CHAPTER THREE

VOCAL REPERTOIRE

Introduction

There were three main objectives in this chapter. First, a method for categorizing the parrots' vocal repertoire was identified. Second, graded vocalizations which make up a large percentage of the repertoire, were examined and their functions are discussed. Third, a number of hypotheses are offered as explanations for the size and complexity of the parrot's repertoire.

While there are numerous studies characterizing the vocal repertoires of a variety of passerines, relatively few have examined non-passerine vocal repertoires. In describing the repertoires of non-passerines, more specifically those in the family Psittacidae, biologists have had to contend with a number of factors overlooked in the characterization of most temperate-zone passerine repertoires. First, in many parrot species both males and females appear to have equally complex repertoires and in a number of these species the repertoires for both sexes may be quite different. In many passerine species, the male sings while the female remains largely silent. Second, in general, parrots do not communicate through the means of notes arranged in the form of songs. Instead their repertoires consist of calls and call sequences which may be likened in structure to words and sentences in human speech. Third, while passerines appear to use their vocal repertoires for gaining and maintaining territory and securing mates, parrots use their repertoires in much broader contexts many of which are associated with group and pair coordination outside of reproductive activities. These three factors complicate the descriptive process as they increase the number of factors which must be considered when grouping and analyzing calls in the vocal repertoire of parrot and other non-passerine species.

Many studies that focus on the characterization of vocal repertoires of parrots group vocalizations with respect to gross audiospectrographic features, i.e. Cameron 1968; Pidgeon 1980; Serpell 1981; Arrowood 1987; Powlesland et al. 1992. However, a few studies have categorized calls according to their function, i.e. Martella & Bucher 1990 and a number of studies have made use of both methods, i.e., Saunders 1983. Vocal repertoires of species not in the family Psittacidae have also largely been

characterized by calls or song types grouped according to audiospectrographic features, i.e. Bertram, 1970; Huxley & Wilkinson 1978; Barklow 1979; Ward 1985.

In this study classifying calls according to their function would not be feasible. Many calls in the repertoire of *A. vittata* are heard in multiple contexts and the majority of calls, if grouped by function would fall into the same category according to this method. Thus calls have been grouped according to audiospectrographic structure.

Gradations within call categories. Cataloging calls that are different in auditory and sonographic features is simply a matter of grouping calls with similar appearances and separating them from those that are dissimilar, however, where two or more calls share physical characteristics which differ only in length or frequency, the decision as to how to group the calls becomes more complicated. The classification of vocalizations for any species is a largely subjective process and can result in the creation of artificial categories. Determining whether a call is a gradation within a call category or whether it is discrete from other calls may minimize the risk of creating artificial categories. According to Miller (1978), most communication systems lie between those with discrete groupings of signals and those with continuous variation. Grading in communication systems is most likely an adaptive feature provided that the gradations of call features are correlated to changes in function, i.e. a single call through subtle changes in one or more parameters can have a large number of different meanings (Miller 1978).

Several studies have grouped calls by how they sound to the human ear, e. g. Powlesland 1992; Cameron 1968 . Although the investigators noted that there was variability in certain parameters within a particular call type, with respect to frequency, length or degree of modulation, they failed to distinguish between consistent variations of a call or standard variants and random or incidental variations.

Cameron (1968) describes 15 calls in the repertoire of the Red-backed Parrot (*Psephotus haematonotus*). Several calls within this repertoire are variable in length and frequency but it is not clear whether this variability occurred randomly or whether it may have been associated with different behavioral activities. Similarly Powlesland (1992) describes three call types used by the male Kakapo (*Strigops habroptilus*) within its lek. One of these calls he described as a “skrark”, a call varying greatly in intensity from “ a few short, soft calls, to loud, drawn-out braying.” There is no reference to possible changes in the behavioral contexts in which these extremes may have been used and it is unclear whether the gradations from ”soft” to “braying” were consistent or random.

In this study I use a hierarchical scheme based on length and frequency measurements taken from various call segments visible on sonograms to separate calls into different categories. Call keys were then used to illustrate how these characteristics were evaluated and subsequently used to separate and group calls.

METHODS

Equipment and Procedure. Tapes recorded following procedures described in chapter three were subsequently analyzed on a Kay Elemetrics sound analyzer. Data sheets were filled out detailing calls made, the time of day they were recorded, individual calling (this information came from field notebooks) if known, and context. Spectrographs were made of call categories produced by the 14 subjects recorded in this study. Call repertoires from each individual were compared from one year to the next, wherever possible, to assess the stability of each birds' repertoire. The following section describes the method used for categorizing calls within the parrots' repertoire.

Categorization of the vocal repertoire. First, spectrographs were sorted according to their general appearance. For example, those calls comprised of a harmonically structured segment joined to a raspy segment were grouped together and separated from calls lacking one or both of these components. These large general categories are referred to as call types throughout this study.

Next, within these large general groups, various characteristics that could be used to separate calls further were identified. These characteristics included among others call length and frequency measurements from relevant call segments Not all calls within different groups could be separated using the same characteristic. These smaller clusters within the call type groups are referred to in this study as call categories. If there was much variation in call parameter measurements between individuals or between calls from the same individual a range was given or an average value was obtained for that measurement. Length measurements were only intended to give a rough estimate as to whether a call was long or short relative to other calls. It was often difficult to judge exactly where a call ended due to reverberations of the harmonics. I measured from the beginning of the harmonic to a point at which the sound intensity became fuzzy or lessened, but this may not have always given a true measurement of length. Thus if measurements of length for different calls were similar I did not use length alone to categorize these calls. I avoided using parameters that had similar values for different calls unless they were used in combination with other parameters which when taken together gave a unique code for each call.

Calls were then further separated by finer details such as degree of modulation occurring in the harmonic structure or the frequency of the fundamental harmonic. Series of calls exhibiting grading in certain features such as changes in call length or changes in pitch were also evaluated at this level. Calls were considered to be graded if they resembled each other in every characteristic, except for frequency and degree of modulation of harmonics and/or call length. Keys were developed in order to facilitate the identification of calls in the future. At the end of each branch in a given key is the smallest independent unit described in the vocal repertoire, the call. Sonograms of calls are provided in Appendix A. Keys used to categorize individual calls within call types are presented in Appendix B. Call codes, e.g., HRP, HP etc., used in this and subsequent chapters are explained in Appendix A.

Categorization of graded signals. Graded signals appear to play a major role in the vocal behavior of *A. vittata*. These signals are used in almost every context ranging from pair-mate communication during food exchanges to vocal exchanges between neighboring pairs. The term graded can be used to describe a variety of differences which occur between similar calls. It is necessary to clarify how the term was used in this study and to define the different types of grading that may have occurred in the parrots' repertoire. In the following section I define the types of gradations that were examined in this study and I describe the call types that contain graded signals.

I divided graded signals into two groups, standard gradations and incidental gradations. Standard gradations of a particular call are forms of that call that could be identified consistently using a dichotomous key and that differ from other graded forms to the same degree each time they are used. For example, calls in the call category HRP20W, HRP20BW and HRP20DW, are graded forms of the same call. Graded features include the fundamental frequency of the BIC region, which in HRP20BW occurs at 2.9 kHz and in HRP20DW at 3.7 kHz and the appearance of the raspy post introduction which is compressed in HRP20BW, and stretched out in HRP20DW. These differences were consistent and the manner in which these calls were used in call sequences provides support for the hypothesis that each gradation when grouped with certain other calls may have a particular significance or function.

Within the category of standard gradations is a small sub-category, that of serial gradations. These gradations occur over a series of calls and appear to be limited to solo sequences of calls given by males. Western males commonly produced a series of HP01AMW calls. This series was most frequently given by the male to signal to the female that he had returned to the nest site from foraging. A typical series may be

composed of five to six calls. The first call in the series had the highest pitch followed by a call that dropped by 0.1-0.2 kHz, which was then followed by another of still lower pitch. By the fourth or fifth call the pitch had leveled off and was maintained at this frequency until the series ended. While there was some variation, each male tended to begin and end at roughly the same frequencies consistently and these frequencies were not the same for each individual (see chapter five). The calls at the end of the sequence had pitches similar to those used by the male in male-female HP01 duets, HP01BW. The calls in the series were similar in every way to these calls except at the BIC segment where the change in frequency was most visible. As the change in pitch tended to be more subtle between signals in serially graded call categories than in those of non-serially graded categories, each call in the series was classified in the same manner, i. e. all calls in a series were abbreviated HP01AMW. Due to their consistent appearance and use it can be assumed that this type of gradation was not incidental. Serial gradations appear to be limited to the HP01 and HRP20 call categories.

Males in the east employed a different type of serial gradation using a call from the same call category, HP01, in male solo sequences. While there was no apparent change in pitch, the between-call interval was graded, being longer at the beginning of the sequence and becoming increasingly shorter towards the end of the sequence. Males in this region also tended to have longer series with up to thirteen calls, allowing enough time for the trend to become noticeable. There was no apparent difference between calls used in duets with females and those used in male solo sequences in this region. See Table 3-1 for a description of graded parameters within each call category.

Incidental gradations were all other types of gradations that did not meet the criteria of the first type. These gradations include but are not limited to the following: 1) In many of the calls produced by females and in a lesser number produced by males , especially calls in the HB and HP categories, frequencies between the harmonics were emphasized giving the call a somewhat “nasal” quality to it. However, the addition of these elements to the calls listed above follow no regular pattern. Nasal calls were used in the same manner as those without the nasal quality. 2) In examining the sonograms of calls it was common to see variation in the modulation of harmonics of the call body or the area between the call body and introduction. However, if this variation was inconsistent from one call to the next or was seen only once, especially if this was a commonly heard call and there were many examples which did not exhibit the same variation in the calls from the same individual, this variation was noted but not taken into consideration in evaluating graded forms of a given call category. 3) The length of calls also varied greatly under different circumstances. For example, during the reproductive season of 1993 the SF2A pair were recorded during some intense periods

of interaction with Pearly-eyed Thrashers. Many calls were lengthened and the harmonics of these calls more highly modulated than usual. One call in particular, an HP01BW call produced by the female was nearly 50 % longer than average. This call was never again recorded in this form nor was it recorded in this form from any other individual. As a result it was noted but was not included in the gradations for the HP01 call category because it was subsequently replaced in the same sequence by calls of shorter lengths. It appears to have been an incidental gradation which may or may not be used in the future and which may or may not have functional significance. As there were a large number of calls and an almost infinite number of graded forms if incidental gradations are taken into consideration, this study will focus mainly on those gradations which fall under the definition of standard gradations as stated above.

In the descriptions of standard gradations, I distinguish between gradations that occur within an individual's repertoire and those that occur between the repertoires of different individuals. I further divide the latter group into interregional gradations and intraregional gradations.

RESULTS

Using the method described above 17 call types were identified. Sixteen of these call types were used by birds in both regions while the remaining call type was used solely by western birds. There were 70 call categories within these call types and 15.7 % of these categories were shared by one or both sexes in both groups. A total of 147 calls were described and of these 8.8 % were common to one or both sexes in both regions. Twenty calls (13.6%) were unique to a single individual (see chapter five for a description of calls unique to individuals).

Fifty-three percent of call categories contained a total of 111 graded calls. Twenty-nine graded calls were produced by one or both sexes in the east, 57.7 % by one or both sexes in the west and 13.5 % by one or both sexes in both regions. Western males produced the greatest number of graded calls, 29.7 % of all graded calls. Western females produced 17.1 %, eastern males produced 11.7 % and eastern females produced 7.2 % of all graded calls. Calls produced by both sexes in a region or a single sex in both regions were not included in these statistics. Appendix A gives an overview of call types and provides examples of calls found within these types. In all cases, calls within a call category (i. e., calls with the same number) represent standard gradations, whereas calls classified in different categories do not represent gradations.

Discussion

In an earlier study on the vocal behavior of the Puerto Rican Parrot, Tomosy (unpublished master's thesis 1989) relied heavily on spectographic features to group similar calls. However, in addition to relying on spectrographic features Tomosy also relied on call function. While it may be reasonable to ascertain function of a small number of calls whereby these calls are restricted to a single context such as squawks given only in flight or those immediately preceding flight, not even these calls are restricted solely to a single context. The vast majority of calls in the parrot's repertoire have multiple contexts and it is not clear how Tomosy used behavioral context to differentiate among calls.

Most of the discrepancies between the results of these two studies may be attributable to how the vocal repertoire was perceived as a whole. Tomosy (unpublished master's thesis 1989) apparently analyzed the repertoire as a group of generally unrelated signals. She describes only one call in each call category noting that there is often great variation in a single category but not describing the type or extent of the variation present. In contrast I considered the parrot's vocal repertoire to be composed of a number of graded signal systems. In these systems the call parameters of one of a number of basic call patterns are modified in a variety of ways to produce different calls that are closer in sound and appearance to each other than to calls from other groups. If indeed this study does provide a more accurate representation of the parrot's vocal repertoire and behavior than that proposed by past studies it may answer some questions regarding the function of the vocal repertoire.

Functions of the vocal repertoire. There are numerous studies describing the repertoires of passerine species. The repertoires of these species range from one to over a hundred song types and the theories used to explain the variability of repertoire size and function are as diverse as the repertoires themselves. For example, the mockingbird (*Mimus polyglottis*), a continuous singer, has a repertoire of over a hundred song types, whereas the chaffinch (*Fringilla coelebs*), a discontinuous singer, has a repertoire of one to six song types (Marler 1956; Slater 1980). It is apparent that these two species use different vocal strategies to attain different ends. The mockingbird sings continuously, not listening for possible replies to its songs, in order to reduce habituation on the part of the listener (Slater 1981). Its song bouts are elaborate displays that most likely are used for the purpose of attracting a mate and not for eliciting vocal responses or imparting information to conspecifics. The chaffinch conversely sings discontinuously, allowing for and eliciting vocal response from conspecifics. Judging from its small size, repertoire complexity is not an index of mate quality. Slater (1981) suggested that content was more important than repertoire size especially in intrasexual interactions. Specifically, Slater (1981) suggested that a young bird is more likely

to be tolerated by neighbors if it learns the repertoire of the bird that previously occupied the same territory. Other theories offered to explain repertoire size and function in other species were summarized by Slater (1981) and include, (1) females prefer mates with more varied repertoires (intersexual selection), (2) males with more elaborate repertoires are better equipped to obtain and maintain territories of high quality (intrasexual selection), (3) males with large repertoires can give the impression that there is more than one individual on their territory thereby excluding intruders (Beau Geste effect) (Krebs 1977), and 4) a large repertoire may give an indication of length of territory occupation possibly deterring intruders. In this case repertoires would tend to become more complex with age (Nottebohm and Nottebohm 1978).

None of the theories described to this point adequately explain the size, complexity or function of the Puerto Rican Parrot's repertoire. In passerines observed complexity is largely within a single call type, the song, with only one or two functions. The number of call types, in contrast, is relatively small. In the Puerto Rican Parrot's repertoire there is complexity among, as well as within, call types. *A. vittata* occupies a habitat of densely vegetated rainforest where the use of visual cues is often not possible. As a result auditory signals may be needed to replace signals that in more open environments would ordinarily be communicated through the use of visual displays. The Indian Hill Mynah (*Gracula religiosa*) inhabits regions of forest, mainly evergreen and semi-evergreen and sometimes wet deciduous forests, in various locations throughout India. It appears to have a complex vocal repertoire with most calls in its repertoire associated with flock cohesion and pair-bond maintenance. This species is most commonly found in small flocks, except during the breeding season when mated pairs (this species is monogamous and individuals form prolonged pair-bonds) split off from the flock to defend their breeding cavity (Bertram 1970). In addition to occupying forested habitats, *A. vittata* and *G. religiosa* are both cavity nesters. One member of a mated pair is in the nest cavity at any one time awaiting the return of its mate who will either take its place in the cavity (*G. religiosa* only) or will deliver food or both. The individual occupying the nest cavity is dependent on vocal cues from its mate to know when to leave the cavity as its mate will generally not enter the cavity before the other bird has left it.

Both of these examples fit Pidgeon's model which assumes species in arid-zones where visibility is not limited will have a more limited repertoire than those in semi-arid environments in which visibility may be somewhat limited (Pidgeon 1980). It is possible that a decrease in visibility from semi-arid conditions to a tropical rainforest may increase the need for a more extensive vocabulary such as the one documented for *A. vittata*. Most calls used by *A. vittata*, and *G. religiosa* appear to be associated with location, cohesion and intraspecific agonistic behavior . Thus it is possible that size and complexity of a vocal repertoire is directly

associated with the social structure of a species, regardless of the taxonomic group to which it belongs (Martella & Bucher 1990).

The complexity of the Puerto Rican Parrot's repertoire surpasses that of most parrot species studied to date, being rivaled by only one other species, the African Grey Parrot (*Psittacus erithacus*) for which a 4 minute recording of a pair from Botsima, Zaire contained 203 motifs of 88 different types (Cruickshank et al. 1993). Cruickshank et al. (1993) suggest that a large repertoire may be sexually selected in the African Grey Parrot, and as a consequence this species incorporates into its repertoire numerous mimicries copied from an array of sympatric species. However, they did not clarify whether the elaboration of the vocal repertoire was in this species intrasexual and/or intersexual selection.

There are at least three possible functions that a vocal repertoire may serve in Puerto Rican Parrots. One function involves mate selection. Neither intersexual nor intrasexual selection through the possession of elaborate repertoire seems to occur in Puerto Rican Parrots. When mates were lost on occasion over the course of this study they were immediately replaced by a new mate and with seemingly little effort the newly formed pairs performed the same duets as had been performed by the old pair with few if any noticeable differences in the vocal repertoire of either sex. It may be that upon losing a mate, females chose a mate with a repertoire comparable to that of the previous mate rather than one that may possess a larger or more complex repertoire. In other words a male that knows the correct response to the female's calls in a duet is more likely to replace her lost mate. Thus a sufficiently sized repertoire is preferred over a depauperate one, but in the case of the Puerto Rican Parrot's repertoire it appears that content, not size is the deciding factor in mate selection.

In addition to mate selection the parrots' repertoire also appears to function in neighboring-pair communication. Lemon (1968) suggested that song matching of neighbors to maintain 'territorial homeostasis' may be the function of repertoires in some species and having a large repertoire would increase the chances that a neighbor's song would be included in that song repertoire and therefore could easily be matched. While Puerto Rican Parrots don't actually maintain territories, neighboring pairs appeared to maintain a distance between each other's nest areas. Judging from the recordings I obtained of vocal interactions between neighboring pairs (the sound intensity was usually too low for the vocalizations to be analyzed although I was still able to identify the calls), they did not come within less than 100-200 m of each other's nest cavities. Generally during pair interactions, the resident pair would be closer to the blind in which I was recording, and the other would be a little further away. Frequently after about ten

minutes of interactions close to one nest area the two pairs would fly towards the other nest area and continue vocalizing. Often one pair would give a sequence of duets and even before this pair had finished the sequence, the other pair would match this sequence. I only observed interactions such as these between close neighbors in one area in the western region (SF2A and SF2B pairs) because all other pairs separated by greater distances.

The third purpose for possessing such a complex vocal repertoire is that different calls may serve different functions. Having a repertoire as large as the parrots' would allow for much variety in call sequence combinations. While not all calls in the parrot's repertoire are context specific the solo and/or duet call sequences in which they occur may show some context specificity. This system of communication may be similar to that of the Mexican Chickadee which uses a combination of notes to produce more than 60 calls. In the parrot's vocal behavior the calls may be analogous to the notes of the chickadee and the call sequence analogous to the chickadees calls (Hailman 1993).

A limitation to this study was that for the most part it was not possible to ascertain the individual identity of conspecifics calling. Only during interactions between the SF2A and SF2B pair was it safe to assume which pairs were involved, and this was sometimes verifiable if observers were in both blinds and indicated the beginning and end of vocal bouts on the data sheets. However, generally pairs or small flocks interacting vocally with a particular resident pair may have included males, females, neighbors, juveniles, related and/or unrelated to the resident pair, and strangers. It would be expected that the resident pair would treat each case differently depending on the identity of the intruders and the threat they may pose to the resident pair if any. Thus it is possible that call sequences may have been more context specific than was shown by this study. Despite these shortcomings, there are a number of calls in the parrot's repertoire that by themselves appear to be used only under certain conditions and this supports the theory that parrots vocalizations may indeed prove to be context-specific. Examples of context-specific calls include single-call alarm calls that are common to all parrots in this study such as **HRP0, KWP0A**, and **GR0** calls, and flight calls, such as **KNP0** calls or take-off squawks, and **BH0** calls or bugles.

Uses of Graded Signals. Many studies on graded vocal systems have focused mainly on graded anti-predator calls and how the animal in question makes use of them, i.e. lapwings (Charadiidae: *Vanellus* spp.), (Walters 1990); Common Loon (*Gavia immer*), (Barklow 1979); domestic chicken (*Gallus domesticus*), (Gyger et al. 1987). These signals are chosen because the predator is usually visible at the time of the recording and the context in which the call is used is easily inferred (Slobodchikoff et al. 1990). The

Common Loon makes use of a graded signal, the tremolo, (an alarm call generally associated with the tendency to flee when threatened). The tremolo has three distinct structural variations formed by the addition of progressively higher, harmonically unrelated frequency components. The pitch frequency of each type varies depending on its duration and the amplitude and interval between calls are correlated with the type given. The three variations appear to be correlated with changes in stimulus intensity (Barklow 1979). Lapwings provide another example of a family that may use graded signals to communicate degree of threat posed by potential predators. Lapwings appear to classify potential predators according to the threat they pose. Variations in the parameters of alarm calls, such as pitch or frequency modulations, indicate a change in call function and may consequently alter the recipient's response (Walters 1990).

Graded alarm call systems have also been well studied in small mammals such as ground squirrels, prairie dogs and monkeys, i.e. California ground squirrels (*Spermophilus beecheyi*) (Leger et al. 1980; Owings and Leger 1980); Gunnison's prairie dogs (*Cynomys gunnisoni*) (Slobodchikoff et al. 1990); vervet monkeys (Seyfarth et al. 1980). Some investigators have studied what types of additional information may be encoded in a graded signal. Marler et al. (1986) found that domestic chickens could communicate information about the quality of food they were given. In a study using Gunnison's prairie dogs as subjects, Slobodchikoff et al. (1990) found that not only could the prairie dogs indicate in their alarm calls that the potential predators were human, but they could also encode their calls to include information about characteristic features of an individual from the group of potential predators.

In the parrot's repertoire gradations occurred in many all-context calls and were not limited to alarm calls. Some calls such as those in the **HRP** call type category occur between regions and sexes and serve to indicate the location of an individual's natal area and the sex of the individual calling (See Chapter 4 and Appendix D). In these calls it is generally the frequency and time components of particular call segments that exhibit grading. Still other types of graded signals within an individual's repertoire such as those used by the male to call the female from the nest cavity when he has returned to the nest site for a food exchange may serve to indicate an individual's motivational state. Graded **HP01AW** calls may be used by the male to indicate his distance from the nest tree which would allow the female to make a decision as to when the male was close enough for her to leave the nest cavity. Females tend to wait until the male is within a few meters of the nest tree before leaving the cavity. The Carolina Wren (*Thryothorus ludovicianus*) learns to sing its neighbors songs and is therefore able to determine more accurately his distance from the singer and to challenge the singer if it is close or ignore it if it is at a distance (Morton 1982). By grading the frequency of calls within certain call categories, the male Puerto Rican Parrot may be increasing the information

available to the female regarding his distance from the nest tree. Different frequencies degrade at variable rates under differing environmental conditions, therefore the greater the number of frequencies included in a call sequence the greater the informational content available in that particular sequence (Morton 1982).

Over half the vocalizations recorded in this study were elicited through interactions with conspecifics. As in the case of the parrot's repertoire it is difficult to ascertain functions of specific graded calls without having more information about the identity and intention of conspecifics. If it were permissible play-back experiments involving the playing of recordings taken from neighboring pairs and non-adjacent pairs may reveal which calls or graded signals are more likely to be used under different social conditions.