. Many parrot species display this advanced learning ability and are prized as pets for this reason. Yet despite their popularity as pets, little is known about how these parrot species use their learning ability in the wild. Even the most basic information, such as the size and composition of the vocal repertoire, is known for only a few species, and there is almost no information on how repertoires might vary between different individuals or different geographic locations.

One species that is particularly well known for its mimicry abilities is the Yellow-naped Amazon *Amazona auropalliata*. For the last five years my assistants and I have studied wild populations of this species in its natural habitat in Costa Rica. The goal of this study has been to describe the communication repertoire of this species and examine how different vocalizations in the repertoire vary geographically. Here I describe some of the most interesting vocalizations and document their distinctive pattern of regional variation, termed vocal dialects.

Several aspects of the biology of the Yellow-naped Amazon facilitate the study of its vocal repertoire. It is found in the tropical dry forest habitat of the Pacific slope of Central America, a habitat that is very conducive to studying parrots because its low forest canopy and long dry season during which many trees lose their leaves. Parrots are much easier to observe and follow in this habitat than in the high canopy of the tropical rain forest.

Two important aspects of the Yellow-naped Amazon's social system, nest territories, and communal night roosts, further simplify the study of its vocalizations. Mated pairs will use the same nest trees, and even the same cavities for several consecutive years. High-quality cavities appear to be an important resource for pairs, and a pair will vigorously defend their nest tree and the area around it against intruding pairs. This defense continues throughout the year, and pairs can often be found vocalizing near their nest areas long after nesting season has ended.

These same pairs will gather each night into large communal night roosts that number from 20 to over 300 birds. These night roosts occur in highly traditional locations that are used throughout the year and in some cases over several years and even decades.

The appearance of birds in these traditional nest and roosts sites on a daily basis makes it relatively simple to get repeated recordings of vocalizations and behaviors from the same birds and to compare these vocalizations to those recorded from birds at

other nests and roosts. We record calling birds on video and audio tapes and take notes on the social behaviors and visual displays that accompany these calls. These tapes are then analyzed using computer programs that transform vocalizations into visual graphs called spectrograms (see Figure 2). Different aspects of calls can be measured from these spectrograms and compared to measurements from the same calls made by members of different pairs and individuals from different roosts. We also conduct playback experiments, in which we broadcast specific calls from speakers placed in trees and note the vocal and behavioral responses of nearby birds to these controlled stimuli.

Using these methods, we have discovered several striking features of the species vocal communication repertoire. One is that wild Yellow-naped Amazons do not appear to mimic other species, nor do they have a particularly large vocal repertoire. In fact, the repertoire is not substantially larger than that of most other bird species, with roughly eight to 10 functional classes of calls.

A single call type, the contact call, composes 40-60 percent of all calls used in any one location. The contact call is a short, loud, relatively stereotyped call that is used in a wide variety of situations, including at roosts, in flight, and near the nest. It appears to function as a marker of social identity that is used to maintain contact with other members of a social group such as a mate or offspring. The acoustic form of this call is fairly consistent among individuals in an area, but as discussed below, shows marked differences among different areas. Figure 2 is a spectrogram of contact calls from three different regions in Costa Rica.

The relative stereotypy of the contact call contrasts strongly with a different functional class of calls, the pair duet. The pair duet is a loud, complex, and highly conspicuous call produced in tandem by the two members of a mated pair. It is used primarily by pairs around their nests, where it appears to function as a marker of territorial ownership. In this respect, as well as in its acoustic complexity, it bears some resemblance to another learned vocal-

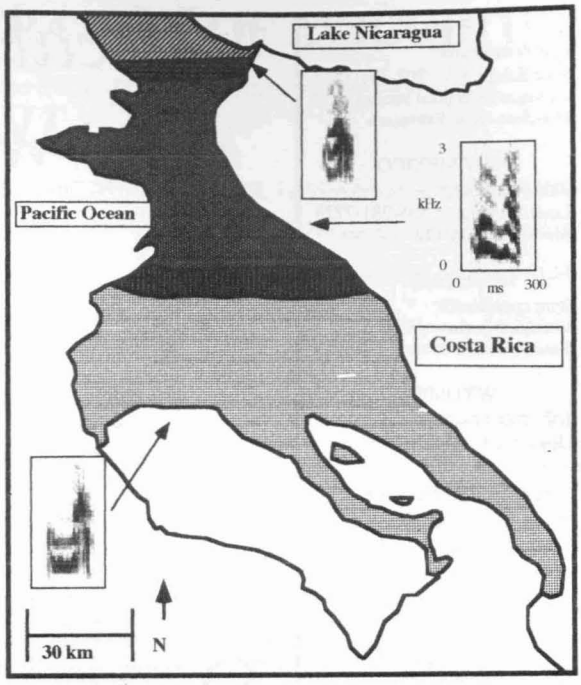

Figure 1: A map of northwestern Costa Rica showing the three vocal dialects (in various shadings) and spectrograms of typical contact calls from each dialect. Spectrograms illustrate time on the horizontal axis and frequency on the vertical axis and are analogous to musical notations. Areas of dialect overlap indicate border areas in which some bilingual individuals are observed. The three dialects illustrated here encompass the entire range of the Yellow-naped Amazon in Costa Rica.

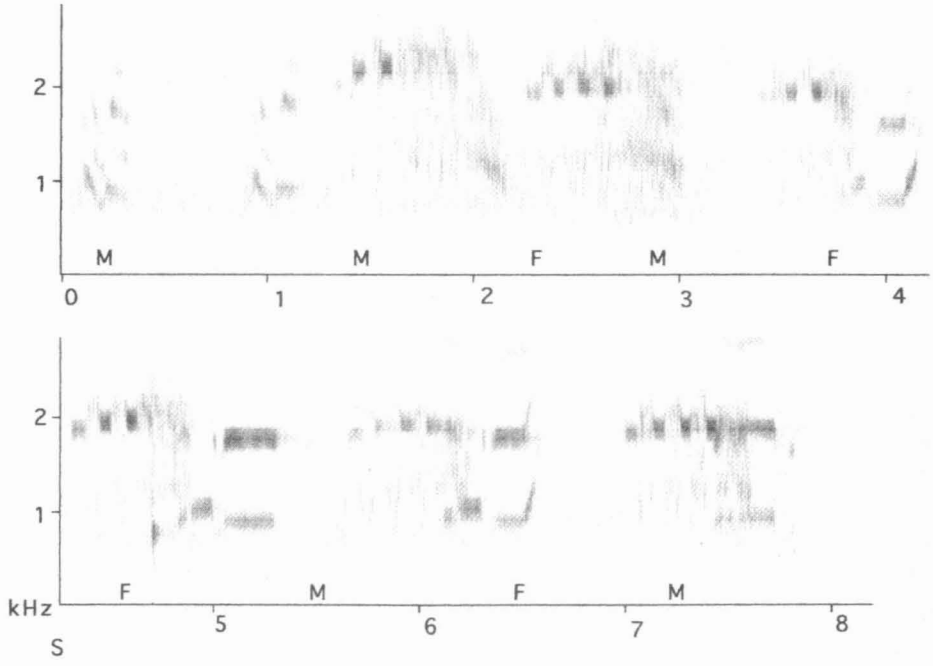

Figure 2: Spectrogram of a single duet from a mated pair of Yellow-naped Amazons in northern Costa Rica. Notes called by the female are marked with an '**F**', while notes called by the male are marked with an '**M**'. The first two notes are contact calls given by the male; subsequent notes compose the duet. The characteristic pairing of female and male notes is readily visible, as is the switch in male note types that occurs between the second and third pairs of duet notes.

ization, the territorial song of male songbirds.

Upon first hearing these pair duets, a casual listener might be struck be the variability between different renditions of these duets, even within a single pair. Our spectrographic analysis of pair duets revealed that they are composed of a small number of sex-specific notes that are combined together using a few simple syntactical rules to form a complex signal (Figure 2).

In one area where we conducted a detailed study of syntactical organization of duets, males used two notes and females used only one. Males and females combine these notes in a repeating and alternating fashion to form duets composed of long strings of paired notes. The males used one of their notes early in these strings and then switched to the other note and used it until the end of a particular duet. Females repeated a single note, but the frequency and the length of the note changed gradually through the course of a duet. Duets varied greatly in the number of pairs of notes from rendition to rendition. The ability to compose a wide variety of complex signals out of limited number of acoustical building blocks is a hallmark of human language but has rarely been found among non-human animals. In the future I plan to conduct a series of playback tests using duets to examine whether parrots are truly communicating different messages with duets of different length and acoustical features.

Perhaps the most striking feature of the vocal repertoire of the Yellow-naped Amazon is how it changes geographically. In 1994 we surveyed 22 communal night roosts spanning the range of this species in Costa Rica and focused on recording contact calls. We found three different types of contact calls being used, each in a distinct region (Figure 1).

At some roosts along the borders of two dialects we found individual birds that used the contact calls of both neighboring regions, but such birds were rare. Such a pattern of geographic variation has been found in some songbird species but never previously documented in a parrot. This pattern has been termed "vocal dialects," in reference to human language dialects. Like human dialects, avian vocal dialects are thought to result from vocal learning, with populations in different areas having different learned traditions.

Intriguingly, in most of the avian dialect systems previously described only a single type of vocalizations, usually the territorial song of males, varies.

In contrast, a second survey we conducted in 1996 showed that not only contact calls, but most of the functional classes of the vocal repertoire were changing along the same geographic boundaries. Pair duets maintained the same syntactical rules across the three dialect areas, but the types of notes used by both males and females differed in each area. Such a pattern of coordinated variation in several classes of the vocal repertoire, while rare among animals, bears a striking resemblance to human language variation. Currently I am investigating the degree to which such variation in learned vocalizations is associated with genetic differences among different populations. Such work will shed light on how such geographic differences originate and how they are maintained through evolutionary time.

There is still much we don't know concerning how Yellow-naped Amazons learn and use their vocalizations. For example, the timing of learning and the models upon which young birds base their learning are still largely unknown. We also have only a rudimentary understanding of how individuals perceive and classify different calls and variants of calls.

What is clear from our studies of wild Yellow-naped Amazons is that their vocal repertoire is a remarkable mix of flexibility and conformity. This mix is demonstrated at the regional level in the vocal dialects, in which each dialect has the same classes of calls, yet the acoustic form of these calls differs dramatically between dialects. This mix is also found at the individual level, where highly variable pair duets are formed from a few note types combined with a few simple rules.

Understanding the role of learning in generating these patterns remains a challenge for future studies.