

CHAPTER FOUR

DIALECTS AND SEX-SPECIFICITY

Introduction

Among their other functions, vocalizations may serve to indicate an individual's geographic origin. In examining vocal repertoires there is often disagreement as to which aspects of the repertoires may be more indicative of the presence of dialects in a particular species. Some investigators have tested song phenotype, others have examined syllables while still others may consider characteristics in both dimensions (Jenkins 1977). In this study an effort was made to examine all aspects of the parrots' vocal behavior including differences found in the repertoire, lexical features, and the sequencing of call notes.

Dialects have been documented in numerous species, e.g., Saddlebacks (*Philesturnus carunculatus*) (Jenkins 1977); Chingolo (*Zonotrichia capensis*) (Nottebohm 1969). For many of these species song ontogeny involves modifications in the innate template following exposure to the songs of conspecific models (Nottebohm 1970; Marler and Mundinger 1971; Kroodsma 1982). New songs are generated in the absence of adult models or by learning errors or by errors in the genetic template (Andrew 1962; Thielcke 1973; Baptista 1975; Lemon 1975). If these new songs are consequently copied by other individuals in a given location as a result of behavioral dominance or the formation of allopatric populations, a new dialect is formed (Jenkins 1978; Payne 1981; Petrinovich et al. 1981). While there is general consensus as to how dialects are generated, how and why these dialects are maintained and what effect they may have on the evolution of a species have been the subject of much debate and speculation in recent years (e.g., Rothstein and Fleischer 1987; Baker and Cunningham 1985). Generally accepted theories for the function, generation and maintenance of dialects include:

1) Dialects represent epiphenomena. This theory proposes that dialects are insignificant by-products of acquiring a song (Payne 1981; Petrinovich et al. 1981; Wiens 1982). However, this theory fails to explain why a genetically dependent song strategy should be replaced by a learning dependent strategy (Jenkins 1977). Many species actively maintain new dialects that become established by recent immigrants

and conversely, newcomers actively learn and use the dialect of their new group. If dialects were mere epiphenomena the impetus to maintain a particular dialect would have been removed. In addition these same species appear to use a genetically controlled song strategy which as adults is replaced by a learning strategy. The epiphenomena theory fails to address this shift in song strategy (Jenkins 1977).

2) Dialects facilitate assortative mating (Konishi 1965; Nottebohm 1969; Baker et al. 1982). Song learning provides the substrate for geographical or long range vocal variation. Juveniles of a particular population may learn the dialect of their home deme during dispersal or mate selection and preferentially remain within their natal area. One possible advantage of this is that genetic adaptations to the local environment might be preserved within the population (Marler and Tamura 1962; Nottebohm 1969).

An example of this theory is a system of dialects that is structured and maintained according to which of its characteristics will be transmitted most efficiently in a given environment. (Bowman 1979; Gish and Morton 1981; Morton 1982; Nottebohm 1985). In a study of three Western Gull (*Larus occidentalis*) subspecies Hand (1981) found that two of the three subspecies, *L. o. occidentalis* and *L. o. wymani*, with similar breeding environments on the west coast of California use call features which tend to facilitate localization by receivers. These two subspecies breed in noisy colonies, often in areas that are dominated by the sound of strong winds and pounding surf, and as a result calls used in threat, alarm or advertisement contexts have frequency contents which promote locatability of the sender. It has been suggested that a receiver that knows the spectral structure of a call at its source may be able to judge its own distance from the sender by comparing relative rates of attenuation of the frequency bands (Wiley and Richards 1978). *L. o. livens*, the third subspecies, in contrast, breeds in the Gulf of California, on beaches within about 30 m from the high tide line in more or less linear colonies. These linear colonies differ in structure from the clustered colonies of *L. o. occidentalis* and *L. o. wymani* in that visual access to potential mates and aerial predators is reduced. Gulf beaches tend to have small, irregular shorelines further reducing visibility between individuals of a colony and ability to visually detect potential predators. As a result it is possible that selection may favor the use of calls in which low frequencies are emphasized. These calls facilitate long distance contact with other individuals in the population, where visual contact is difficult and density of individuals in breeding colonies is low (Hand 1981). Furthermore, in the relative absence of environmental noise such as pounding surf or strong winds in the Gulf, low frequency vocalizations can be successfully transmitted (Hand 1981).

In addition to preserving genetic adaptations to certain environmental factors recognizing kin through dialect identification allows certain sedentary species such as the Saddleback (*Philesturnus carunculatus*) (Jenkins 1977) to avoid pairing with close relatives. In other species individuals may set up territories in close proximity to kin, reducing the need for aggression between pairs in a given area (Treisman 1987).

3) Dialects are maintained through the copying of songs of established males for the purpose of gaining status, acquiring territory and acquiring mates. In order to acquire a territory and/or a mate males must establish their status. Therefore it is advantageous to copy a male of high rank, i.e. one holding a territory and/or having a mate. This method of dialect maintenance suggests that song learning may continue after the juvenile period if there is dispersal from the parental population (Verner 1975; Payne 1981; Baptista 1985).

This theory emphasizes social adaptation as a function of dialects. According to Rothstein and Fleischer (1987) there are two mechanisms by which this can occur. Rothstein and Fleischer (1987) coined the phrase deceptive convergence to describe the first of these mechanisms, known earlier as competitive mimicry (Payne 1982), or deceptive mimicry (McGregor and Krebs 1984; Baker and Cunningham 1985). Dialects result from males imitating the vocal repertoire and/or behavior of a dominant male to improve their status in a population (Jenkins 1982; Payne 1981). By doing so sub-adult males that have recently dispersed from their parental population, immigrants from other populations and non-dispersing juveniles trying to establish territories or acquire mates attempt to deceive others in the population into interacting with the mimic as if it were a dominant male. These dialects prove to be unstable over time as the dominant male develops novel vocalizations to compensate for the mimicry (Rohwer 1982).

The second of these mechanisms, honest convergence, promotes the preservation of a local vocal variant because the ability of individuals to use this dialect proficiently provides a 'reliably honest signal of high social status and mate quality' (Rothstein and Fleischer 1987). According to Rothstein and Fleischer (1987), the signal is honest because the repertoire is complex and can not be easily imitated by recent immigrants (Craig and Jenkins 1982) or juveniles (Kroodsma and Pickert 1980). This mechanism for social adaptation accounts for long-term stability of local dialects because if non-dispersing adult males were to alter their dialects they would no longer be identifiable as experienced or dominant members of a population (Rothstein and Fleischer 1987). The Indian Hill Mynah (*Gracula religiosa*) and the Brown-headed Cowbird are examples of species that may be included in this category.

Up to this point I have focused mainly on the existence and maintenance of dialect systems in passerines as dialect studies in non-passerines are few in number. In 1982 Mundinger compiled a list of species in which dialects have been documented. There were a total of six non-passerine species in four families compared to as many as 118 species in 24 families of passerines. One of the non-passerine species documented to use dialects was in the same genus as *A. vittata*, *A. amazonica*, or the orange-winged amazon.. In this study, while the main focus was on the syringeal morphology and phonation of *A. amazonica*, Nottebohm (1976) mentions briefly that there appeared to be a dialectal differences in the flight calls of these parrots across contiguous populations. Nottebohm (1976) describes the differences as "...differing in detail and manner of delivery." He suggests that young birds in the wild may copy the calls from birds with which they interact socially. A similar trend may explain the presence of dialects in the Puerto Rican Parrot. Although birds from both regions fly from one region to another freely during the non-breeding season it is possible that they do so in a flock of conspecifics with which they interact most closely during the reproductive season. Given a larger population size the groups in the Luquillo Forest may form contiguous dialectal populations similar to those that exist for *A. amazonica* and dialect groups may be formed by young birds copying the dialect of birds with which they interact most closely. This scenario appears to fit most closely with the theory that dialects serve to promote social adaptation and this is most likely achieved via honest convergence, a mechanism proposed by Rothstein and Fleischer (1987). However, in their discussion on honest convergence, Rothstein and Fleischer (1987) seemingly confine their examples to males of passerine species. As a result it is necessary to broaden the scope of this mechanism to include females of non-passerine species which presumably learn their vocal repertoires in much the same way as males except that they most likely copy their vocal repertoires from adult females in their natal area as opposed to adult males. It appears that young parrots learn their vocal repertoire from reproductive pairs in their natal area and pair with birds using the dialect of that area. Individuals that lose mates tend to form new pair-bonds with individuals possessing repertoires closely matching that of their previous mates (pers. obs.).

Sex-specificity within dialects. Prior to dividing the reproductive population regionally to test for differences within and between groups it is necessary to group the population by sex. The justification for this sex-specific division is that as with many other monomorphic species active in environments where visual contact is limited or lacking e.g., densely vegetated environments, it is likely that there is some degree of sex-specificity present in the vocal behavior. Examples include nocturnal seabirds such as storm-petrels (*Oceanodroma* spp.) (Taoka and Okumura 1990); monomorphic Whooping Cranes (*Grus americana*) (Carlson and Trost 1992); and bush-shrikes (*Laniarius* spp.) which are essentially monomorphic and

inhabit areas of dense vegetation (Sonnenschein and Reyer 1983). In these diverse groups it appears that sex-specificity in vocal repertoires may compensate for a lack of available visual cues. In addition to sex-specific vocal repertoires there is often a sex-specific component to the vocal behavior of these species that could conceivably be used by conspecifics and biologists to determine an individual's sex. However, the sex-specific component of vocal behavior may have significance beyond identification of sex. In many monomorphic, monogamous species that either defend a territory year-round or that return to the same location each breeding season, call sequencing can provide information with respect to not only the sex of the bird vocalizing but also to the reproductive status of the individual, i.e., whether an individual is a member of a mated pair, is defending a territory or is a member of the non-breeding population (Farabaugh 1982).

Duets. One of the dominant forms of call sequencing between reproductive pairs in Puerto Rican Parrots and other species with similar life histories is duetting. A duet generally consists of an exchange of sequences of call notes (Farabaugh 1982). The calls supplied by each individual can be similar or sex-specific. Farabaugh (1982) defined duets as 'bouts (vocalizations that are clumped rather than randomly distributed in time) of certain elements in the repertoire of one bird that frequently overlap with bouts of certain elements in the repertoire of its mate'. The definition provided by Farabaugh (1982) also requires that duets be performed by members of a mated pair or a family group. Counter-singing by neighboring males or pairs is not considered to be duetting under this definition (Payne 1971; Brown and Farabaugh 1991). Duets can take one of many forms and are not restricted to acoustic displays (Kunkel 1974; Baptista 1978; Wickler 1980; Todt and Fiebelkorn 1980; Farabaugh unpublished. data), bill clattering of storks, and drumming of woodpeckers are considered to be examples of duets (Haverschmidt 1947; Kilham 1959). Duetting may have a number of functions and while many of these functions were proposed with passerines in mind, especially with regard to territoriality some functions proposed may be applicable to the Puerto Rican Parrot and other non-passerine species that do not defend territories.

For example, duetting may help to synchronize reproductive physiology of mates. This could occur via some vocal-endocrinological feedback system as has been demonstrated for budgerigars and ring doves (Brockway 1969; Lehrman & Friedman 1969). Schwabl et al. (1992) found that participation of female Tropical Bush Shrikes (*Laniarius funebris*) in certain duet-types thought to occur during intense territorial threat, was positively correlated with female testosterone levels. Thus it is possible that singing of female shrikes in the context of territorial defense is facilitated by testosterone (Harding 1983; Kriner & Schwabl 1991; Schwabl 1992).

In addition maintaining the pair-bond through duetting also has implications for species which maintain prolonged family bonds whether they maintain permanent territories or not. Family- and individual-specific contributions in duets between family members appear to allow Common Crows (*Corvus brachyrhynchos*) and Pinon Jays (*Gymnorhinus cyanocephala*) to maintain family integrity following the fledging of young (Good 1952; Balda and Balda 1978; Brown 1979; Farabaugh 1982). It is well documented that reproductive pairs of Puerto Rican Parrots and their young remain in close contact for several months subsequent to the fledging of the young and it is conceivable that the vocal behavior of this species plays an important role in maintaining family groups especially when group members are out of visual contact. While it is not known whether duetting occurs between family members other than mated pairs during the non-breeding season it is possible that offspring of a given pair recognize the vocalizations of their parents and this recognition may play an important role in keeping a family group together.

The function of a particular duet may also be indicated by the arrangement of male and female elements (Farabaugh 1982). According to Farabaugh (1982) duets can be placed into one of two groups, antiphonal, where calls or songs are alternated without overlap or simultaneous, where calls or songs can be either partially or completely overlapping one another. While there is general agreement about the two extremes of duet-types, i.e., duets that do not overlap are antiphonal and those that overlap completely are simultaneous, there appears to be some confusion as to which category duets with partially overlapping of elements should be placed. Farabaugh (1982) places these duets in the category of simultaneous duets. In contrast, in a study of vocal behavior in California Quail (*Lophortyx californica*) Stokes and Williams (1968) referred to duets in which there was a partial overlap of elements as antiphonal. In this study I consider duets to form a continuum with antiphonal and simultaneous duets being extremes at either end of the duetting spectrum. While it appears that reproductive pairs of parrots tend to favor the use of asynchronous duets as a means of pair communication more often than not there is some degree of overlap between each individual's contribution, and simultaneous duets are not uncommon.

Thus as part of an examination of dialects, regional differences in vocal behavior with respect to duetting and solo sequences (these are discussed in further detail in the results section) are examined in this chapter.

Methods

Repertoires were compiled for nine birds, SF1A female (assumed to be the same individual over both reproductive seasons), SF1A #1 male, SF1A #2 male, SF2A pair, SF2B pair and the QG pair, in the western region of the Luquillo forest and for four birds, EM pair and EF #3 pair, in the eastern region (see Chapter three and Appendix A for information about these individuals). Differences between same-sex birds from the eastern region were compared to those of same-sex birds from the western region. Birds were compared to same-sex birds, except where a call was used by all birds, as the repertoires of males and females in general were more dissimilar than those of same-sex birds and therefore more difficult to compare in terms of geographic variation.

Comparing differences in content of call repertoires within and between groups. Repertoires of same-sex birds from one region were compared to other same-sex birds of that same region to determine if birds from one region used a common dialect. Both groups were analyzed in this manner and the repertoires of birds from each group with similar repertoires were compared to those from the other group to determine how many if any dialects were present in the population.

In addition to the general composition of the vocal repertoire (i.e. numbers and description of all call types, call categories and calls) time and frequency parameters of three calls in call category HP01 were analyzed to test for differences within and between both groups. This call category was chosen because three calls contained within this category are very similar in appearance across both sexes and groups, these calls are used in all contexts and in similar call sequences across both regions and they were the most frequently heard call used by all individuals, providing the largest sample size of calls possible for all birds.

Comparing differences in vocalization behavior within and between groups. Male and female solo and duet call sequences were examined for differences between and within groups to determine if these exhibited geographic variation in addition to the call repertoires themselves. The terms described in the following section refer to the units of duets that were compared within and between regions.

Terminology - duets. During this study I did not record any duets between resident pair-mates and any other individuals. Therefore I am assuming that duetting, at least during the reproductive season, is limited to pair-bonded individuals and those attempting to form pair-bonds.

I. In this section the basic units of duet-bouts are defined from the smallest unit to largest unit.

Duet element. - this is the smallest subdivision in duet-bouts. Each call that makes up a single couplet or duet is an element, i.e., a single duet consists of a female element, B, and a male element, A. For the remainder of the definitions given in this section, the symbol A will represent a male element and the symbol B will represent a female element.

Duet couplet. - a vocalization unit used by mated pairs during the reproductive season in which a single call or element is contributed by each pair member. In addition the elements generally precede or follow each other closely or are slightly overlapping. For example, BA BA BA. The two main exceptions to this definition are couplets emitted by a pair during intense vocal battles with conspecifics or interactions with thrashers which may be composed of two elements given simultaneously, e.g. \overline{BA} (the line represents overlap) and conversely, those duets emitted by distantly separated pair-mates in which there is a significant lag time between the elements in the duet. For example, B A B A. Both of these exceptions are nonetheless still considered to be duet couplets. See Figs 4-1, 4-2, 4-3, 4-4.

Duet complex. - this unit is composed of >1 consecutive couplets, i.e., a sequence of generally two duets in which the time between couplets is equal or less than the time between calls in a couplet. The duet complex is frequently preceded by a call given by the male which is considered to be part of the complex because of its close proximity to the first duet. For example, ABABA. See Figs 4-5, 4-6.

Duet-phrase. - this sequence consists of a string of duets either in the form of couplets or complexes including the initiator, which are not separated by > two seconds. For example, A A A BA BA or A A A BABA. See Figs 4-1, 4-2, 4-5, 4-6, 4-9, 4-10, 4-11, 4-12, 4-13.

Duet-bouts. - this is a sequence containing one or more phrases whereby the phrases are not separated by > ten minutes.

II. Initiators. Initiators are single solo calls or a sequence of single solo calls which precede a duet-couplet or complex. In about 78% of cases begun in this manner, males produce the initiators. These calls may play a role in stimulating the other pair-mate to begin duetting. There are two types of male initiators, male type I and male type II.

Male type I initiators. - these are composed of a sequence of solo calls which are most frequently used by males in male solo call sequences. When the female hears these sequences she often interrupts the sequence and begins duetting with the male. The male usually duets with his mate answering her calls with the calls he would normally have used to finish the male solo call sequence. Figs 4-7 and 4-8 are examples of solo sequences given by eastern and western males respectively. In Figs 4-9 and 4-10 eastern and western males respectively, begin these same solo sequences but are interrupted by their mates and the male solo sequence develops into a pair-mate duet.

Male type II initiators. - these are single calls or call sequences other than those typically used in male solo call sequences that appear to be used mainly to initiate duet sequences with pair-mates. An example of a typical type II initiator in the western region is HRP26AW M20AW which is shared by all males in this region. See Figs. 4-5, 4-6, 4-11, 4-12.

Female duet initiators. - similar to male initiators, these calls given by the female may help to initiate and synchronize a pair's duets. See Fig. 4-13.

Results

In this section differences in call repertoire will be examined within and between regions. This will be followed by a comparison of vocal behavior and call sequencing within and between regions.

The following is a summary of the calls recorded in this study according to region and sex. For a more complete description see Table 4-1 and 4-2. Table 4-3 provides a summary of call repertoires for individuals recorded in this study.

Differences in content of call repertoires within and between groups.

Call types. There were seventeen call types, sixteen of which were common to both regions but not necessarily to both sexes in those regions. One call type, Q, which contains two call categories and a total of five calls was exclusive to both sexes in the western region. Calls belonging to one of the categories of this call type, Q0, were among the most frequently used calls in the repertoires of western birds and were possible counterparts to calls from the KLP0 category, exclusive to eastern birds. Calls from both the KLP0 and Q0 categories were used in male solo call sequences, in duets with pair-mates and these calls were frequently the last calls given before taking flight. Two call types, W and WHP were exclusively used by females. There were no types exclusive to males.

Call categories. Of 74 existing call categories, 28 or 37.8 % were used by at least one bird in both regions. Four categories, BZ0, HP0, Q0, and Q01 were exclusive to birds of both sexes in the western region, while only a single category, KLP0, was exclusive to both sexes in the eastern region. Ten categories in the BH, GR, HN, HRP, KNP, and LR call type groups were used exclusively by western males, six in the HN, HRP, M, and SPS call type groups were used exclusively by eastern males, 18 categories in the BH, HRP, KNP, KWP, LR, W, and WHP call type groups were used exclusively by western females and six categories in the HRP, KWP, SPS, W and WHP call type groups were exclusive to eastern females.

Calls. Few calls were common to all birds in both regions. Of 147 calls identified in this study (see chapter three) five calls representing five different call types and 5 different categories within these types were used by all birds in both regions, BZ01, GR0, HP02B, KWP0A, and MOB. One of these five calls, KWP0A, was used exclusively as an alarm call, and a second call, GR0, was used only during nest inspection and upon returning to a nest cavity during incubation when a disturbance has caused the resident pair to leave the nest cavity for an extended period of time. A third call in this group, MOB, was used exclusively as a contact call and was often the first call heard in the morning. It was also commonly heard when pair members were separated and just after chicks have fledged and were still in the vicinity of the nest tree. The two remaining calls, BZ01 and HP02 were used in multiple contexts. HP02 was one of the most frequently used calls in all repertoires. Four calls, HRP0A, LR0A, Z01A and Z01B, were used by all eastern birds and western males but were not used by western females.

Four calls were used by either sex exclusively in both regions while three additional calls were used by the majority of females or males but not by both sexes. While one call, GR01BF, was shared by all females, another call, HP01DF, was shared by all eastern females and a single western female. The female call GR01BF, shared by all females, was always answered by the male call, SPS21B, which was recorded from all males in both regions except for the EF #3 male (n=31). The EF #3 male uses a gradation of SPS21B, SPS21AE, to answer the female's GR01BF call (n=7) (see Figs 4-14, 4-15). Three alarm calls, HRPOCM, HRP26B, and M20C, were shared by all males and two calls, KLP20B and SPS21B were shared by all western males and the EM male, but were not recorded by the EF #3 male. While SPS21B was recorded 61 times collectively from all males except the EF #3 male, KLP20B, was recorded only once from the EM male. While it appeared that this call was absent from the EF #3 male's call repertoire other explanations are plausible. This call may have been used infrequently by

males in the eastern region due to a lack of appropriate behavioral stimulus that would normally have elicited it.

The numbers of calls and call categories used by both sexes but not shared between regions were similar in both regions. Twelve calls were used exclusively by birds of both sexes in the eastern region. These 12 calls fall into the following call categories: BH0, HP01, HP02, HRP02, KLP0, M01, and TL0. Eleven calls were exclusive to both eastern males and these calls fall into the following categories: GR23, HN20, HRP02, HRP22, HRP23, KNP21, KWP20, M21, SPS20, and Z0. Four calls were exclusive to one male or the other. HN22E, HRP0BME, and HRP21FE were recorded from only the EM male while SPS21AE appeared to be exclusive to the EF #3 male. Six calls were shared by both eastern females, HRP2DE, HRP2EE, KLP01BFE, M01CFE, W7E and Z01DFE. Seven were exclusive to one female or the other. HRP3BE, HRP4AE, KWP2E, KWP3E, SPS1E, and WHP2E appear to be used exclusively by the EM female while HRP4BE was used solely by the EF #3 female.

Fourteen calls were used exclusively by birds of both sexes in the western region. These 14 calls fall into the following categories: BH0AW, BZ0, HP0, HP01, HP02, KNP0, M0, Q0, and TL0. One call, Z0AW, was used by all western males and was recorded once from the QG female. Thirty-four calls were used exclusively by all western males and these fall into the following categories: BH20, GR01, GR20, GR23, HN0, HN21, HP01, HRP02, HRP20, HRP21, HRP26, HRP24, KLP01, KLP20, KNP21, KWP0, KWP20, LR0, LR20, SPS0, and Z01. Seven calls were not used by all males or were exclusive to certain individuals. BZ0AMW was recorded only from the SF1A male #2, and BZ20AW was recorded from all western males except for the SF2A male, which substituted another call, BZ20BW, for it. BZ20BW was recorded only from this individual. GR22W was recorded from only a single male, the SF1A #2 male, and GR24W appeared to be exclusive to the SF2A male. M20BW was recorded only from the SF1A #1 male and Z0CMW was used exclusively by the SF2B male. Thirty calls were used by all western females and these calls fall into the following categories: BH1, BZ0, HN0, HRP1, HRP2, HRP3, KNP1, KNP2, KWP1, KWP4, LR1, LR2, LR4, M01, SPS0, W1, W2, W3, W4, W5, and W6. Five calls were not used by all western females or were exclusive to a certain individual. HP01EFW was used by all western females except for the SF2B female which appeared to substitute LR3W for it. LR3W was recorded exclusively from the SF2B female. KWP5W was recorded from only the SF1A female and LR1CW was recorded from only the SF2A female. WHP1W was recorded from only two females, the SF1A female who used it infrequently and the QG female who used it frequently in duets with its mate.

Regional differences in graded calls within a category. Sixteen out of seventeen call types contain graded signals. The call type WHP, used solely by females, was comprised of two non-graded calls and was the only call type that does not contain graded signals. HP and HRP were the only call types that contain graded signals in the repertoires of all birds in this study. In the east both males and females have graded signals in the HP, HRP, KLP and TL call types. In the west males and females have graded signals in the BZ, HP, HRP, LR, and Q call types.

The repertoires of eastern males have a total of five graded call types which contain seven call categories for a total of 17 graded calls. The call categories include: HN20(2), HP02(2), HRP0(3), HRP02(2), KLP0(4), SPS21(2) and TL0(2). The number of calls within each category is in parentheses following the category abbreviation.

The repertoire of western males have a total of 11 call types which contain 18 call categories and 48 calls were contained within these categories. These categories include: BZ0 (2), BZ20(2), HP01(2), HP02(3), HRP0(2), HRP20(4), HRP21(5), HRP26(2), KLP20(2), KNP21(4), KWP0(2), LR0(2), M0(2), M20(3), Q0(4), Z0(2), and Z01(3).

The repertoires of eastern females contain six call types, consisting of nine call categories which hold a total of 19 calls. The call categories include: HP01(2), HP02(2), HRP2(2), HRP4(2), KLP0(4), M01(2), TL0(2), and Z01(3).

The repertoires of western females contain six call types, consisting of eight call categories which hold a total of 26 calls. The call categories include: BZ0(4), HP01(3), HP02(3), HRP1(4), HRP2(3), LR1(3), Q0(4), and W(2).

The call type group BH, not represented in the categories above, contains a pair of interregionally graded calls, BH0AW and BH0BE, among other non-graded calls. These calls were generally given only in flight, although there were exceptions.

Regional differences in parameters of graded calls within a category. While the majority of regional and/or sex-specific calls within the same call category were visibly different, i.e. differences were apparent without the need for parameter measurements, a small number of graded calls appear alike in

structure requiring comparisons of parameters to confirm that they were in fact gradations within the same category, not examples of the same call. For this purpose I chose to make a comparison of HP01 calls. This call category is represented by five calls, three of which were closer in appearance to each other than to the two remaining calls. These three calls appear to be regional and sex-specific counterparts or gradations of the same call. Eastern males and females use the graded form, HP01CE. Western males use two graded forms, HP01AMW which was used in male solo call sequences and HP01BW, which was used in duets with pair-mates. Western females use the graded form HP01BW calls in duets with pair-mates and in solo call sequences. In contrasting the western gradations to the eastern gradations in the HP01 category I compared the first and second HP01AMW calls from all western male solo call sequences to all eastern male HP01CE calls as eastern males use only one graded form. I also compared western female HP01BW calls to eastern female HP01CE calls.

To compare these calls I chose to analyze only frequency parameters because the call bodies and BIC regions of these calls appeared to be similar in length and the introductory post and inflections tended to have a high degree of variation in length even between calls from a single individual. As a result I measured the frequency of the first harmonic of the BIC region and the difference in frequency between the second harmonic of the call body and the first harmonic of the BIC region. Box and whisker plots in Figures 4-16, 4-17, 4-18, 4-19 are used to illustrate differences in means of frequency parameters between same-sex individuals in the same region and between regions, and the regional differences are illustrated in Figures 4-20, 4-21, 4-22, 4-23. Although the sample sizes used in these analyses are very small, the results indicate that there may be significant regional and sex-specific differences in frequency content among HP01 calls.

While HP01 calls were useful in formulating a method of quantifying differences in frequency parameters in calls recorded in different regions, there were enough additional structural differences between these regional-specific gradations that were apparent without quantification. This allowed me to recognize regional differences in a call with very small sample sizes, even without statistical tests. Some of the more obvious differences between regional gradations of this call included the shape of the call body and the structure of the introductory inflections (see fig. A-2). In addition to being graded from one region to another these calls were also serially graded within a region, in male solo call sequences. In the west, males tended to grade the harmonics of the BIC region, decreasing the frequency from the beginning of the sequence to the end of the sequence. Males in the east employed a different type of serial gradation. In the solo call sequences of eastern males there was no apparent change in pitch, but the between-call interval

was graded, being longer at the beginning of the sequence and becoming increasingly shorter towards the end of the sequence. There was no apparent difference between calls used in duets with females and those used in male solo sequences in the eastern region . In the west, when duetting with the female, the male tended to use HP01BW calls which closely matched the BIC frequency of the female's calls.

Other types of gradations within a call type appeared to be similar across both regions. For example, gradations in calls of the HRP call type group occurred most often in the frequency of the BIC region, the length of the raspy post and the length of the call body in both regions.

I did not find any apparent trends in frequency content or call length that could be used to distinguish the majority of calls of western birds from those of eastern birds. It appeared that the frequency modulations and overall shape of the call were more indicative of whether the bird using a given call had acquired its repertoire in the eastern region or in the western region.

Regional differences in vocal behavior and call sequencing.

One of the most apparent regional differences in the vocal behavior of pairs was that in contrast to western pairs, pairs from the eastern region seldom spent time vocalizing around the nest tree. Often, especially in the case of the EF #3 pair, the male would arrive for food exchanges in silence and the only indication of his presence would be a string of soft chatters which I was able to hear through the listening device attached to the nest cavity, and which the female could presumably hear from inside the nest cavity. On occasion the male would vocalize using male solo call sequences, most commonly strings of HP01CE calls, but duets were rarely heard near the nest area. While under normal conditions the EM pair was similar with respect to their vocal activity I was able to obtain more extensive recordings in March 1992 during a severe warble fly infestation in the nest cavity which resulted in nest failure.

A second difference in vocal activity between eastern and western pairs appeared to result from the amount of interaction these pairs had with other breeding pairs and/or non-breeding individuals or flocks in the vicinity of nest areas. In the eastern region nest trees were relatively isolated. During this study I heard intruders only once from the EF #3 blind and this was a distant encounter, too far from the microphone to record. In the EM nest area during the warble fly infestation, there was a single intruder, thought by biologists to be a young bird from the previous year's clutch. This bird made several attempts to enter the EM nest cavity and was chased out of the area each time by the male. However, for this pair, this was the only vocal encounter with intruders that I heard and was able to record over the course

of this study. Therefore it is conceivable that birds in the eastern region have a larger repertoire than I recorded, or at least that pairs in this region shared more calls with each other than my data indicate. It is also possible that during the nestling period when the female left the vicinity of the nest tree to forage that the pair vocalized more extensively. In contrast, the amount of vocal activity of the western pairs in the vicinity of the nest tree was always high. With the exception of the QG pair all nest areas were either bordering each other or they were in an area that appeared to attract flocks of non-breeding birds. As a result each resident pair had much interaction with intruders and/or neighboring pairs.

In the following section I will examine regional differences in call sequencing. As there were differences between males and females with respect to sequencing I will compare the call sequencing of western females to eastern females and western males to eastern males. As described in the introduction, for both members of a pair there were generally two modes of communication heard during the reproductive season. The first is solo call sequencing and the second is duetting with a pair-mate. Here I focus on solo call sequences.

Solo call sequences. In the western region male solo call sequences were heard frequently during the reproductive season. They usually preceded each food exchange in which the female was incubating eggs or brooding nestlings inside the nest cavity and the male needed to indicate his return to the vicinity of the nest tree. In contrast, female solo sequences were relatively rare. During the course of this study female solo call sequences, which were similar in content and structure to those of males, were heard only when the female briefly abandoned the nest cavity during the incubation or early nestling stage due to a disturbance in or around the nest tree, while the male was presumably out of the area foraging. In such instances the pair became separated and the female returned to the nest area seemingly without the male. I assumed that the male was absent because he was not heard vocalizing with the female and in each case, n=4, the male would be heard producing flight calls (BH0AW or BH0BE) or bugling returning to the nest area some time later.

In the eastern region I did not record or hear a single instance of a female vocalizing in the male's absence. As a result I can compare regional differences only in the solo sequences of males. In both regions I was able to separate male solo sequences into five general groups according to call content. The first group of solo call sequences in the west consisted of a string of HP02 calls. Calls in this string were relatively widely spaced and strings could consist of ten or more calls. While eastern males used HP02 calls they generally did not produce them in series. It appears that the eastern male's counterpart to the

western male's HP02 sequence was a sequence of HP02DE calls. As with the sequence of HP02 calls these calls were relatively widely spaced and could occur in strings of ten or more calls. Both of these sequences frequently preceded the second group of solo sequences.

In the west the second group of call sequences generally consisted of a string of HP01AMW calls preceded by an introductory call such as an HP02 or HP0 call. There were generally 2-5 HP01AMW calls in a single string and the frequency of the BIC region was graded from one call to the next, tending to decrease from the first call to the last. In the east, almost without exception the string of HP01CM calls, regional counterparts to HP01AMW and HP01BW, was introduced by a pair of HP02DE calls. There were between 6-20 HP01CME calls in a string with an average string containing about 13 calls. Unlike HP01AMW and HP01BW calls, HP01CME calls were consistent in frequency with no audible or visible changes in the BIC region from the first to the last call in a string. However, there was a slight gradation in the length of time between calls which appeared to decrease from the beginning of a string to the end.

Calls in the HRP call type group in combination with other call types make up the third and fourth sequence types. In the west, the third group of sequences was comprised of strings of HRP20AW calls preceded by an introductory call, HP0W. In these sequences usually 2-3 HRP20AW calls were used in a single string and one string was often repeated several times before the bird changes to a different group of call sequences. In the east 2-3 HRP02AE calls were preceded by an introductory call, HP02DE and these strings were used in a similar manner as strings of HRP20AW calls were used by males in the west.

Sequences in the fourth group were made up of a variety of calls in the HRP, HN, and Z call type categories. In the west sequences in the fourth group were comprised mainly of HN0AMW, HRP20A-DW calls, HRP21AW, HRP21CW, Z01A and Z01B calls. Some common arrangements of these calls include: HRP20CW HN0AMW Z01A, HRP20DW HRP20AW Z01A, and HRP21AW Z01A HRP20AW HRP21CW (see fig. 4-8). In the east there appeared to be fewer variations in call sequencing within the fourth group. The most commonly heard sequence was HN20AME HN20AME HN20BME HRP02AE or HRP22E Z01A. While the order of these calls generally did not vary from this, certain calls such as HN20BME or Z01A were frequently repeated in the sequence, i.e. sequences like HN20AME HN20AME HN20BME HN20BME Z01A Z01A Z01A were not uncommon (see fig. 4-7).

Sequences in the fifth group were made up of a gradations of calls within a single call category in both regions and these call categories were region-specific. In the west these sequences were composed of long strings of primarily Q0AW calls, punctuated occasionally by a Q0BW call. The calls in these strings were widely spaced, sometimes separated by over a second and strings often contained over 20 calls. Usually Q0BW calls followed two relatively closely spaced (< 1 second apart) Q0A calls and this sequence was preceded and followed by strings of more widely separated Q0A calls. In the east, KLP0E calls were substituted for Q0W calls. Strings of KLP0BE calls were occasionally interspersed with KLP0CE calls and KLP0DE calls. Calls in these sequences tended to become more and more widely spaced until the male ceased to call or left the area. There could be from 5-15 calls in a sequence.

Pair-mate duet sequences. Ideally, with a large sample size, it may be possible to record a pair's entire duet repertoire, however, because the recordings I collected failed to include all pairs in every behavioral context, they tended to be biased towards certain behavioral contexts for almost all pairs in this study. For example, 17 out of 29 recordings of duet bouts for the SF2A pair were made during intense interactions with a pair of thrashers while both pairs were attempting to occupy the same nest cavity. As a result of these intense interactions the pair spent much time vocalizing in close proximity to the cavity and the microphone and I was able to obtain a relatively large sample size of duets for these birds, although the recordings tended to be restricted to this and one other behavioral context. In comparison, the QG pair rarely vocalized in close proximity to the nest cavity with the exception of two days during nest inspection in February of 1993. In 1992 the nest inspection stage was relatively quiet possibly due to the presence of Red-tailed Hawks (*Buteo jamaicensis*) that were routinely heard circling the area. While the QG pair did not vocalize frequently in the vicinity of the nest cavity I could hear them vocalizing continuously in the distance. Therefore it is likely that while their duet repertoire may have approached the complexity of that used by the SF2A pair the sample of recordings I did obtain may not have been truly representative of the pair's duet repertoire.

Due to the discrepancies in data collection described above it was necessary to limit comparisons of duetting behavior between regions to how duets were composed and structured by pair-mates. Comparing complexity and size of duet repertoires at the call level within and between regions may be misleading in this study. The following is a summary of general trends in duetting behavior with respect to call ordering and duet structure within and between regions.

First, with respect to call sequencing, while the majority of duet phrases or bouts were begun by male initiators it was usually the female that initiated each individual duet couplet or complex following the initiator. However, there were exceptions to this and these exceptions in both regions occur usually under intense situations. Generally in the west, intense situations may include vocal battles with intruders or intruding pairs that take place in close proximity to the resident pair's nest tree. In the eastern region intense situations included nest checks and an intrusion into the EM nest cavity by a young bird from the previous year's clutch. Generally even when the male did initiate the first duet in a sequence, the duets following the initial duet were initiated by the female. See Figs 4-5, 4-6, 4-9, 4-10, 4-11, 4-12.

Second, with respect to duet composition, pairs from both regions tended to use similar call pairs in duets, e.g., if a western female begins a duet with an HRP1AW call this was most likely to be answered by an HRP call from the bird's mate. In the east the female's HRP02AE call was frequently answered by male-specific calls from the HRP call type group. The calls were different but the call types were the same. Only one duet sequence was common to both regions at the call level, GR01BF SPS21B, and this was true of only the EM pair in the eastern region as the EF #3 male used SPS21AE, an alternative gradation of SPS21, to answer the female's GR01BF call. See Figs 4-14, 4-15.

A third similarity in duetting behavior between the regions was noticeable when the members of a pair were visually separated. When duetting, pair-mates were generally in sight of each other and may even have been perched next to each other on the same branch, however, on occasion the female would call from inside the nest cavity to the male perched in a nearby tree or the male (rarely the female) would fly towards another pair or intruder in the distance leaving the female in the proximity of the nest tree and the pair-mates would continue to duet even at a distance. In these instances the calls making up a duet, which were normally closely spaced or sometimes slightly overlapping became more widely spaced. Figures 4-5 and 4-6 show typical duets between pair-mates. Note the slight overlapping of the female's calls with those of her mate's. In contrast Figures 4-1 and 4-2 show duets produced by pair-mates while out of visual contact. Note that the inter-note space has increased significantly from zero to about 0.2 seconds for the eastern pair and about 0.4 seconds for the western pair. When visually separated this inter-note length can range from about 0.2 seconds to 0.5 seconds. In 21 of 23 instances where pair-mates were duetting out of sight of one another, the average inter-note length was 0.34 seconds \pm 0.02 seconds. In addition calls that tend to attenuate more slowly over a distance were chosen over other

calls. It appears that a small number of calls were used during these instances, calls generally in the KWP, KNP, LR, HRP, HP, and W call type groups.

Discussion

Dialect formation. Results from the data analyzed in this chapter suggest that while there appear to be two dialects present in the population of parrots recorded in this study, the call sequencing or vocal behavior (i.e. how calls from the vocal repertoire are used in communication) of the two dialect groups is similar. In most species how and why dialects are maintained becomes apparent following an analysis of how young birds of a given species acquire their vocal repertoires and of the social system of that species. For a particular species details such as degree of relatedness between groups with different dialects (i.e. whether one group evolved from the other or two groups with different dialects came from the same parental population) or whether two groups with different dialects interact (i.e. interbreed, forage together, or flock together during the non-breeding season) are generally known. In most studies the relationship between two groups of conspecifics with different or similar dialects is known and it is possible to speculate as to the origin and function of a dialect system within these species, e.g. Saddlebacks (Jenkins 1977), White-crowned Sparrows (Baker and Cunningham 1985). However, for the population of Puerto Rican Parrots inhabiting the Luquillo forest details such as the relatedness of the two dialectal groups are largely unknown, and while it is agreed that there is some movement of birds from one region to the other during the non-breeding season it is unknown whether there is interbreeding or mixing of individuals from different regions or dialect groups during the breeding season. In addition there are few data available from past studies on how and when parrots in the wild acquire their vocal repertoire or whether this repertoire can be modified after it is acquired.

Historical records indicate that cavities were occupied by parrots in the same areas as they are today, only in larger numbers, as far back as the 1940s and likely before this. The first written inventory of nests was conducted by Rodriguez-Vidal in the mid 1950s and it confirmed the existence of nests in both eastern and western regions in approximately the same proportion as they are found today, i.e. there is a higher concentration of nests in the western region than in the east. However, it is unclear as to whether both groups originated from the same parental population or if one gave rise to the other. It is also unclear as to how many if any breeding groups were found between the western and eastern breeding groups and to what extent these groups may have interacted with each other. It is possible that in place

of a two dialect system that exists today there may at one time have been a continuum of vocal repertoires in which the repertoires of individuals within a group may have differed by one or two calls. The difference in repertoires between individuals of adjacent groups might have been relatively low compared to groups that were widely separated and out of contact for much of the year.

Data collected during this study suggest that the vocal repertoire used by reproductive pairs during the breeding season may be acquired by birds in their natal territories. During the 1993 breeding season a flock of non-breeding birds was recorded numerous times in the vicinity of two breeding areas and birds presumed to be young females were heard producing high pitched and uncrystallized versions of calls normally produced by adult females. It is possible that there are alternative explanations for the quality of calls these individuals were making, but the majority of birds in the group, 10-15 individuals, made calls in a similar manner. In addition a single individual recorded on four separate occasions in the western region was heard producing calls normally associated with eastern males. Presumably this bird had learned the vocal repertoire used by paired males during the reproductive season in its natal territory but had remained in the western region, possibly as a result of a very low population of non-breeding birds or available mates in the eastern region.

While not much is known of the vocal behavior during the non-breeding season it is likely that repertoires may consist mainly of calls from the chit-chat repertoire described in chapter four and possibly some alarm calls that are common to all birds. On several occasions I have heard groups of birds both during the breeding season and outside of the breeding season using what sounded like short chip-like calls that I associate with the chit-chat repertoire. However, I do not have recordings of these instances and was not able to analyze these vocalizations, nor do I know what the composition of the groups were, i.e. a group may have consisted of western, eastern or a mixture of eastern and western birds. In these groups a number of birds were calling simultaneously and there was seemingly no sequencing equivalent to that present between mated pairs during the breeding season, i.e. no antiphonal duets or solo call sequences. Another reason the breeding season repertoire may differ markedly from the repertoire used during the non-breeding season is that the stimuli eliciting vocalizations during the breeding season would appear to be quite different from the stimuli that elicit vocalizations during the non-breeding season. During the breeding season, much of the pair-mate communication, especially in the form of duets, at least in the western region, is an advertisement or aggressive signal directed at neighboring pairs or intruders that approach too closely to nest sites. During the non-breeding season birds tend to form large flocks, especially while foraging, and calls used during the breeding season in an

aggressive manner would seem inappropriate for this non-breeding season context. In addition a difference in vocal dialects may inhibit the formation of such mixed flocks, which might cause selection for convergence in vocalizations used in the non-breeding season. It is well documented that there is mixing of birds between regions during the non-breeding season.

In the following section I will offer a possible explanation as to how dialects may have formed in this population of parrots. I will attempt to explain the differences in the dialects from one region to the other, the manner in which these dialects may be maintained and the possible reason for their maintenance in the context of theories proposed in the introduction of this chapter. In studying the vocal repertoire of each individual I have found that a small number of calls are specific to each bird (see footnotes for Table 1). The calls specific to a particular individual appear to be either calls that are used in addition to the basic call repertoire common to all same-sex birds of that region, or they are substitutions for calls common to all same-sex birds of that region except the individual with the substitute call in its repertoire. In this case the substitute call often resembles the call it is substituting for closely. It is not known exactly how this substitute call may have been incorporated into an individual's repertoire but it is conceivable that when the bird was acquiring its vocal repertoire it made an error in copying a given call. Since the call sounded similar enough to the original perhaps it was never corrected and was subsequently incorporated into the individual's repertoire. An example of call substitution in the west is that the SF2B female substitutes LR3W for HP01EFW, and in the east, the EM female uses HRP4AE and the EF #3 female uses HRP4BE. As there are only two known breeding females in the east it is unknown which call is the original and which is the substitution. Figures 4-14 and 4-15 provides an example of this in males, where SPS21AE is specific to the EF #3 male. This call appears to have replaced SPS21B in this male's repertoire.

It is conceivable that at some point in time a young bird will copy one of these substitutions, incorporate it into its vocal repertoire and subsequently pass this call on to future generations. A possible example of this is provided by the usage of the call, WHP1W. This call was recorded from only two females in the western region and it is quite possible that the SF1A female produced this call exclusively until it was copied by a younger female, the QG female. It is assumed that the SF1A female is considerably older than the QG female as the SF1A female is possibly one of, if not the oldest, of the nesting females in the west while the QG female is the latest female to pair and produce young in the western region. In this manner the vocal repertoire of a region is continually changing at a relatively slow rate. Since so-called copying errors or copying of calls that were at one time exclusive to an individual are unlikely to be

transmitted from one region to another eventually the vocal repertoires from each region diverge and may become separate dialects. As it is not known if the western and eastern groups originated from the same parental population, different parental populations or one came from the other, it is not possible to assess how long it has taken for these two dialect groups to form independently from each other.

Dialect structure. In comparing the two dialects some broad generalizations can be made. First, there are twice as many calls present in the repertoires of western birds as there are in those of eastern birds. While this could be largely an artifact of eastern reproductive pairs tending to vocalize less in the vicinity of the nest site, i.e. the blind and microphone, than birds in the west so that the repertoires of eastern birds are underestimated, a previous study carried out by Tomosy in 1987 suggests otherwise. Tomosy recorded much of her data from birds in the east and she described a single vocal repertoire for the Puerto Rican Parrots which more closely resembles that of eastern birds than western birds. I conclude that while the difference in number of calls between western repertoires and eastern repertoires may not be as great as indicated in this present study there is still a significant difference in the number of calls between the two regions (see Table 2). In the east females have only 4-5 fewer calls in their repertoires than males, whereas in the west this difference increases to 15-17. The average western male has a repertoire of 65 calls while the average western female has a repertoire of 50 calls (see Table 3). The average eastern male has a repertoire of 38 calls and eastern females have an average of 33 calls (see Table 3).

It is possible that birds from the western region have a larger repertoire as a result of their interactions with a larger group of conspecifics that interact most closely during the reproductive season and possibly stay in close contact during the non-breeding season. If every individual in a given social group has at least one call in its repertoire specific to that bird, in a larger social group a young bird would have an opportunity to incorporate a greater number of calls into its repertoire than a young bird in a smaller social group. In other words a young bird that acquires its repertoire in the western region has at least six additional calls that it could add to its repertoire in addition to the call repertoire common to all birds of that sex. In contrast a young bird acquiring its repertoire in the eastern region has fewer calls available for it to copy. This could explain the discrepancy in numbers of calls in vocal repertoires between regions, however, it does little to explain why the difference in call numbers between males and females is greater in the western region than it is in the eastern region.

The majority of graded signals produced by western males were used during a variety of intense interactions with conspecifics and other species such as thrashers. In the east, during this study there was

an extremely low rate of interaction with conspecifics and thrashers. Thrashers were seemingly not present in the vicinity of the EM nest tree and I never witnessed any interaction between thrashers and parrots in the vicinity of the EF #3 nest tree although there were thrashers nesting in the area. In contrast, in the western region some reproductive pairs interacted with thrashers during a large part of the breeding season, often vying for the same cavities. In addition, in the west it was common for neighboring males and possibly a number of non-breeding individuals to accompany a resident male back to the vicinity of the resident male's nest cavity, presumably after foraging together within a flock. I could often hear neighboring males, particularly adjacent neighbors, e.g. the SF2B and SF2A males, producing flight calls, KNP0AW, upon returning to their respective nesting areas at approximately the same time. Following this the respective mates of these males would leave their cavities and the pairs would fly towards each other vocalizing loudly. I never encountered an equivalent interaction between pairs or other conspecifics in the eastern region. As a result it is possible that the lack of social or threat stimuli in the vicinity of nest cavities in the eastern region may have limited the types and number of vocalizations that I was able to record during this study.

With respect to vocal behavior, it appears that birds from both regions use similar types of call sequences although the call content in these sequences varies from one region to the other. One notable difference between the regions with respect to vocal behavior is an increased degree of call repetition in call sequences of eastern birds. In eastern male solo call sequences of the fourth type described above, each call of a sequence is in about 83% of cases (n=53) repeated at least once before a new call is introduced. In western male solo call sequences of this type however, calls are repeated in only 3% of male solo call sequences (n=87). It is more common in western male solo call sequences for the calls to be followed by other graded calls rather than the same call. In male solo call sequences of the second type (see above) eastern male sequences often contain twice as many HP01 calls as those of western males. Also with only a few exceptions (HRP1AW HRP20BW and HP01BW HP01BW duets) western pairs rarely repeat a duet combination. In contrast, eastern pairs commonly repeat the last duet combination of a duet sequence. As it appeared that eastern males were often further from the nest cavity when they began calling their mates than western males, it is reasonable to assume that a longer sequence might ensure that their mates hear them to know when they are approaching for food exchanges, but this does not explain the repetition in duets of pair-mates. There were certainly enough duet combinations used by eastern pairs that they could have substituted other duets for the repeated combinations. Thus the repetition was not due to a lack of calls. One possible explanation is that in the western region pairs tend to nest in closer proximity to each other. Thus with few exceptions most duet combinations will be

heard easily by other birds in the area and using a variety of calls may increase a pair's locatability. However, in the east nest cavities are at much greater distances from each other and possibly only a few calls transmit effectively over these distances, these being the calls used in the repeated duets at the end of a pair-mate duet sequence.

Evolutionary considerations. While in some species it appears as though dialects may facilitate assortative mating in order to maintain an adaptation it is difficult to imagine such a scenario among the parrots recorded in this study. Acoustic properties of the regions are quite similar and while there may be some subtle differences these do not appear to affect how the relatively loud, high energy calls of the parrots transmit within their environment. With the exception of crickets, there are no other species whose vocalizations are as loud as the parrot's, and other environmental sounds such as rivers or wind tend to be composed mostly of white noise that would not appear to effect the transmission of parrot calls. During a large part of the breeding season crickets can be heard for a period of about 20 minutes in the early evening. During this time the most commonly produced calls from the parrots appear to be low frequency alarm calls with dominant frequencies of about 1.5-2.0 kHz. The chirping of the crickets, is generally in a frequency band around 7-8 kHz and this masks any high frequency harmonics that may exist in the parrot's calls. It is unclear whether these alarm calls were chosen for their high energy low frequency harmonics to compensate for the loudness of the crickets chirps. While rain can make it difficult to hear parrot calls, the parrots tend not to call in heavy downpours, although there are exceptions to this. Apart from environmental sounds the only other noise that may have been loud enough to mask the parrots' calls was present at only one nest site in the eastern region. This noise is transmitted continuously from a radio control tower near the nest site. While this interference was not audible to the human ear it appeared as a wide band of frequencies around 13-16 kHz on sonographs.

Other hypotheses are not as readily dismissed as the acoustic adaptation hypothesis. Treisman (1987) suggests that the use of dialects may facilitate assortive mating whereby individuals set up territories in close proximity to kin, reducing the need for aggression between pairs in a given area. While it is highly likely that the parrots within a region are all related to some degree due to the small population size, parrots generally do not hold territories and mated pairs appear to be relatively tolerant of other parrots in the vicinity of their nest tree provided the intruders do not approach too closely or give vocal signals that identify the intruders as a possible pair. It is unclear whether there is more aggression among unrelated neighbors than related ones. As mated pairs tend to return to the same cavities each breeding season unless a mate is lost or the cavity is destroyed, neighbors are generally familiar with each other and

aggression appears to be kept at a minimum. There may be heightening of aggression when new pairs are heard in the area and are searching for nesting cavities.

While the relatedness of pairs in a region is unknown for this population, if it is assumed that birds tend to learn their call repertoires from adults in their natal region then it follows that individuals tend to find nest cavities within their natal region, and that relatedness is higher within than between dialect groups. During 1993 a bird, presumably a male from the eastern region, was heard in the vicinity of two nest trees in the western region during four different recording sessions. The resident pairs of these nest trees did not appear to react aggressively at hearing this bird, possibly because it was not answered by a mate and was not considered to be a threat. It is unclear whether this bird would pair successfully with a western female despite the differences in vocal repertoires. Generally when the male of a mated pair is lost the female will re-pair almost immediately with an available male even if the original male is lost during the breeding season. A male that replaces another tends to have a similar repertoire to the male he is replacing, which may reduce the amount of time pair-mates expend on learning each other's repertoires, and may promote synchrony of the sex-specific calls in duets. Whether this male could actively change its repertoire to match that of other males and thus increase its chances of acquiring a mate is unknown.

If calls of mates do converge, Rothstein and Fleischer's (1987) honest convergence theory may apply with some modification to take into account the fact that females in addition to males acquire a large and complex vocal repertoire. In this case the dialects would remain essentially stable as birds enter the breeding pool either as a member of a new breeding pair or as a mate replacement for an individual already included in the reproductive pool. In the latter case, an individual's chance of replacing another bird would seem to be greatly increased if the bird could adequately mimic the calls of the other bird's former mate.

Conceivably in the case of a species, such as *Amazona vittata* perhaps where young birds tend to remain in a close family group for an extended period of time, learn their call repertoires from adults in their natal regions, and subsequently establish breeding cavities within the same region, Treisman's (1987) kin recognition theory and Rothstein and Fleischer's (1987) honest convergence theory might both apply. They are not necessarily mutually exclusive. Additional studies may confirm that these two theories together may offer an explanation as to the function and maintenance of dialects in this population of parrots.

Further research needs to be conducted in order to determine how young birds acquire their vocal repertoires. If they disperse before acquiring their repertoires then it may be necessary to determine whether birds such as the eastern male heard in the western region could in fact modify their repertoires to match the western repertoire or whether this would possibly act as a barrier to acquiring a mate outside of an individual's natal area. If it is confirmed that an individual's vocal repertoire identifies it as a member of a particular social group from its natal area this may support the theory that one function of dialects in this species may be social group identification, as is the case in human populations where accents can be used to identify a segment of the population, usually associated with groups of people living in a particular area, e.g., a Brooklyn accent or a southern drawl etc. Determining how young birds acquire their repertoires and how they learn to associate certain calls with particular contexts may enable biologists to make decisions about how birds that are being bred in captivity might be housed in order to better prepare them for release and survival in the wild.