CHAPTER FIVE

INDIVIDUAL RECOGNITION

<u>Introduction</u>

In at least twelve orders of birds, individual specificity in vocalizations has been demonstrated. In general, perhaps because the environment in which they are found often allows for little or no visual contact, many monomorphic, long-lived, monogamous tropical bird species such as *A vitatta*, appear to rely heavily on vocal cues for communication and individual recognition (Beer, 1970). In a number of cavity nesters, including nocturnal species and species occupying habitats of dense vegetation, vocal signals gain greater importance in pair communication during the breeding season (Brooke,1978).

Nocturnal species such as shearwaters (*Puffinus* spp.), petrels (*Oceanodroma* spp., *Pterodroma* spp. and *Hydrobates* spp.) and storm-petrels (*Procellaria* spp.) use varying degrees of vocal identification for defending their nesting burrows, and distinguishing their mates from potential intruders (Brooke, 1978; Brooke, 1986; Grant et al., 1983; Hall-Craggs et al., 1976; James et al., 1984; James et al 1985a; James et al., 1985b; Simons, 1981; Taoka et al, 1990; Taoka et al., 1989a; Taoka et al., 1989b;). Manx Shearwater (*Puffinus puffinus*) females can distinguish the calls of their mates whereas males do not respond selectively to their mates' calls. This may be due to the different roles the sexes play during the breeding season. The male establishes ownership of the burrow during the pre-laying period. When the female arrives from the sea she needs to locate her mate from the previous year. Males call frequently from within their burrows, and the females are able to recognize individual males in their burrows in order to locate them. The selective ability of the female to respond only to the correct male implies that for males, the within bird variation in certain call features is less than the between bird variation. Upon visual inspection of the spectrographs of males' calls it appears that there are a number of individually distinct frequency and temporal components that may provide a basis for their recognition by females, but it is not known which the females use (Brooke, 1978).

Short-billed White-tailed Black Cockatoos (*Calyptorhynchus baudinii latirostris*) are cavity nesters as are Puerto Rican Parrots. Female Short-billed White-tailed Black Cockatoos rely on auditory cues produced by their mates to coordinate feeding bouts during the breeding season. The female alone incubates and broods the eggs and chicks and she must depend mostly on the male for sustenance. Should the male fail to return to feed the female she would be forced to leave the nest cavity to forage at the risk of losing eggs or chicks (Saunders, 1983).

Some of the studies cited above have been conducted with the objective of finding a means that is less risky than conventional censusing methods to identify individuals of endangered, rare vulnerable species (Gilbert et al., 1994; Saunders, 1987). Other studies have been conducted simply to learn more about a species' ecology and behavioral traits (Hand, 1981, Brooke, 1978). Frequently a method useful to biologists for identifying individuals of a species arises out of these studies, though this is not the primary objective. The latter studies usually employ some form of playback experiment in which individuals of a given species exhibit some degree of recognition of known individuals. For example, in a study on Stripe-backed Wrens (*Campylorhynchus nuchalis*) it was shown that males of the species can discriminate among neighboring males and non-adjacent males and furthermore can discriminate between neighboring males. That is, the response of a given male to a neighboring male singing in a location other than its own territory will elicit a response similar to one that would be elicited by a stranger (Wiley, 1977). Other types of playback experiments performed to test for individual recognition involve parent offspring recognition, for example, in creching species such as the Adelie Penguin (*Pygoscelis adeliae*) the adults of young congregating in large creches need to be able to recognize their own offspring (Penney, 1968), and mate recognition in species such as shearwaters and cockatoos, both cavity nesters where mates need to be able to recognize each other in the absence of visual cues to reduce the time spent away from their unprotected nest (Brooke, 1978; Saunders, 1983).

In this study I had planned to use playback experiments to support the theory that the parrots were able to recognize conspecifics via their vocalizations. In watching the behavior of breeding females prior to this study, I had observed that when incubating eggs or brooding young in nest cavities females appeared to be able to discriminate between intruders in the vicinity of or flying over a nest cavity and their mates calling them from their nest cavity for food exchanges even in the absence of visual cues. Males would leave the nest site for periods of time presumably to forage for food. Frequently these males would be accompanied by a small group of conspecifics. Upon returning to the nest site a number of the birds accompanying the resident male would fly over the nest site while others would land on trees near the nest cavity and begin vocalizing. However, the resident female would not respond until her mate landed in a nearby tree or in the nest tree and began vocalizing. A negative or non-response from the female in this context is one in which the female in the nest cavity remained silent. A positive response is one in which the female vocalized, the vocalizations ranging from loud mumbling to loud calls, though loud calls given by females inside the nest cavity were uncommon. At one nest site, EM, an intruder landed on the entrance vine leading into the nest cavity. Upon hearing the vocalizations of this individual the female left her brood immediately and chased it some distance from the nest tree. In the absence of visual cues it appears that the resident female had little difficulty recognizing that this individual was an intruder and not her mate. Despite the fact that the playback experiments I had planned to conduct would not have exposed the parrots to any unfamiliar conditions that they would not normally encounter over the course of the breeding season, the USFWS deemed the playback experiments to be too intrusive and would not permit the use of them. As a result this part of the study was restricted to the recognition of individuals by biologists with the only evidence supporting recognition of individuals in the birds themselves being anecdotal as described above.

In general individual recognition of parrots in the wild through visual cues is difficult. Biologists are usually restricted to a blind or tree-top platform during censuses. The blind restricts the ability of an observer to see much beyond the entrance vine and outside of the nest cavity while from the tree-top platforms one can not do much more than count parrots as they fly by usually at a great distance. In the hundreds of hours I spent in observation blinds I was able to observe only three birds, presumably not members of the breeding population, with aluminum bands. A flock of birds often seen foraging near the SF1A pair's nest tree contained several banded individuals. One of these individuals later pair-bonded briefly with the SF1A female but was subsequently replaced by another bird. The former bird was easily recognizable as it was wearing a radio-collar from a previous study. The majority of birds in this flock were neither banded nor did they have any additional distinguishing features and were thus not readily identifiable. In addition to three members of this flock, several birds of the breeding population were banded and two had worn radio-collars. While bands supplied information such as the location of an individual's natal area if it hatched in the wild, they gave little information that could be used to identify individuals. Thus a method that does not depend on visual cues for the identification of individuals is preferable for this and many other cryptic species. In this chapter a method for recording and analyzing characteristics of call repertoires for each individual in the breeding population is described. Much like a finger print record, this method would prove to be a useful tool for censusing and identifying members of the breeding population. With a record of each known individual's repertoire (a partial repertoire may also be sufficient) subsequent recordings made in the field could be compared to these records to determine which individual had been recorded and to add new individuals to the data files when recordings could not be identified as one of the individuals previously recorded.

It is possible that slight individual morphological differences in the vocal apparatus used by birds are sufficient to allow for individual-specificity within their vocalizations (Nowicki, 1987). Saunders and Wooller (1987) note that the phenomenon of imitative learning in some passerines may make the recognition of individuals by their vocalizations unlikely. It is possible, however, that the features of vocalizations analyzed by biologists are usually those relating to frequency and temporal characteristics alone and that these characteristics, especially where complex calls are concerned, may not provide enough information for biologists to be able to discriminate between individuals. As a result in this chapter I compare the results of three techniques as a means of identifying individuals. These three methods include 1)bird - call pairing, 2)examination of frequency content and temporal characteristics through the use of sonograms and 3) examination of the sound energy of an individual's calls using linear predictive coding. After showing the advantages and disadvantages or limitations of each method when used separately I demonstrate how by using these techniques jointly, it is possible to make more efficient use of all the characteristics present in the signal rather than relying on a single characteristic.

Methods and Results

This section is divided into three parts. Each part describes one of the three methods used for identifying individuals. The results directly follow the description of the methods used.

Bird-call pairing. This method in which a bird may be identified by a call unique to it, relies on the assumption that there are calls in each bird's vocal repertoire that are used solely by that individual and that call repertoires remain stable once acquired. For a call to be used by biologists to identify an individual it should be used frequently, i.e., at least once per recording session and preferably in multiple contexts. If a particular call is recorded infrequently and in only one context it is likely that I may not record this call at least once per breeding season. As a result I might make the assumption that the bird in question had been replaced or had abandoned its cavity when it may simply indicate that the context in which this individual makes its unique call did not occur during a particular breeding season or on any of the days I was recording it. If a particular call is heard at least once per recording session at the same nest cavity and is not recorded from any other individual it is safe to assume the call is being made by the same individual each season. If a call commonly recorded in two consecutive seasons from the same individual, is not heard in the third season it is conceivable that either the individual using the call was replaced or the individual and its pair-mate abandoned the nest cavity. In the latter case this could be determined by examining the recordings of the pair-mate's vocal repertoire to note any changes over the three breeding seasons.

Methods. First, I analyzed recordings made over the course of this study and noted all calls that were seemingly unique to individuals. I then removed vocalizations that I did not hear more than once. Ideally I would have preferred to remove calls that I did not record at least once per breeding season but some individuals disappeared during the course of this study and I have recordings of these individuals from only one breeding season.

Next I divided the list of unique calls into two categories, substitutions and individual-specific calls. Substitutions are calls unique to an individual that appear to be used as replacements for similar calls used by all other same-sex birds from the same region (see Table 5-1). The individual using the replacement or substitution does not appear to have the more commonly used call in its repertoire. Substitutions often sound similar to the more commonly used call they appeared to be replacing and they tend to be associated with similar call sequences. For example, HP01EFW is a call used by all western females except the SF2B female. This call is often the first call given by the female after landing upon returning to the vicinity of the cavity and is frequently the first call or initiator of a duet sequence between pair-mates. The SF2B female appears to use LR3W as a substitute for HP01EFW. LR3W sounds similar to HP01EFW though, structurally it appears to represent a hybrid form between HP01EFW calls and calls in the LR call type group. The elongated, buzzed introduction was similar to that of the HP01EFW call, however, the call-body shape and the lack of a post prompted me to place LR3W in the LR call type category.

Individual-specific calls, the second group of calls unique to individuals, did not appear to be substitutes for other calls but rather may serve to increase the size of individual call repertoires. An example of an individual-specific call is BZ0AMW recorded from only the SF1A #2 male. This buzzy call was used frequently by this male while it was perched outside the cavity and its mate was inside the cavity and also after heavy downpours. It did not appear to be a substitute for another call and it did not closely resemble another call in the BZ call type group. While it is conceivable that substitutions may have resulted from copying errors, the evolution of individual-specific calls is not so obvious.

A major limitation to this method is that it can not be used to document the movement of unknown individuals. It is restricted in use to known individuals, i.e., individuals that are members of mated pairs, where the vocal repertoires of these individuals can be collected and subsequently used to determine factors such as whether pairs remain constant over breeding seasons and whether they return to the same nest cavity each year.

Results. The best candidates for this method were pairs from which I recorded vocalizations given in multiple contexts over multiple breeding seasons and these included the SF2A and SF2B pairs. I noted at least one call unique to each individual in these pairs (see Tables 5-1 and 5-2). These unique calls were used frequently by the individuals and in more than one context, allowing me to reliably identify the individuals by their use of these calls. Using this method I was able to identify the SF2A and SF2B pairs during vocal interactions. For example, if I were recording from the SF2A blind and heard two pairs vocalizing, one the SF2A pair and the other using at least one call unique to one of the pair-mates of the SF2B pair, I was relatively certain that the second pair was the SF2B pair. In addition, this method confirmed that these pairs remained faithful to their respective nest cavities over the course of this study.

Due to the limited number of quality recordings obtained from some pairs this method was not always a reliable tool for identifying individuals. First I will discuss the validity of using this method to identify individuals in the remaining western pairs and then I will analyze this method with respect to pairs in the east.

Western pairs. The bird-call pairing method had limited application in the case of the QG pair. Most recordings analyzed for this pair were obtained in February 1993 during the nest inspection stage. Thus most of the recordings were acquired in a limited number of contexts, i.e., there were no apparent interactions with conspecific intruders or neighbors, no interactions with thrashers or other contexts other than those associated with the activity of nest inspection. Possibly because this pair nested in a cavity relatively isolated from other active cavities in the western region, the birds tended to vocalize more frequently at a distance from the nest cavity and the recordings as a result were faint. Thus if there were calls unique to either pair-mate but that were produced only in contexts associated with conspecific interactions I may not have recorded these calls because they were given at closer proximity to other active nest sites. As a result neither pair member appeared to use calls unique to them. However, the QG female produced a call, WHP1W, that I had, prior to the 1993 breeding season, recorded from only the SF1A female. This call was recorded only three times from the SF1A female but was used frequently by the QG female in pair-mate duets during and subsequent to nest inspection. Thus the QG female's use of the WHP1W call makes this female unique because if other females in the region, besides the SF1A female, also used this call it was used relatively infrequently since I did not have any recordings of it from the other females. Therefore if they produced the WHP1W call, they used it infrequently, at a rate similar to that of the SF1A female. In other words it may be the use-rate in addition to the uniqueness of the call that may allow biologist to use this method for individual identification.

Another example of call use where a call is not exclusive to an individual but appears to be used in an exceptional manner involved the QG female's use of the Z0AW call. Prior to February 1993 I had recorded this call from only western males however, I subsequently recorded this call from the QG female on one occasion in a duet with her mate. As I did not record it from this individual more than once I do not consider it useful in individual recognition, but had it been used more frequently, though it was not unique to this individual, it appeared to be unique among females of this region and it would have been a useful marker for this individual.

The bird-call pairing method may be applicable to the SF1A pair during the 1992 and early to mid 1993 breeding seasons. The first male produced at least one unique call, M20BW, and did not produce the BZ0AMW call, unique to second male that replaced the first male in the 1993 breeding season. The SF1A female also produced calls unique to it, but these calls were recorded only in the 1992 and early 1993 seasons. From the middle to the end of the 1993 season my access to the SF1A blind was limited because biologists were actively responding to an increase in thrasher activity and rate of predation on parrot eggs and young at this nest and the blind was being used for this purpose. The recordings I obtained during this time did not contain any of the previously documented calls unique to either pair-mate. However, there was a call, BZ0AMW, previously unrecorded that appeared to be unique to the male. The male used this call frequently in the recording sessions conducted during the month of June 1993 but only sporadically in the month of July. The recording of the previously unheard call from the male coincides closely with the time that the first male was replaced by a second male. However, it is not obvious from the recordings whether the female abandoned the cavity also, i.e., the pair abandoned the cavity leaving it to be occupied by another pair, or whether the female lost her original mate and subsequently re-mated.

Eastern pairs. Although I recorded eastern pairs over multiple breeding seasons and in multiple contexts I actually had few quality recordings from them because they tended to vocalize more frequently at a distance from the nest cavity. In addition because there were only two pairs in this region it was difficult if not impossible to ascertain which calls were substitutions and which calls would be more commonly used in a larger population. For example the EF #3 female used a call, HRP4BE while the EM female used an almost identical call, HRP4AE, in similar contexts. However, without more paired females in the population it is not possible to determine if one of these calls resulted from a copying error while the other represented the standard form of the call. Nonetheless it was possible to identify these females by their use of these different forms from the same call category and unless the population were to grow and these calls were copied, making them common to all females this method for identifying individuals may be considered a reliable tool individual recognition. Both eastern males also used calls unique to them but, again there were few recordings of these calls and these recordings were acquired over a 2-3 recording sessions, thus I did not hear the calls at every recording sessions and had my recording days been fewer in number (< 10 sessions) I may not have any record of these calls.

Frequency content from fourier transforms (sonagrams). This method is similar to the one used to categorize calls in the vocal repertoire (see Chapter 3). Recordings were converted to sonagraphs and the frequency and time parameters of these calls were analyzed to determine if there were differences that may be used to reliably identify individuals.

Methods. All measurements were made on calls in the HP01 call category because they were the most frequently produced by all birds. Six frequency parameters were evaluated. Figure 5-1 illustrates how these parameters were measured and figures 5-2 - 5-13 show frequency ranges for each parameter. The calls from five females, SF2A, SF2B, SF1A, QG, and EF #3 were analyzed. Calls from females in the eastern region were difficult to obtain because these females did not produce solo sequences in the vicinity of the nest tree and overlap from the male's calls in duets made it difficult to obtain accurate measurements. Calls from seven males, SF2A, SF2B, QG, SF1A1, SF1A2, EM and EF #3 were analyzed. After taking measurements of six frequency parameters for each individual the means of these measurements were compared pair-wise using the Mann-Whitney U test.

General results: The results are summarized in Tables 5-3 - 5-5. The results suggest that differences in frequency in one or more parameters between individuals of the same sex can be identified.

Comparison of variables among males: Variables 1 and 3 appeared to provide the most reliable basis for individual recognition among western males. With the exception of variables 2 and 5, the parameters of eastern males' calls differed significantly from those of their western counterparts. Variable 6 did not vary among western males but differed significantly between western and eastern males and among eastern males. All individuals differed from other individuals in at least one variable except for the SF1A male #1 and the SF1A male #3. Thus there was at least one variable that could be used to differentiate between the majority of individuals contrasted in this analysis.

Comparison of variables among females: As only one eastern female's calls were used in this analysis it was not possible to separate individuals by region. Therefore the analysis examines all females as a group without respect to region. Variable 2 appeared to be the single best parameter for distinguishing females. Variables 1, 4 and 6 were also useful. As with males, all individual females differed from other individuals of the same sex by at least on variable.

Differences in average frequency of one or more parameters between individuals does not necessarily allow for separation of individuals unless opportunities for recording are unlimited. After evaluating the means of the parameters for each individual I attempted to cluster the data around the mean. I then analyzed ten calls that had been omitted from the data set used to find the means and attempted to add these calls to a cluster which most closely matched the parameters of the calls. Eight out of ten calls fell into two or more clusters, including the cluster to which the calls belonged, i.e., that of the same individual. Two out of eight calls were closer to clusters to which they did not belong. Thus it appears that while this method indicates that there are individual differences in some parameters of HP01 calls, evaluating frequency content of fourier transforms does not allow for fine enough discrimination between frequencies to efficiently separate individuals.

Linear Predictive Coding analysis. Frequency measurements made on sonagraphs do not easily enable individual identification, however, they do allow for separation by sex and region as was shown in chapter 4. Linear predictive coding or LPC is the auto-regression of the auto-correlation of a signal where the waveform is analyzed in its entirety taking all of its properties into account as opposed to analyzing characteristics such as frequency or time spectra independently. As the resolution of frequency /time analyses is not fine enough to separate individuals the LPC technique permits components of the signal other than frequency to be analyzed more closely. This technique is explained more completely in appendix C.

Methods. The majority of data for these analyses were acquired over the 1992 and 1993 breeding seasons. In 1994 I recorded at only two nest sites, SF1A and another site previously unoccupied but that was being inspected by a pair. Only recordings with minimum background noise (e.g., calls with rain or other disturbance that actually distorted calls were not used), made relatively close to the microphone and with only one individual calling at a time (e.g., calls made in duets with mates were not used because of overlap and potential loss of information) were used in these analyses. As a result, sample sizes are very small usually with fewer than ten calls per individual. No effort was made to filter background noise, e.g., wind, rivers, or to standardize conditions as I wanted to determine how robust this method for identifying individuals was under a variety of field conditions. If this method for individual recognition proves robust even under the constantly changing conditions in a rainforest then it may eventually provide a quick and reliable method for biologists to ascertain an individual's identity in the field.

LPC techniques have routinely been tested for use in human voice recognition and while the recordings used are not always of the highest quality, the conditions under which they are made are usually controlled, e.g., speakers are recorded in a sound-proof room and all speakers are recorded under these same conditions. To test for robustness I noted which recordings appeared both sonagraphically and audibly to be the cleanest, i.e., recordings with the clearest sonagraph and little background noise, and which were the noisiest, i.e., recordings with low signal to noise ratio and with the bird at a distance. The clearest recordings came from the SF1A #1, SF2B, and QG females and the SF1A #2A, SF1A#2B, SF2A, SF2B, and EF #3 males. Recordings from the SF2A, EF #3 and SF1A #2 females and those from the SF1A #1, QG and EM males I considered would be more likely to show higher variability between calls from the same individual because of the relatively low signal to noise ratio.

After selecting the recordings for the analyses I used results from sonagraphic analyses conducted on sex and region-specific calls, HP01 (see chapter 4), to divide pair-mates into four groups, eastern males, eastern females, western males and western females. Various features of the sonograms were shown to be reliable indicators of region of origin, e. g., shape of the extensions and call body harmonics (see Fig. 3-2). Variable 1 as shown in Fig. 5-1 was shown to be a reliable indicator of an individual's sex (see Chapter 4). In general if the fundamental frequency of the BIC region of HP01 calls was higher than 3.2 kHz in western birds, the call was most likely produced by a male and if it was below 3.2 kHz, the call was probably produced by a female. The fundamental frequency of the BIC region in HP01calls from eastern birds did not allow for as consistent separation between the sexes as in the west because there was a smaller difference in this parameter between males and females. However, in the calls produced by females this parameter tended to be equal to or less than 2.9 kHz while in calls produced by males this parameter tended to be equal to or higher than 2.9 kHz. Thus after determining a bird's origin by examining structural features of sonagraphs, the bird's sex was determined by measuring the fundamental frequency of the BIC region and the parrots were grouped accordingly.

Prior to analyzing data using LPC techniques, calls were passed through both a pre-emphasis and low-pass Chebyshev filter (see Appendix C). I set the Chebyshev filter to emphasize harmonics of calls between 2.5 kHz and 3.5 kHz for females and 2.5 kHz and 3.7 kHz for males. This frequency range encompasses the loudest part of parrot vocalizations and reduces the possible effects of low frequency distortion. I chose to make 3.5 kHz and 3.7 kHz as upper limits because in some cases if birds were recorded at a distance or were facing away from the microphone higher frequencies were faint or non-existent whereas calls recorded from birds at close range often included frequencies above 10 kHz. Thus in truncating the frequency range I was able to standardize the number of frequencies analyzed. Calls were then smoothed using a hamming window.

Next, preliminary tests were run on the calls to determine the optimum number of coefficients required to conduct the LPC analysis. In a study on individual and sex recognition in humans, 12 coefficients were found to be the optimum number, i.e., the number of coefficients that gave the most consistent results (Tran, 1995). I selected a number of HP01 calls from five individuals at random and analyzed these calls using from 10-20 coefficients. Using fewer than 10 coefficients, I obtained inconsistent results. Perhaps because there may not have been a sufficient number of coefficients to model the vocalizations and it is possible that at a low number of coefficients, different parameters are measured each time resulting in inconsistent results. Using more than 17 coefficients appeared to increase variability of parameters from one call to the next possibly as a result of fragmenting calls into components too small to give meaningful results. Thus I chose to use 15 coefficients to model the parrots' vocalizations, though using 14 or 16 coefficients probably would not have changed the results significantly.

Next, calls were converted to 15 LPC coefficients and these coefficients were plotted and analyzed (see Fig. 5-14). Although calls range from 0.25-0.3 seconds in length I graphed only the first 0.2 seconds of calls because after 0.2 seconds the coefficients tended to become more variable and less consistent in calls from the same individual, i.e., there did not appear to be any patterns repeated in calls from the same individual and it was often difficult to ascertain where the call ended. In addition abbreviating calls permitted the relevant segments to be stretched and more easily examined. I graphed groups of coefficients that were similar in shape and separated these from other groups of coefficients with differently shaped contours to reduce loss of information due to overlap interference. I grouped the coefficients as follows, coefficient 1 was grouped by itself (Fig. 5-15A), coefficients 2-4 were grouped together (Fig. 5-15B), coefficients 5-7 were grouped together (Fig. 5-15C), coefficients 8-9 were grouped together (Fig 5-15D) , coefficients 10-12 were grouped together (Fig.5-15E), coefficients 13-14 (Fig. 5-15F) and coefficient 15 was plotted alone (Fig. 5-15G).

After grouping coefficients by shape I attempted to determine which group or groups of coefficients minimized variability within an individual's calls and maximized variability between calls from different individuals. In addition I examined groups, e.g., males versus females and east versus west, to determine if individuals from different groups were more easily identifiable by the same or different groups of coefficients. In comparing groups of coefficients from one call to the another I compared number and position of peaks, and the contours of coefficients with respect to each other, i.e., where coefficients intersected and the direction of their slopes with respect to each other (see Appendix D).

Next using the group containing coefficients 10-12, I divided calls into sections corresponding to regions on the sonagraph (see fig.5-14). I chose these coefficients because they gave consistent results within and between individuals. I compared sections within and between calls of individuals and found the segment of the coefficients corresponding to the BIC region of the sonagraph to have the highest variability between individuals and the lowest variability within individuals (Fig. 5-16). In addition, its characteristic contour (see Appendix D) was easy to locate in graphs of the coefficients and the BIC region was free of editing errors that are present at the beginning and end of some calls. These errors occurred when the beginning or end of a call was cut off either because the calls were produced in a duet and there was overlap whereby I would cut the overlapping part or if there was some distortion in these regions. If there was distortion over the entire call it was not used in these analyses.

After, isolating the BIC region I took the first derivative of the LPC coefficients (Fig. 5-17). The first derivatives of the coefficients give the slope of the coefficients and they can be plotted in much the same way, giving a slightly different perspective to the analysis. These graphs can then be compared within and between individuals in the same manner as the LPC coefficients were analyzed. In addition I performed principle component analysis on the first derivatives of the LPC coefficients in order to reduce the number of variables common to the derivatives and to define the structural relationship between variables. The graphs resulting from the PCA analysis of the first derivatives can be examined in a manner similar to the method used for evaluating the LPC coefficients (see Appendix D).

Results: Some results were given in the methods section above as they supplied data for other analyses, however, in this section I discuss these results in greater detail. When examining the groups of LPC coefficients I found several groups to be variable and inconsistent between and within individuals. These groups contained coefficients 1-4 and 15. I graphed these coefficients to show inconsistencies in the contours of the calls(see Fig. D-1- D-8) Other coefficients were more consistent within the calls from an individual and served to distinguish individuals from the rest of their group, e.g., male, female, east or west. These coefficients fell into four groups, 5-7, 8-9, 10-12, and 13-14 (see Fig. D9 - D-24). The coefficients in these groups tended to run parallel to each other with little overlap over the majority of the call. When there was overlap either one coefficient was superimposed on another for a brief period of time or coefficients intersected and deviated from each other. The latter created a pattern which is frequently unique to all calls from a given individual particularly with respect to the BIC region of coefficients 13 and 14 and may be used in combination with other aspects of the coefficients for individual identification (see Figs. D-21 - D-24).

Before examining calls for characteristics that may be unique to individuals I attempted to determine if there were differences in consistency between these coefficients with respect to group. For example, I compared coefficients 10-12 of calls produced by western males to those produced by eastern males and calls produced by eastern females to those produced by western females. I did not observe differences in the contours of these coefficients between sexes within a region, however, there appeared to be a difference in contours of calls between regions. This difference was most visible in the BIC region. In the calls of eastern birds the BIC region had an n-shaped curve whereas in calls from western birds this curve was u-shaped. I found that these region-specific curves were detectable in coefficients 5-12 and they were prominent in both sexes from both regions. In addition to the differences observed in coefficients 5-12 there was also an observable difference in the BIC region of coefficients 13-14. In calls from western birds, coefficients 13 and 14 tend to intersect and do not run parallel to each other in the BIC region, however, in the same region of calls from eastern birds these coefficients are more widely spaced and run parallel to each other with no visible intersections. A possible explanation for these differences is that the eastern and western calls differ slightly in sonagraphic structure, particularly in the introduction and BIC region and this difference may be reflected in the LPC coefficients. Though there are differences in frequency range in males and females within a region, the overall structure of the call remains unchanged as does the contour of the LPC coefficients.

I then examined the contour of the BIC region and identified patterns in the coefficients that were repeated consistently in different calls from the same individual but that appeared to differ from one individual to another. The introductory extensions of calls may also contain information useful in separating individuals but the segment was often distorted or shortened in the editing stage of the analysis most often because the call was overlapped by another bird's calls. With the exception of the first 0.05 seconds, coefficients in the segment corresponding to the call body in sonagraphs appeared similar in all birds and I did not find this segment useful in separating individuals.

Using the graphs of the BIC region, including the plots of coefficients 10-12, the first derivatives of these coefficients and the graphs of the PCA of the first derivatives, I was consistently able to recognize patterns in the LPC coefficients which could be used to distinguish individuals. On occasion when the contour of coefficients from one individual resembled the contours of another individual's calls I was generally able to use other data, such as looking at contours of other coefficients over the entire call to determine the identity of the caller. I did not however, have a sufficient number of calls produced by birds in this study to test the reliability of this method because all available calls were used in the characterization of each individual's vocalizations.

While most results obtained in this section supported my previous assumptions that unless otherwise noted pair-mates in this study remained unchanged and faithful to their nest sites, there is one discrepancy. This discrepancy involves the SF1A pair. The male of the original pair disappeared near the end of the 1993 breeding season and was replaced by a second male. In the 1994 breeding season a third male replaced the second male. The female was thought to have been the same bird throughout the three breeding seasons. However, data from the LPC analysis suggest that both male and female occupying this cavity in 1994 were different individuals from those composing the original pair. In examining coefficients 5-14 I found differences in numbers of peaks and in the juxtaposition of coefficients, two characteristics that I used to successfully separate other individuals in this study (see Figs D-36 - D-38). As a result it is conceivable that the original SF1A female and her second mate may have abandoned the nest cavity they had occupied over the 1992 and 1993 breeding seasons and the cavity may have been occupied in 1994 by a new pair.

Discussion

LPC analysis versus sonagraphic analysis. One of the objectives of this chapter was to evaluate techniques for identifying individuals via their vocalizations. As was found in this and a multitude of other studies involving the vocal recognition of individuals, sonographic analysis does not provide fine enough resolution of frequency-time response to allow for sufficient separation of individuals, e.g., Gilbert et al., 1994; Carlson, 1991; Eakle, 1989. In this study, information gleaned from sonographic analysis was generally limited to descriptions of calls, sex of individuals and region in which an individual had acquired its repertoire.

Having many features in common with human speech it stands to reason that parrot vocalizations may be analyzed in a similar manner to facilitate individual recognition. I found the LPC analysis previously used successfully in human speech recognition, to be the most promising in the vocal identification of individual Puerto Rican Parrots. In addition, the LPC analysis method seems to be robust with regard to recording and environmental conditions. I made no attempt to standardize recording conditions. In a wet and rugged environment such as a rainforest, equipment (tapes, tape recorders etc.) is constantly being subjected to high levels of humidity and manhandling, e.g., being dropped from great heights, being dropped into rivers etc., and I wanted to mimic field conditions as closely as possible. If this method of individual recognition is to have practical application in the field it should be able to withstand normal field conditions. I attempted to reduce call variation due to certain field conditions such as rain, or other disturbances that visually (on the sonagraph) and/or audibly distorted calls. For a few individuals I was unable to find samples of suitable calls, i.e., calls recorded relatively close to the microphone with minimal background noise. Even despite these less than ideal recording conditions the LPC analyses gave consistent results providing further support for the robustness of this technique.

LPC coefficients. In summary I found that LPC coefficients 5-14 were the most useful in separating individuals, i.e., these coefficients were similar between calls from the same individual but differed in calls from different individuals. Coefficients1-4 and 15 tended to be variable in calls from the same individual and were largely indistinguishable between individuals. Perhaps these coefficients were modeling the background noise which accompanied most calls and as a result calls recorded at different times with different noise levels would be variable, making individual recognition difficult. Coefficients 5-14 may not have been as sensitive to the background noise or other distortion and may have therefore been more representative of the unique characteristics of an individual's calls.

While the first 0.2 seconds of an individual's call may be used to distinguish it from other individual's, it appears that an even smaller segment of a call can provide sufficient information for individual recognition. In analyses using coefficients 10-12, the BIC region alone was determined to be effective in separating individuals. When combined with other analyses such as taking the first derivative of these coefficients within the BIC region and subsequently running a principle component analysis on the first derivative, the BIC region appeared to contain adequate data for individual recognition. In addition to the BIC region, it appeared that the introductory inflections may also contain individual-specific information, however, because of the location of the BIC region in HP01 calls it was less likely to be distorted by editing or the calls from a bird's mate. Many calls analyzed could only be examined using the BIC region and call body because the introductory extensions were abbreviated by recording errors or were overlapped by pair-mates.

I was unable to test this theory using known individuals. However, this hypothesis might explain why the calls of pair-mates overlap when the birds are within sight of each other but are quite separate when the birds are at a distance and presumably out of sight of one another. If the inflections and BIC regions of HP01 calls act as call signatures for individuals, pair-mates may duet with no overlap of calls at a distance to reduce the amount of information lost in the region of overlap, whereas they would have little need of this information if they were perched next to each other or were within sight of each other.

The next step. My study generated many hypotheses that remain untested, such as the one just discussed, but there is little chance that these will be tested on the Puerto Rican Parrot in the near future due to its critically endangered status. However, it is possible that these hypotheses could be tested on a closely related species such as *A. ventralis*. The next step in developing a technique to identify individuals in the wild is to simplify the process of decision-making. It took me many long hours to be able to recognize what I considered to be relevant features in the contours of LPC coefficients. As a result I believe it would be unrealistic to give a number of calls, graphed in the form of LPC coefficients, to a group of naïve observers and ask them to group the calls by individuals, a standard practice used to determine whether patterns observed by the investigator are valid and not just a result of the researcher's biases. Due to the complexity of the pattern recognition with regard to LPC coefficients, decision-making may be accomplished more easily by computers. One method that may be used involves the employment of neural networks. Using neural networks a computer can be trained to recognize an individual's calls in its many forms and distinguish this individual's calls from those of others parrots.

On a practical level, being able to identify individuals by their vocalizations can aid biologists in recognizing individuals in the wild and following their movements. This may help to eliminate the need for assumptions (most likely erroneous ones) such as those made in this study about the identity and faithfulness of pair-members and their use of cavities. From a behavioral standpoint, confirming that it is possible for biologists to recognize individuals by their vocalizations strongly suggests that it is likely the birds themselves are able to recognize each other via this method. In addition if further experimentation did support the theory that the inflection of the HP01 call contains an individual's unique 'signature' , it may be possible to determine by means of play-back experiments if other parts of the HP01 calls or other types of calls may be encoded to transmit species-specific, region-specific or dialectal, or sex-specific information.