# A Structural Description and Reclassification of the Wolf, Canis lupus,

**Chorus Howl** 

by

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#### ABSTRACT

The wolf (Canis lupus) group vocalization referred to as the chorus howl has historically been described as a form of howl, whereby two or more pack members vocalize together. A playback experiment, using artificially created human howl imitations, elicited vocal responses from three captive packs and provided evidence that choruses include not only howls but also squeaks, barks, bark-howls and growls. In 17 choruses recorded in this study, howls were the dominant vocal type in terms of overall number of vocalizations in the choruses (mean= 56 ± 14%, n= 1702), followed by squeaks (mean=  $36 \pm 11\%$ , n= 1202), barks (mean=  $7 \pm$ 8%, n= 284), growls (mean=  $0.6 \pm 1.2\%$ , n =11) and bark-howls (n= 2). The duration (s) and frequencies (Hz) of the vocal types contained within the choruses corresponded to previously reported values. This would indicate that the information contained within the chorus may be a function of the vocal composition. The data were also mildly suggestive of vocal mimicking in wolves along a graded continuum of duration and frequency modulation. From the observations made in this study it is recommended that the vocalization know as the chorus howl be reclassified as the "chorus" and given its own category rather than being included in the howl vocal type.

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#### INTRODUCTION

#### The Classification of Animal Vocalizations

The classification of vocalizations has been the undertaking of many researchers who study animal communication and behavior. The acoustic parameters of animal vocalizations are measured in terms of temporal duration, and frequency (Hz) and amplitude modulation. Vocalizations that have similar structural characteristics are then grouped together and referred to as a vocal type. In theory, vocalizations that exhibit less within variability than between variability when compared to other vocalizations make up these vocal types. The vocal type names are often based on the sound itself and what it sounds like to the person doing the classification. For example, wolves (Canis lupus) exhibit a vocal type referred to as the squeak (Crisler, 1958). This high frequency, short duration vocal type sounds like the high pitched whine of a dog, yet, it was called the squeak. Some authors however call this vocal type the whine (Schassburger, 1987). This has caused some confusion. It is of vital importance that authors use the same terminology to describe the same vocal types for a particular species. The use of similar or the same words to describe the vocal types of different species also occurs. For example, red howler monkeys, Alouatta seniculus, (Sekulic, 1982) and lions, Panthera leo (McComb et. al., 1994) both roar to advertise territory ownership. Classification generally follows structural, contextual and functional descriptions. To effectively classify animal sounds these sounds

must first be organized according to acoustic (structural) properties, then they must be linked to associated behaviors to give a comprehensive description of the animal's vocal repertoire.

The more we know about the type of vocalizations a certain organism uses and the behavioral contexts under which each vocal type is observed, the more we'll understand the types of information (something an animal receives that affects the internal motivation of the animal and its subsequent behaviors) conveyed by the communication system. In this study, the vocal repertoire of the wolf is under investigation. The main focus is on the chorus howl, a group vocalization that has been historically classified as a type of howl, but which may indeed contain far more vocal types than simply howling. To proceed, the ecology, behavior and described vocal types of the wolf must first be understood.

#### Wolf Social Organization and Behavior

The wolf, the largest of the non-domestic canids, is a highly social carnivore for which acoustic communication plays an important role. Wolves usually live in family units called packs, which typically include one mated pair and offspring from several years' litters. Wolf packs vary in size, usually ranging in size from 2 to 10 individuals, although packs as large as 36 individuals have been reported (Rausch, 1967, cited in Mech, 1974). A social hierarchy exists within the pack with the dominant male and female, or alpha pair, at the apex.

In forested areas, and elsewhere where wolves are non-migratory, wolves are territorial; each pack defends an exclusive home range, or territory. On the tundra, wolves are migratory by necessity because their main prey, caribou (Rangifer tarandus granti), are also migratory. In forested areas, territories are variable in size, typically ranging from 125 to 240 Km<sup>2</sup> with some as large as 555 Km<sup>2</sup> in northern Minnesota (Mech, 1977a). The actual size of a territory is reportedly governed mainly by pack size and prey abundance (Messier, 1985). Individual ranges are relatively stable in terms of both size and location over time (Mech, 1977a; Harrington & Mech, 1979) and are actively defended from conspecifics (Mech, 1977a; Fritts & Mech, 1981). There is evidence that there exists an area of overlap between the territories of neighboring wolf packs and that this area, called a buffer zone, is contested (Hoskinson & Mech, 1976; Mech, 1977b; Peters & Mech, 1975). Wolves spend less time at the periphery of their territories than further within the defended range to avoid potential encounters with neighboring packs. The buffer zone is the site of most interpack strife (Mech, 1994). Research has shown (Hoskinson & Mech, 1976; Fuller & Keith, 1981) that these buffer zones are selectively utilized by lone, dispersing wolves, sympatric species such as coyotes (Canis latrans) and prey species (example, white-tailed deer, Odocoileus virginianus). The buffer zone provides a corridor for prey since they are less likely to encounter resident wolves in this area. The maintenance and advertisement of these territories is accomplished through scent marking, primarily urination (Peters & Mech, 1975) and vocal

communication, primarily howling (Joslin, 1967; Theberge & Falls, 1967; Harrington & Mech, 1978a, 1978b, 1979, 1983). Social interactions within the pack and agonistic interactions between packs make it important for the wolf to have a sophisticated vocal repertoire, which includes both long-distance and short-range vocal types.

#### Wolf Vocalizations

Vocalizations play a large role in the social interactions amongst wolves and, consequently, they possess a varied vocal repertoire. Wolf vocalizations have been classified into four basic types: barks, growls, squeaks (also called whines/ whimpers) and howls (Fentress, 1967; Theberge & Falls, 1967; Field, 1978; Klinghammer & Laidlaw, 1979; Harrington & Mech, 1978a), with subdivision into as many as 11 different types (Schassburger, 1987, 1993). The following descriptions form the bulk of information available on wolf vocalization types to date. While there have been several studies that described the acoustic parameters of wolf vocalizations, these have primarily focused on two of the four basic vocal types, the howl (Joslin, 1967; Mech, 1970) and the squeak (Coscia et. al., 1991; Goldman, 1993; Holt & Harrington, unpubl. data).

#### (a) Bark

The bark has been described as a short, noisy, explosive sound (Harrington & Mech, 1978a; Schassburger, 1993), typically less than 1s

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(Tembrock, 1963; Schassburger, 1993). It is a vocalization with a low frequency, between 320 to 904 Hz (Tembrock, 1963) with emphasis near 500 Hz (Harrington & Mech, 1978a). The bark is uttered singly or in sequences. Behaviorally, the bark is generally considered an agonistic, alerting vocal type that may serve to attract attention toward the vocalizing animal (Bekoff, 1974). It has been noted that barking wolves are almost always visually conspicuous (Harrington & Mech, 1978a). Researchers have noticed that when they approached dens (Murie, 1944) or home-sites (Joslin, 1967) when pups were present, or when they approached kill-sites, wolves barked (Mech, 1966). These and other similar observations suggests that the bark may serve as a defense, threat, warning and/or alarm call. The bark is also observed in conjunction with howling. When these two vocalizations are uttered together, with no temporal separation, the resulting vocalization is called the bark-howl.

The bark-howl is composed of 1 or a series of barks that become incorporated into a long, steady howl with slow frequency modulation. Structurally, the bark-howl is a variable, long duration (2.5 to 4.5 s), low frequency (210 to 400 Hz), composite vocalization made up of between 1 and 6 barks, in series, followed by one howl (Holt & Watson, unpublished data). Bark-howls are sometimes uttered in sequences. The bark component is a short (0.02 to 0.05 s), low frequency ( $f_0 = 280$  Hz) vocalization with a narrow frequency range (250 to 293 Hz). From the spectrograph, the frequency rises sharply at onset and either curves downward or levels out at the end (Holt &

Watson, unpubl. data). The howl component is harmonically structured (1 to 3 harmonics), of long duration (2 to 4 s), and low frequency ( $f_0$  306 Hz, range 195-460 Hz) (Holt & Watson, unpubl. data).

The bark-howl has been observed from both wild and captive animals. Murie (1944) and Mech (1966) observed bark-howling when they closely approached wolves. Harrington and Mech (1978b) made similar observations when they closely approached (within 50 m) a pack of wolves with pups. In captivity, when wolves are approached by unfamiliar persons (Field, 1978), and when persons approach the den when pups are present (Holt & Watson, unpubl. data), one or several wolves bark-howl. In the study by Holt & Watson, it was also observed that in 27 of 44 occurrences of bark-howling, the animal vocalizing was the alpha male who positioned himself in a visually conspicuous position (the remaining cases were either started by a subdominant male, n=5 or an unidentified animal, n=8). Also, there was a trend toward a decrease in the number of cases of bark-howling as the pups got older and spent less time inside the den. These observations would suggest that the bark-howl is some form of alarm, or threat call, perhaps to draw attention away from the den and vulnerable pups.

#### (b) Growl

The growl has been described as a deep, course sound (Harrington & Mech, 1978a). Structurally, the growl has a reported frequency range

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between 250 and 1500 Hz, with the fundamental around 800 Hz (Tembrock, 1963). Schassburger (1993) characterized the growl as having a fundamental frequency in the range of 70 to 2175 Hz. Loudness and spectral form affect the range of the growl; Joslin (1967) suggested that the growl is audible at less than 200 m. The growl is also described as a long duration, continuous vocalization lasting from <1 to several seconds (Field, 1978; Schassburger, 1993). It is thought that the primary contexts in which growling occurs are warning, defense, threat, attack and dominance (Fentress, 1967; Fox, 1971; Field, 1978; Harrington & Mech, 1978a; Schassburger, 1993). It has been noted that assertions of dominance, defense of food, and other agonistic behaviors are often accompanied by growling (Harrington & Mech, 1978a). A growl from the mother wolf can send pups to the den in times of danger. Field (1978) observed that there was a peak in the number of growls during the fall and during the month of February, while growls were also more numerous during the late afternoon and early evening when feeding behavior was more evident. Also in the study, males growled more often than females. In general, not much attention has been directed toward research into the growl.

#### (c) Squeaks

Squeaks, also referred to as whines and whimpers, are short, high frequency vocalizations which play a role in close social interactions within the pack. Structurally, the squeak is harmonic, of short duration (0.1 to 0.5 s)

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and high frequency (2500 to 5500 Hz), and is often produced in sequences of varying length (Fentress, 1978; Fentress, Field & Parr, 1978; Field, 1978; Goldman, 1993; Holt & Harrington, unpubl. data). Squeaks have been shown to be individually distinct vocalizations for adult wolves, with the fundamental frequencies being significantly different between individual wolves (Goldman, 1993; Holt & Harrington, unpubl. data). Behaviorally, the squeak has been described in several contexts, between pups and adults and between adults. Pups respond differentially to the squeaks of the mother and to the squeaks of other adult female care-givers, with the mother's squeaks being able to draw the pups out of the den (Fox, 1971; Goldman, 1993). Wolves exhibit cooperative pup rearing and it is significant that they recognize the voice of the mother and other familiar adults. Also, pups can elicit a response from adults with their squeaks. Fox (1971) noted that when pups are cold, hungry, or in pain, they squeak to solicit care from the adults. Coscia (1995), however observed that pups elicit more parental care with screams than squeaks from birth to 21 days of age, when squeaks first begin to appear in the vocal repertoire. Pups have also been observed squeaking when the adults return to the home-site, perhaps as a greeting (Peterson, 1974; Voight, 1973). Between adults, the squeak has been observed in close contact interactions. such as greetings, submissive behavior by subordinate animals, and during courtship (Harrington & Mech, 1978a). Following Morton's (1977) motivational-structural rules, the squeak is considered a 'friendly', nonaggressive vocalization that is used for short distance communication within the pack.

#### (d) Howls

Howls, the most conspicuous of the wolf's vocalizations, have been the most extensively studied of all the wolf vocal types. The wolf how has been described as a highly variable, long-distance vocalization. Howls may carry over distances up to 10 Km (Joslin, 1967; Harrington & Mech, 1978a). Structurally the howl is classified as a continuous, harmonic vocalization with a frequency range between 150 and 780 Hz (Theberge & Falls, 1967; Harrington & Mech, 1978a; Schassburger, 1987, 1993) and up to 12 harmonic overtones (Theberge & Falls, 1967). In a study by Theberge and Falls (1967), some 700 howls were recorded from three wolves and it was found that the duration of the howls ranged from 0.5 to 11 s, indicating that the duration is quite variable. However, howls are generally considered to be vocalizations of long duration, with 93% of adult howls lasting at least 3 s, and the majority of those being between 4 and 6 s in duration (Theberge & Falls, 1967; Harrington & Mech, 1978b). Howls are often uttered in sequence, termed a bout. Joslin (1967) found that for a wild wolf replying to his howl imitation, the bout lasted 35 s, with the wolf uttering several howls. Harrington and Mech (1978b) found similar results in Minnesota where individual reply bouts lasted approximately 10 s, with one wolf uttering 35 individual howls over a span of 3.5 minutes (this howl bout was not elicited by the authors).

Research has also shown that the amount of howling follows daily and seasonal patterns. In terms of daily patterns, Harrington and Mech (1978b) found that for two packs in Minnesota (Harris Lake and Jackpine packs) the majority of howling occurred between the hours of 20:00 and 11:00, indicating that wolves howl predominantly more at night and early morning. Other authors have found similar trends for captive (Zimen, 1971) and wild wolves (Rutter & Pimlott, 1968). Seasonally, howling increases from the fall into winter (October to February), and peaks around the breeding season, in January/ February (Harrington & Mech, 1978a,b). Similar results were observed with captive wolves. Klinghammer and Laidlaw (1979) observed that unaccompanied howls increased (from <5 to between 30 and 40 per week) during the breeding season.

Howls have been ascribed several functions. It's been argued that howls function primarily in the advertisement and maintenance of territories, as well as in pack cohesion (Joslin, 1967; Theberge & Falls, 1967; Harrington & Mech, 1978a,b, 1982; Harrington, 1989). Howls serve to both increase and decrease the distance between animals and appear to function both within and between packs. It is thought that howls carry information such as individual identity (Joslin, 1967; Theberge & Falls, 1967; Rutter & Pimlott, 1968; Voight, 1973; Tooze et. al., 1990), location and the motivational state of the animal (Harrington, 1987).

Wolves howl alone (solo howling) and as part of a group (chorus howling). Solo howls are thought to serve several functions. One such

function would be that of pack assembly. It was observed that when captive (Young, 1944) and wild (Murie, 1944; Mech, 1966) wolves were separated from their pack mates, they howl. Murie (1944) described 5 separate occasions when an individual wolf howled after having been separated from its pack mates and was later reunited with the pack as a result. In a similar fashion, howls may play a role in the formation of new packs (Zimen, 1971). Two basic classes of solo howls have been described, flat howls and breaking howls. Flat howls have a relatively unmodulated frequency, whereas breaking howls are more modulated (Harrington & Mech, 1978a). Flat howls were found to have a lower mean fundamental frequency and occur when a wolf closely approaches an intruder, possibly indicating a context of high aggression. Breaking howls tend to be higher in frequency (Harrington & Mech, 1978a). Morton (1977), theorized that animal vocalizations follow motivational-structural rules and that lower frequency vocalizations indicate a more aggressive context. Tooze (1987) described a third type of solo howl, called the 'woa-woa' howl, which was characterized by one short howl followed by between 5 and 13 aborted howls. These were considered rare, being more frequently heard from single wolves isolated from their pack mates.

When two or more wolves in a pack howl together, the resulting vocalization occurs as a chorus. The chorus howl has been described as a vocalization in which one wolf begins howling, with other pack members joining in, until several, or all the members of a pack are howling together

(Joslin, 1967). It has been described further as a highly contagious event within the pack (Crisler, 1958), accompanied by tail wagging and face nuzzling (Harrington & Mech, 1978a). Chorus howls are proposed to play a significant role in interpack communication, primarily functioning in territory defense (Joslin, 1967; Theberge & Falls, 1967; Harrington & Mech, 1978a). Structurally, chorus howls are highly variable in terms of frequency modulation, duration of response, number of individuals in the pack that participate and the manner in which the animals enter into the chorus (Theberge & Falls, 1967; Harrington, 1975; Harrington & Mech, 1982, Harrington, 1989). Howls that begin the chorus tend to be lower frequency, longer and less modulated than subsequent howls, which tend to be shorter duration and more modulated than solo howls (Joslin, 1967; Harrington & Mech. 1978: Tooze, 1987). The chorus, while variable in duration, averages between 60 s (Minnesota: Harrington & Mech, 1978a) and 85 s (Ontario: Joslin, 1967). The chorus may provide information on pack identity, location, motivation and potentially pack size (Mech, 1970), although the latter has been questioned (Harrington, 1989). Two forms of the chorus howl have also been proposed: harmonious and discordant (Schassburger, 1993). It has been suggested that elicited choruses are more discordant than spontaneous ones (no apparent stimulus) (Schassburger, 1993; for red wolves (Canis rufus), McCarley, 1975).

#### Rational of Present Study

The chorus howl has historically been treated as one form of howl vocalization (Murie, 1944; Joslin, 1966; Theberge & Falls, 1967; Harrington & Mech, 1978a, b; Schassburger, 1987, 1993; Tooze, 1987). While much is known about the wolf howl structurally and of the behaviors associated with it, the chorus howl has not been deconstructed to observe the extent to which the chorus incorporates the various vocal types described for the wolf. Reference has been made to vocal types other than the howl being heard during the chorus. Tooze (1987) observed that wolves bark frequently during choruses and that these barks, while isolated from the howls, are often interspersed with squeaks. Joslin (1967) observed that in some instances, barks terminate howling sessions and bark-howling can be heard interspersed with howls when humans approach closely (Mech. 1966; Murie, 1944; Joslin, 1967; Harrington & Mech, 1978b). Reference has also been made to squeaks occurring during chorus howls. Harrington and Mech (1978a) observed that young and subordinate animals squeak while attempting to lick the face of other wolves during a chorus howl. Perhaps one of the reasons why the chorus howl has been described as a form of howl is because of the distances from which choruses are generally heard and recorded. At distances > 1 Km the predominant vocalization heard and recorded is the howl. Vocalizations like squeaks and growls would not be heard at these distances and it is only when choruses are observed and recorded at close range (within <1 Km) that these associated vocal types can

be more closely analyzed. The purpose of this study then, was to perform a structural analysis of the chorus howl to identify the component vocal types associated with the group vocalization.

#### **METHODS**

#### **General Description**

This study employed playback to elicit chorus howl responses from captive wolf packs. The elicited responses were then recorded on both video and audio cassette tapes. The video taping was conducted within 5 to 10 m of the wolves, while they were vocalizing, giving good recording quality and ensuring that any vocal types considered short range calls would be recorded with the definition required for spectrographic analysis. During spectrographic analysis, the elicited chorus howl responses were deconstructed to determine the nature of the variability of vocal types contained within the chorus. General behaviors associated with these responses were also recorded and described.

### Study Sites/ Subjects

The study included data from three captive packs of wolves, housed at three different facilities across the United States. These were 1) Wolf Park, Indiana, 2) the International Wolf Center, Minnesota, and 3) the Wolf Education and Research Center, Idaho. The study sites were chosen primarily on the basis of the facility layout. Each of the three facilities housed either a single wolf pack, or the wolves were housed such that it was certain which animals were responding to the stimuli. All facilities provided information about pack structure, feeding schedules and routine handling procedures. The playback experiments were conducted between August and December 1995.

During the course of this study, several other facilities were considered, all of which were rejected upon visitation because of their layout. These included the Wild Canid Survival and Research Center (Missouri), Carlos Avery Game Farm (Minnesota), Bear Country U.S.A (South Dakota) and the Metro Toronto Zoo (Ontario). The playback experiment was also attempted with wild radio-collared wolves in Superior National Forest, Minnesota (U. S. Geological Survey, Biological Resources Division project) where problems with budget constraints and adverse weather conditions prevented the collection of useful data.

#### (a) Wolf Park

Wolf Park, located near the town of Battle Ground, Indiana, is a privately owned, publicly funded facility. Wolf Park is open to the public for wolf education and provides students with the opportunity to complete internships and practicums in the areas of ethology and animal handling. At the time of the study, the facility maintained a pack of 8 related (alpha pair and sibling, as well as several generations of offspring) socialized wolves as well as several other wolves housed singly or in pairs some distance from the

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large pack. Also housed at Wolf Park were 2 coyotes (*Canis latrans*), 1 Red fox (*Vulpes vulpes*) and a herd of 22 North American bison (*Bison bison*).

The 8 wolves in the main pack (Table 1) were the study animals. Preliminary observation showed that the presence of the singly housed and paired wolves did not interfere with the study pack's responses to stimuli, or with subsequent recording. The pack was maintained in a semi-natural, sparsely treed (mostly deciduous), 2.6 ha enclosure which encompassed a small lake to which the wolves had access. There were several wooden den boxes in the enclosure. The wolves were fed once weekly a diet of road-killed deer (*Odocoileus virginianus*) and the carcasses of domestic livestock donated from farms in the vicinity. The wolves were socialized to humans and received close physical contact with several people on a weekly basis. The playback experiment was conducted between August 4 and August 25, 1995.

#### (b) International Wolf Center

The International Wolf Center, located in the town of Ely, Minnesota, is a not-for-profit organization. The center is open to the public as an information/ learning facility, and to students for internships. At the time of the study the IWC maintained a pack of 4 related (siblings), socialized wolves (Table 2) housed in a forested, semi-natural 0.5 ha enclosure, which included automatic water dispensers and a den box. Twice weekly, the animals were fed a diet of road-killed deer, prepared high protein dog kibble, and various assorted fresh meats. The wolves were socialized to humans and received close physical contact with several people on a daily basis. The playback experiment was conducted between September 15 and October 31, 1995.

(c) Wolf Education and Research Center

The Wolf Education and Research Center is located at the base of the Sawtooth Mountains, in Stanley, Idaho. The center was open primarily to students and volunteers at the time of the study. A pack of 6 (related siblings and non related individuals) socialized wolves (Table 3) was maintained in a heavily forested, semi-natural 6.9 ha enclosure which contained several den boxes, and water dispensers. The animals were fed a weekly diet of roadkilled deer and other assorted meats, as well as prepared dog kibble. The wolves were socialized to people however, they received minimal close physical contact. The playback experiment was conducted between November 18 and December 1, 1995. Table 1. The structure of the study pack at Wolf Park, August 1995.

SEX	AGE (YEARS)	SOCIAL STATUS
MALE	7	ALPHA
FEMALE	7	ALPHA
MALE	2	SUBDOMINANT
MALE	2	SUBDOMINANT
MALE	1	SUBDOMINANT
MALE	1	SUBDOMINANT
FEMALE	1	SUBDOMINANT
FEMALE	7	OMEGA

<u>Table 2</u>. The structure of the study pack at the International Wolf Center, October 1995.

SEX	AGE (YEARS)	SOCIAL STATUS
MALE	2	ALPHA
FEMALE	2	ALPHA
FEMALE	2	SUBDOMINANT
FEMALE	2	OMEGA

<u>Table 3</u>. The structure of the study pack at the Wolf Education and Research Center, December 1995.

SEX	AGE (YEARS)	SOCIAL STATUS
MALE	4	ALPHA
FEMALE	3	ALPHA
MALE	4	SUBDOMINANT
MALE	3	SUBDOMINANT
MALE	3	SUBDOMINANT
MALE	3	SUBDOMINANT

#### Stimulus Creation

The stimuli for the playback experiment were created primarily to elicit chorus howl responses from the captive packs involved in this study. They were also created to determine whether the number of wolves howling, the fundamental frequency and the coefficient of frequency modulation of the stimulus influenced the structure of the responses, in particular, whether wolves in any way mimicked the parameters of the stimulus. For example, do wolves modulate their choruses more in response to more modulated stimuli? Many animals mimic the vocalizations of conspecifics, other species and even background noises (Zahavi & Zahavi, 1997).

The stimuli for the playback experiment were artificially created from recorded human imitations of wolf howls. Artificially created stimuli are now recognized as having many advantages over natural signals for playback experiments, particularly because they avoid a number of design problems arising from the multidimensional nature of natural signals (Gerhardt, 1992). Advantages include: 1) the quality of the stimuli can be kept constant, 2) the total duration of the stimuli can be set to ensure a level of sensory input appropriate for the study species (Pepperberg, 1992), and 3) the identities of participants in creating the stimuli can be tailored for the particular experiment (McComb, 1992).

Human howl imitations were chosen because they can be produced with relative ease, and can be manipulated to great extent. Human howls are also effective at eliciting responses from wolves (Pimlott, 1960). Such howls have been used as stimuli to study many aspects of wolf vocal behavior: general characteristics of the howl (Joslin, 1967; Theberge & Falls, 1967; Harrington, 1975), aggression (Harrington, 1987), the effects of howling on territory maintenance (Harrington & Mech, 1979, 1983), estimation of pack size (Theberge & Strickland, 1978) and to census wolf packs (Harrington & Mech, 1982; Fuller & Sampson, 1988).

The human howl imitations were recorded at Wolf Park with the cooperation of the facility director and four employees/ volunteers. All stimuli participants had previously demonstrated skill at eliciting responses from wolves with their howl imitations. The human howls were recorded on two separate days (one day recordings would have been preferred however the human howlers had conflicting schedules making this unfeasible), and factors such as environmental conditions (wind velocity and temperature), distance (10m) and recording volume were kept constant to ensure consistent recording quality. The stimulus howls were recorded on Sony UCX-S90 audio cassette tapes, using a Sony Professional Walkman (WM-D6) and a tripod mounted Sennheiser Super Cardioid shotgun microphone fitted with a Sennheiser MZW 415 windscreen. The voltage required to power the set-up was obtained by attaching both the Walkman and the microphone to a Nagra/Kudelski amplifier/monitor which was, in turn, attached to a 12 Volt vehicle battery.

One male individual produced two howls, one (Howl 1) was unmodulated (CoFM=1.2%) and was labeled as Stimulus 1, and the other

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howl (Howl 2) had a higher level of modulation (CoFM=2.6%) and became Stimulus 2. Four individual howls (CoFM<6%) were recorded, one from each of the four remaining participants. These howls (Howls 3-6) were used to produce Stimulus 3 and Stimulus 5. Stimulus 4 (2 wolves) and Stimulus 6 (5 wolves) were recorded as ' natural ' choruses. In both cases the individual that produced Howl 1 and Howl 2 began the chorus. A second individual (producer of Howl 3) joined in the chorus to produce Stimulus 4, whereas for Stimulus 6, four individuals (producers of Howls 3-6) joined the chorus in succession, varying their howls over the course of the chorus.

The finalized stimuli were produced using the Sound Forge<sup>TM</sup> 2.0 (Sonic Foundry, 1994) computer software package. Stimulus 1 and Stimulus 2, representing one wolf howling, were synthesized as follows: previously recorded Howl 1 and Howl 2 were saved individually as 16 bit wave form files. Each howl was copied 5 times and a sequence of 6 identical howls, separated by 1s intervals, was synthesized for each howl. The sequence synthesized from Howl 1 became Stimulus 1, with a total duration of 36 s and the sequence synthesized from Howl 2 became stimulus 2, with a total duration of 41 s. Stimulus 3, representing 2 wolves howling, was synthesized by taking the howl sequence recorded from Howl 1 and overlapping it with a sequence synthesized in the same way, using Howl 3. The overlap was offset so that the Howl 3 sequence started 3 s after the onset of Howl 1 sequence. The total duration of Stimulus 3 was 42 s. Stimulus 5, representing 5 wolves howling, was synthesized using the same procedure as that for Stimulus 3.

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Howl 1 sequence, Howl 3 sequence, and three additional howl sequences from three different individuals were overlapped in a staggered manner to give a final chorus (Stimulus 5) with a duration of 51 s. Stimulus 4 (2 wolves) and Stimulus 6 (5 wolves) were recorded as ' natural ' choruses. Neither was modified. Stimulus 4 had an overall duration of 45 s and Stimulus 6 had duration of 46 s. The six resulting stimuli (Table 4) were recorded from Sound Forge<sup>™</sup>, through a Sound Blaster<sup>™</sup> card onto Sony UCX-S90 audio cassettes. Table 4. Description of the stimuli used for the playback experiment.

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STIMULUS	PACK SIZE	FREQUECNY (Hz)	COFM (%)	DURATION (S)
1	1	437.5	1.2	36
2	1	463.6	2.6	41
3	2	524.4	3.4	42
4	2	567.1	7.9	45
5	5	543.9	8.1	50
6	5	575.1	23.5	46

## Playback Experiment Procedures

The stimuli were broadcast to the packs using a Sony Professional Walkman, through a Nagra/ Kudelski (DMS) amplifier (frequency response 20-20000Hz) set on external output to accommodate a 20Watt Alpine car audio speaker. Peak sound pressure levels were kept constant at 100dB, at 1m from source. The speaker was positioned 0.75m from the ground and tilted at a 45° angle to simulate the approximate height and position of a wolf howling. It has been observed that even slight differences in the position of the speaker during broadcast of a signal can result in substantial changes in the level of sound received by the subjects (Wiley & Richards, 1978). The broadcast signal was directed toward the pack's enclosure from a distance of 300m from the periphery. This distance allowed for a more natural sound being received by the pack, as increasing the heterogeneity of the environment would induce echoes and cause attenuation of the signal characteristic of the natural situation. Observations prior to the individual playback experiments confirmed that the stimuli could be heard throughout the entire area of each enclosure. Also, Harrington and Mech (1983) found no evidence that a wolf pack's probability of reply, in response to a stimulus, depends on the pack's location within its territory. Because of this, the position of the pack within their enclosure was not taken into account at the onset of stimulus broadcast.

Responses were recorded on both audio cassettes (Sony UCX-S90) and on video cassette, with video equipment provided by the individual

facilities. Both the video recording equipment and video cassettes used were different for each pack. For each response, the video recording equipment was positioned within 5m of the enclosure perimeter. The exact location was chosen for its unobstructed view of the area within the enclosure in which the wolves spent the most time (these data were obtained by personal observation and information provided by the facility staff). The video camera was positioned at the same location for each session, regardless of where the wolves were within the enclosure at the beginning of the broadcast session. Wolf Park and the International Wolf Center provided a volunteer to operate the video camera. At the Wolf Education and Research Center, the video camera was tripod mounted.

The playback experiment followed a set protocol. Each pack received a total of six different stimuli over the course of six separate playback sessions. Each playback session went as follows: It began with an initial 10 minute observation period, during which the location of the wolves within the enclosure, their behavior, and environmental conditions were noted. A playback period followed with the broadcast of a pre-selected stimulus (chosen by random number generator). If a vocal response was elicited, the wolves were observed for 10 minutes after the conclusion of the response and the session was ended. If no vocal response was elicited an alternative procedure was followed. Rather than having a 10 minute observation period, then ending the session, a 20 minute observation period was followed by the rebroadcast of the stimulus. If a vocal response was elicited a 10 minute

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observation period followed and the session ended. This procedure was repeated one more time if a vocal response was not elicited by the rebroadcast. Each playback session was separated by at least 48 hours to avoid habituation.

The playback sessions were conducted between 1 hour before sunset and 1 hour after sunrise. Wolves are most active during these periods (Harrington & Mech, 1979; 1982) and at these times environmental conditions are more stable. Wind is reduced and temperature inversions near the ground, which can have an effect on attenuation, are less common (Wiley & Richards, 1978).

## Data Analysis-Acoustic

The data obtained from the playback experiment were taken directly from the video cassettes. The audio cassettes provided acoustic back-up. The video cassettes were viewed on a Panasonic video monitor. The acoustic component of the video was digitized using the Signal<sup>™</sup> (Engineering Design, 1990) sound analysis system, which includes the Real Time Spectrograph<sup>™</sup> (RTS<sup>™</sup>), designed specifically for the spectral analysis of animal vocalizations. RTS<sup>™</sup> permits on-screen viewing and measurement of each sound sample. The analogue signal undergoes a 512 point Fourier transformation, producing a digitized signal, which is displayed on-screen in the form of a frequency-time plot (spectrograph). For each vocal response, a spectrograph scrolled across the screen in real time. This spectrograph could be 'frozen' to record the specific frequency (Hz) and time (s) measurements using crosshair cursors.

The acoustic data measured from the spectrographic analysis of responses from the playback experiments were:

- <u>1.</u> Total duration of response (s), measured as the duration between the initial vocalization after the onset of the stimulus broadcast and the last vocalization that was followed by a 5s interval in which there were no vocalizations. The time to reply was also measured as the time from the stimulus broadcast onset to the beginning of the response.
- 2. Total number of individual vocalizations of each of the 5 identified types: howls, barks, bark-howls, growls and squeaks. These vocal types were identified both by ear (all have characteristic sounds) and by spectrographic (Figure 1) comparison between each vocalization in the response and a set of standard vocal types based on previous research into acoustic parameters (Table 5).
- <u>3.</u> The mean fundamental frequency  $(f_0)$  of all vocalizations within the response. The  $f_0$  (Hz) was sampled at 0.1s intervals for the duration of each vocalization; these were combined to give an overall mean frequency of the whole response.
- <u>4.</u> Durations of all vocalizations within the response (s), which were divided into vocal types and averaged to give a mean duration of vocalizations in the response.

5. The coefficient of frequency modulation (CoFM) was calculated for all vocalizations with a duration >1s. The CoFM measures the rate of frequency modulation relative to the mean fundamental frequency of the individual vocalization (Appendix 1 for CoFM equation).

The 17 choruses analyzed were considered together because they constitute one category of wolf vocalizations regardless of how they were elicited. The percent occurrence of each vocal type (howl, bark, bark-howl, squeak and growl) was measured for each chorus, then the mean was taken of the vocal types to give a general description of the choruses.

The vocal types within the choruses were analyzed separately to determine their structural characteristics. Values for mean duration and frequency, and the CoFM (for vocalizations >1s in duration) were calculated for each vocal type. This permitted comparison with previously established values for these vocal types.

The stimuli in the study were designed to elicit chorus responses from the packs as well as to make preliminary observations into the possibility of vocal mimicking in wolves. To make these observations, the choruses elicited from each pack, were pooled by stimulus (example: Stimulus 3, n=3) and analyzed for total duration and CoFM. These values were then plotted against values from the stimuli.

# Data Analysis-Behavioral

The following behavioral information was obtained from the video record of each response.

- 1. The animal which began the response (if visible).
- 2. The total number of animals that participated in the response (if visible).
- 3. The position of the wolves in relation to each other during the response, and their associated postures and behaviors. For example, were the animals laying down, standing, tails wagging, face nuzzling, etc.

Figure 1. Spectrographic representation (stylized) of characteristic forms of the A) bark, B) growl, C) squeak, D) howl and E) bark-howl vocal types.



Time (s)



Figure 1.

<u>Table 5</u>. Structural characteristics of the bark, growl, squeak, howl and barkhowl vocal types (from Tembrock, 1967; Schassburger, 1993 and Holt & Watson, unpubl. data.).

VOCAL TYPE	FREQUENCY (HZ)	DURATION (S)	SPECTRAL TYPE
BARK	145-2720	<1	NOISY- HARMONIC
GROWL	250- 1500	< 1- SEVERAL	CONTINUOUS SPECTRUM
SQUEAK	2500- 5500	0.1- 0.5	HARMONIC
HOWL	150-780	0.5- 11.5	HARMONIC
BARK-HOWL	210-400	2.5- 4.5	NOISY- HARMONIC

Table 5.

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## RESULTS

## Composition of the Chorus Howl

The data show that the group vocalization referred to as the chorus howl is actually comprised of a variety of vocal types in addition to howling and should be categorized simply as a "chorus" rather than as a form of howl. Figure 2 demonstrates the variety of vocal types contained within a chorus. In all choruses analyzed (n=17), at least two vocal types were always present: howls and squeaks. Howls comprised the largest number of vocalizations (calculated as [the number of sounds of one vocal type  $\div$  the total number of vocalizations] x 100%) within the chorus (mean=56%± 14%), followed by squeaks (mean=36%± 11%), barks (mean=7%± 8%), growls (mean=0.6%± 1.2%), bark howls (mean=0.04%± 0.11%) and miscellaneous vocalizations that could not be categorized (mean=0.3%± 0.6%). Using total duration of each vocal type to show the composition of choruses, it was found that howls represent 75.6 % of the durations of the choruses, followed by squeaks at 23 %, barks at 1.2 % and growls at 0.3 %.

In at least one chorus from each pack, the howl was not the most numerous vocal type. For the Wolf Park pack, two of five recorded choruses had a higher percentage of squeaks than howls (Figure 3). Barks were only heard during one chorus. In this case, however, the barks made up 21% of the vocalizations. <u>Figure 2</u>. Spectrographs of the beginning, mid section and end of a chorus vocalization, showing the variability of vocal types contained within.

- 2A) Chorus beginning
- 2B) Mid chorus
- 2C) End of chorus



Time (s)

Figure 2A.



Time (s)

Figure 2B.



Time (s)

Figure 2C.

Figure 3. The vocal type composition (%, based on the number of each vocalization) of each chorus recorded at Wolf Park (August, 1995). For Stimulus 1 and 2, no vocal response was elicited. \* indicates a spontaneous chorus. This chorus, for which there was no apparent stimulus, was recorded during observation (before stimulation). The table below gives the number of each vocal type in the choruses.

Stim.	Howl	squeak	bark	Bark-	growl	misc.	Total
				howl			
1	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0
3	53	15	9	0	0	0	77
4	77	97	46	0	1	0	221
5	20	7	0	0	0	0	27
6	130	67	0	0	1	0	198
*	27	46	0	0	0	0	73



VOCAL TYPES (%)

Figure 3.

This chorus also contained growls (3 growls out of a total of 220 individual vocalizations); growls were heard in only one other chorus. No bark howls were uttered in any of the choruses.

For the International Wolf Center pack, the choruses were all (n=6) dominated by howls (Figure 4). All choruses contained from 48 to 64 % howls with a variable percentage of squeaks (20-45%). Five of the choruses also contained barks, two contained growls, and one bark howl were heard. As for the Wolf Park (WP) pack, the growls were heard in choruses that also contained barks, and in one of these, a bark howl. The Wolf Education and Research Center (WERC) pack (Figure 5) showed a pattern of vocal types similar to that at both the International Wolf Center (IWC) and Wolf Park. Similar to WP, two of the six choruses contained a higher percentage of squeaks than howls. However, in terms of the number of choruses that contained barks, the WERC pack showed more similarity to the IWC pack. Barks occurred in varying amounts (3 to 19%) in four of the six choruses and growls (range 1 to 4%) were heard in all choruses that contained barks. One of these choruses (both growls and barks present) also contained the only other bark howl heard during the study. As with WP, a natural chorus (no apparent stimulus) was recorded at WERC, which consisted entirely of howls and squeaks.

<u>Figure 4</u>. The vocal type composition (%, based on the number of vocalizations) of each chorus recorded at the International Wolf Center (Sept./ Oct. 1995). The table gives the number of each vocal type for each chorus.

Stim.	Howl	squeak	bark	bark-	growl	Misc.	Total
				howl			
1	21	15	4	0	1	0	41
2	108	37	38	0	0	0	183
3	93	81	7	0	0	3	184
4	134	97	39	1	3	3	277
5	81	43	3	0	0	0	127
6	109	89	0	0	0	0	198





VOCAL TYPE (%)

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Figure 5. The vocal type composition (%, based on the number of vocalizations) of each chorus recorded at the Wolf Education and Research Center (November 1995). No vocal response was elicited by Stimulus 1. \* indicates a spontaneous chorus. This chorus, for which there was no apparent stimulus, was recorded during observation.

Stim.	Howl	squeak	bark	bark-	growl	misc.	total
				howl			
1	0	0	0	0	0	0	0
2	121	132	25	0	3	0	281
3	141	63	0	0	0	0	204
4	141	160	73	0	4	4	382
5	199	81	42	0	3	0	325
6	197	152	11	1	15	4	380
*	52	23	0	0	0	0	78







## Properties of Chorus Vocal Types

The vocal types contained within the chorus vocalizations were analyzed individually and compared to previously reported structural properties. Frequency and duration were the main properties examined. For howls, CoFM was calculated.

## (a) Howls

The howl was the major vocal type observed in wolf choruses. Three forms of howls were described from the data; one form closely resembled the solo howl, a second form the breaking-howl, and a third form resembled the 'woa-woa' howl described by Tooze (1987). The solo howl accounted for 96% of all recorded howls. One breaking-howl and a total of 62 'woa-woa' howls completed the total (n=1702).

The solo howls (n=1639) in the study had a mean  $f_0$ = 512 ± 231 Hz, a mean duration of 1.78 ± 1.02 s, and the CoFM averaged 3.2%. The one observed breaking-howl had a  $f_0$ = 486 ± 103 Hz, a duration of 1.24 s and a CoFM = 6.1%. Tooze (1987) described the 'woa-woa' howl as a howl that begins with a short howl which is followed by between 5 and 13 very short 'aborted' howls. The woa-woa howl in Tooze's (1987) study was heard from an animal that had recently been isolated from its pack mates. The present study identified potential woa-woa howls in the chorus. The

'woa-woa' howls observed in choruses (n= 62) had a mean  $f_0$ = 504 ± 215 Hz, a mean duration of 1.45 ± 0.8 s and a calculated CoFM = 8.1%. These 'woa-woa' howls were described as between 5 and 9 very short (<0.6s), chevron shaped howls, separated from each other by time intervals so short in duration that each syllable appeared joined. These howls occurred in all but 2 choruses and tended to occur in the middle of the chorus. Figure 6 shows spectrographic differences between a characteristic solo howl, breaking-howl and woa-woa howl from this study. It was also observed that when wolves woa-woa howl they keep their heads in the characteristic up-tilted position and the sound is produced by sequentially opening and closing the mouth (Figure 7).

(b) Squeaks

The squeak vocal type was the second most abundant vocalization observed in the choruses. The squeaks analyzed for this study (n= 1202) had a  $f_0$ = 2465 ± 1123 Hz and a mean duration of 0.76 ± .23 s. Squeaks were uttered singly or in trains of between 2 and 5. Observations showed that the squeak is heard over relatively short distances. At 3-5 m distance, squeaks were readily heard by observers, whereas at distances of 300 m or greater, they were difficult to hear (squeaks were barely discernable from the stimulus broadcast area, positioned at 300 m from the outer perimeter of the wolf enclosure). Figure 8 shows squeaks characteristic of those recorded in the study.

Figure 6. Spectrograph comparing a solo howl, a breaking howl and a woawoa howl.

- A) solo howi
- B) breaking howl
- C) woa-woa howl



<u>Figure 7</u>. Sequence of photographs showing the position of the head and mouth of a wolf uttering a woa-woa howl. The wolf in question is a subdominant male at the Wolf Education and Research Center.



Figure 7.

Figure 8. Spectrograph of squeaks contained within a chorus. In this spectrograph the squeaks appear in a train of 4 individual squeaks, at a frequency of 2500Hz.



Time (s)

(c) Barks, Bark-howls and Growls.

Barks were observed in 10 of the 17 choruses recorded. No barks were uttered in either of the 2 spontaneous choruses. Barks (n= 284) were short duration (mean =  $0.17 \pm 0.07$  s), with a mean f<sub>0</sub>= 340 ± 51 Hz. Barks were uttered singly or in trains from between 2 and 17 individual barks. Figure 9A shows barks from one animal that were uttered in a train of 12 barks, followed by a train of 3, followed by a single bark uttered during a chorus.

Two bark-howls were observed in the study, they consisted of 3-4 barks followed by one long howl (Figure 9B). One bark howl was uttered in the middle of a chorus that contained a large percentage of barks (13%), as well as 4 growls. The second bark howl was observed under the same conditions (chorus with barks and growls).

Growls were observed in 8 of the 17 choruses recorded. No growls were uttered in the spontaneous choruses. Of the growls (n= 11) analyzed for this study it was found that growls had a variable duration (from 0.46 to 1.55 s, mean 0.93 s) and a low frequency ( $f_0$ = 237 ± 18 Hz) with a broad spectrum. Figure 9C shows a growl characteristic of those seen in the study. It is of importance to note also that growls were heard along with squeaks, during episodes of tail-wagging, face nuzzling behaviors. Schassburger (1993) stated that growls occur solely in aggressive contexts and that squeaks occur solely in non aggressive contexts, yet here they occur together.

The vocal types observed in the chorus howls were compared to the accepted standards for those vocal types. Table 6 shows values for frequency and duration for the howl, squeak, bark, and growl from previous reports and from this study. All the values found for frequency and duration of the vocal types contained within the choruses fall within the prescribed ranges (Table 6). In this study, barks were described as having a mean  $f_0$ = 340 ± 51 Hz. This corresponds to the frequency found by Tembrock (1963) which ranged from 320 to 904 Hz.

Figure 9. A) Spectrograph of a train of barks contained within a chorus.

- B) Spectrograph of a bark-howl uttered during a chorus.
- C) Spectrograph of a growl uttered during a chorus.

Sounds at 2500 Hz are crickets.



Figure 9 A.



Time (s)

Figure 9B.


Time (s)

Figure 9C.

<u>Table 6</u>. Comparison of the published values for frequency and duration for the howl, squeak, bark and growl, to the corresponding values observed in this study. For the howl, a = solo, b = breaking-howl, c = woa-woa howl.

- <sup>1</sup> Schassburger (1993)
- <sup>2</sup> Tembrock (1963)

VOCAL TYPE	FREQUENCY F <sub>0</sub> (HZ)		DURATION (S)	
	PREVIOUS	PRESENT	PREVIOUS	PRESENT
HOWL	150-780	a. 281-743 b. 383-589 c. 289-719	0.5-11.5	a. 0.76-2.80 b. 1.24 c. 0.65-2.25
SQUEAK	2500-5000	1342-3588	0.1-0.5	0.53-0.99
BARK	145-170 <sup>1</sup> 320-904 <sup>2</sup>	287-391	<1	0.10-0.24
GROWL	250-1500	219-255	<1-several	0.43-1.43

### Structural Characteristics of Choruses

Data were collected on the duration of the choruses, the time required for packs to reply to stimuli, the overall frequency of the choruses, and modulation. Choruses had a variable duration, ranging from 45 to 210 s, with a mean of 101.5  $\pm$  44.4 s. This mean duration is longer than averages found by Joslin (1967) (85 s for free-ranging packs in Ontario) and Harrington & Mech (1978b) (60 s for free-ranging packs in Minnesota). The time to reply was highly variable; packs began to reply an average of 36.5  $\pm$  29.4 s (n=15) after the onset of the stimulus broadcast. This mean is 0.5s longer than the shortest of the stimulus. Ten of the 15 choruses elicited by a stimulus began before the stimulus had ended. The remaining choruses began after the stimulus ended. This is consistent with findings by Harrington (1989), who found that wolves often begin howling before the stimulus is terminated. The wolves in the latter study were free-ranging and the stimuli were human howls uttered *in situ*.

The overall mean frequency of vocalizations in each chorus was also variable, ranging between 506.1 and 1415.9 Hz, with a mean of  $881.9 \pm 250.1$  Hz. Because the mean frequency of a chorus took into account all vocalizations uttered, the relatively high frequency range reflects the inclusion of the many high-pitched squeak vocalizations that were present in most choruses. The CoFM, calculated as a mean for all choruses, indicated a modulation rate of  $5.9 \pm 2.5\%$ / second. This number is low due to the

exclusion of squeaks, growls and barks in the calculation because these vocalizations were generally less than 1s in duration. Thus CoFM was calculated solely on howls greater than 1 s in duration.

## Effect of Stimuli on Choruses

The stimuli were designed not only to elicit chorus responses from the wolf packs but also to observe whether or not wolf packs mimic the stimulus they reply to. The stimuli increase in duration and CoFM from Stimulus 1 to Stimulus 6. If wolves mimic the stimulus, a trend should have been observed in both duration and CoFM. The data for duration exhibit a slight trend. However, duration was the longest (mean =  $136 \pm 34.8$  s; n=3) in response to Stimulus 4, shortest in response to Stimulus 1 (47.8 s, n=1), shorter than the duration of the spontaneous chorus (mean =  $95.7 \pm 28.7$  s; n=2). The data for CoFM showed a very slight trend toward higher CoFM of the chorus as the CoFM of the stimulus increased (Figure 10). In the case of CoFM, the less modulated choruses were the spontaneous choruses (CoFM = 1.8%) and the most modulated were those in response to Stimulus 5 (CoFM = 6.7%). The CoFMs for the remaining responses fell between those for Stimulus 5 and the spontaneous choruses. These trends may indicate mimicking, however the sample size for each stimulus may not give means that accurately represent the trend.

Figure 10. Duration and CoFM for chorus responses to each stimulus.





## **Behavioral Characteristics of Choruses**

Where the identity of the animal who began the chorus was known, six were started by the alpha male and two were started by a subdominant male. At Wolf Park and the Wolf Education and Research Center, wolves often stood on structures within their enclosure to vocalize. These structures were either artificial, like den boxes, or natural such as fallen trees. This was not observed at the International Wolf Center, even though there were such structures in the enclosure. These wolves did, however, stand in a section of the enclosure that was higher in elevation than the area in which they spent their time during observation periods. Also, wolves were in a standing position when vocalizing during choruses, except in one case. At Wolf Park, the alpha male started a spontaneous chorus while lying down. As other wolves joined the chorus it continued to remain lying down throughout the chorus. Figure 11 shows the alpha male (lying down, foreground) and a subdominant male vocalizing during the chorus.

Data were collected on the number of pack members that participated in the choruses. It was observed that at Wolf Park, the omega animal (lowest ranking animal), an adult female wolf, never participated in the choruses with the other wolves. This wolf was mobbed repeatedly by the other pack members when she was in close contact with them and was therefore seldom seen in their vicinity (personal communication from P. Goodman). Also at Wolf Park, not all pack members participated in the one observed spontaneous chorus. Only four of the seven wolves participated, the alpha male, alpha female and two subdominant males. For the packs at the international Wolf Center, all wolves participated in all the choruses. At the Wolf Education and Research Center, the wolves were not visible during two of the choruses so it was not possible to determine if all animals participated. However, in the remaining four choruses all wolves participated.

Choruses were characterized by much social interaction among pack members. Face nuzzling and tail wagging were observed in all choruses. The animals also stood close together during the chorus, within two to three body lengths. It was also observed that the wolves, upon hearing the onset of the stimulus, stood, ears erect, tail down and stared in the direction of the stimulus broadcast. This behaviour was repeated at the end of the chorus response and in seven of the 17 choruses, this was seen during a pause (>1s) near the end of the choruses. In those choruses which had a pause greater than one second, the wolves abruptly stopped vocalizing, stared in the direction of stimulus broadcast, and then resumed vocalizing. This would indicate that the wolves remained aware of the direction in which the stimulus was broadcast and that they were still attending to it. The wolves during the choruses remained in close contact with each other. Figure 11. Photograph showing the alpha male and a subdominant male during a spontaneous chorus. The alpha male remains lying down while howling.



Figure 11.

### DISCUSSION

### Summary of Major Findings

The choruses of wolves contain howls, squeaks, barks, bark-howls and growls. These vocal types occur in varying amounts with howls being the most numerous. Choruses also contained a high percentage of squeaks and barks. The choruses that contained barks were often accompanied by growls and in two cases, bark-howls. Spontaneous choruses, those not elicited by any detected stimulus, were composed of howls and squeaks only. When the vocal types contained within the choruses were analyzed separately, they corresponded to previous descriptions made for those particular vocalizations. Three forms of howls were identified, the solo howl, the breaking-howl and the seldom described woa-woa howl. The woa-woa howl contributed to the variability of frequency modulation within the choruses. The description of squeaks as short distance vocalizations was further elucidated. Squeaks that occurred during choruses were heard at distances of between 10 and 20 m but were not heard at a distance of 300m. This was found by watching the video and listening to audio cassettes of the responses concurrently. This confirms their use for close contact communication.

The packs in this study responded vocally at a higher rate to stimuli containing more than one animal which suggests that choruses are more effective at eliciting choruses from packs than are the howls of lone animals. The data were also mildly suggestive of vocal mimicking, or more specifically, vocal matching in terms of overall chorus length and frequency modulation. Behaviorally, pack members rallying around each other characterized choruses. Face nuzzling, tail wagging and other close contact behaviors such as submissive displays were common. Typically, wolves stood to howl, with head tilted back, ears erect and tails down. The one exception was a spontaneous chorus started by the alpha male who was lying down at the beginning and remained lying throughout the chorus. The vocalization known as the chorus howl is composed of several vocal types and while the howl is the defining feature of the chorus, it should be reclassified as a "chorus" rather than being referred to as a type of howl as it has been described hereto-fore.

# Choruses, Structure and Behavior

Choruses were found to be variable in overall duration, vocal composition and frequency modulation. The choruses contained varying combinations of howls, squeaks, barks, bark-howls and growls. Howls were the most numerous vocalizations, followed by squeaks, barks, growls and bark-howls. This combination of vocalizations may be important in the overall message contained within the chorus. The inclusion of several vocal types may serve to alter the motivational states of the animals in the pack and thereby alter the chorus. This, in turn, may affect the message received by neighboring packs. For example, a chorus that contains growls and barks may be more aggressive in context that one that contains only howls and squeaks.

Choruses were variable in overall duration, ranging from 45 to 210 s. The longest choruses were those with the most vocalizations (range from 27 to 382 vocalizations). Most chorus responses were also started before the stimulus had ended. This indicated that wolves may not attend to the overall duration of a stimulus chorus; rather they may listen for the motivational state of the stimulus pack. The pack may be angered, excited, scared, all motivations which may be transmitted by the chorus.

The choruses were variable in terms of frequency modulation, however the mean was lower than expected (5.9  $\pm$  2.5%). The mean was expected to be higher because of the highly modulated nature of the choruses. The modulation of the choruses was calculated as the CoFM of all vocalizations greater than 1s in duration. This calculation however did not give a true measure of the chorus modulation because squeaks and barks, which can comprise up to 50% of a chorus and are generally less than 1s in duration, were not represented in this calculation. In future calculations of the frequency modulation of choruses all vocalizations, both greater than and less than 1s in duration, should be included to get a more accurate CoFM which may aid in better defining differences in choruses. This is especially important for choruses now that there is evidence that choruses contain a significant number of squeaks and barks, which are less than 1s in duration and potentially add to the information transmitted by the chorus. Information could potentially be carried in the overall modulation of the chorus, as defined by the CoFM.

In terms of overall structure, Schassburger (1987, 1993) defined two types of choruses, harmonious and discordant. A harmonious chorus is one in which the howls are uttered in sequence, one over the other, with very little modulation, while a discordant chorus is one in which the howls are uttered in a discordant manner, with much frequency modulation. Lehner (1978, 1982) described the same scenario for coyotes with the group howl and the group yip-howl. In this study, these two forms were not distinguished. All choruses were discordant, even the spontaneous choruses, which Schassburger suggested were harmonious. It would be better to say that choruses follow a graded continuum of frequency modulation which may have something to do with the combination of vocal types within and may vary with the arousal level of the pack.

Choruses have been described as beginning with one animal uttering one or several solo howls, which are followed by howls uttered by one or more pack members (Joslin, 1967). Choruses in this study were not always started in this fashion. In one response, the initial vocalization was a growl, uttered by a subdominant male. Squeaks and howls of other pack members quickly followed this. Some researchers have alluded to other vocal types being incorporated into the chorus. For example, Mech (1966), Murie (1944), Joslin (1967), Harrington & Mech (1978a) and Tooze (1987) made mention of barks occurring during choruses. In none of these studies however were the barks associated with the choruses and the possibility of the combination of barks and howls together in a chorus was not completely explored. Typically, vocal types other than howls are only made reference to in association with the chorus but not being a part of the chorus. This is akin to suggesting that the message in a piece of music that is meant for an orchestra is conveyed solely by the piano and that the sounds carried by the other instruments, while associated with the music, are somehow removed, or extraneous to the main message. The combination of sounds conveys the entire message.

Behaviorally choruses have been described as highly contagious events within the pack (Crisler, 1958), ones which are accompanied by much face nuzzling and tail wagging (Harrington & Mech, 1978a). The data from this study were consistent with these descriptions. Wolves would typically rally around each other, face nuzzle, and tail wag. This was observed most often at the beginning of the chorus and after the chorus had ended. The behavior of the wolves during these close contact associations may serve to further stimulate the pack into responding and perhaps the vocal types associated with these behaviors serve to unify and/ or enhance the motivation of pack members. For example, if these rallying sessions are accompanied by a large number of growls and barks, perhaps the resulting chorus will be more aggressive (lower frequency) as the motivation of the pack members becomes more aggressive.

Regardless of what the wolves were doing prior to stimulus broadcast (usually sleeping, resting, eating, sometimes playing or greeting), upon

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hearing the stimulus, the wolves always reacted the same way. They would look up, stand, ears erect, tails down, and stare for varying amounts of time in the direction of the stimulus broadcast. The prior activities did not seem to have any effect on the resulting chorus. Responses uttered when the wolves had been sleeping prior to stimulus broadcast were as modulated, etc, as when the wolves were more active (greeting, playing). The response would typically begin before the end of the stimulus. Perhaps the wolves were listening for the first few howls of the stimulus to gauge the motivation, distance, or perhaps the identities or the number of animals vocalizing. Once the chorus had begun, the wolves would sometimes stand on available structures (better vantage point), and they would keep their relative positions without a great deal of movement, other than vocalizing. When the wolves stopped vocalizing, they would look in the direction of the stimulus broadcast before resuming pre-chorus behaviors, such as eating or sleeping. This staring suggests that the wolves remember the contexts under which they started the chorus and that perhaps they are still attending to the original stimulus.

Vocal signals carried over long distances must contain all the necessary information without the aid of visual and olfactory cues. For this reason, it is theorized that these vocalizations should be structurally stereotypic to minimize the ambiguity of the message that structural variability introduces. This stereotypy of long distance vocalizations was observed for arboreal dwelling primates (example, *Cercocebus albigena*) where visual

cues are absent between groups because of the forested habitat (Waser, 1977; Waser & Waser, 1982). Wolves living predominantly in forested habitats occupy territories that cover up to several hundred square kilometers. This limits the use of visual cues when conveying information between packs. According to Waser's (1977) theory then, the chorus of wolves, which is the main mode of transmitting information over long distances between packs, should be fairly stereotypic in structure, that is, the vocalization should not be variable structurally in terms of frequency modulations and vocal composition. This, however, is not the case: choruses of wolves are indeed quite variable in both frequency modulation and vocal composition. The question is why are choruses so complex if the primary message is to be transmitted over long distances? The answer may lie in the nature of the vocal types contained within the chorus and to whom the information is directed. The chorus contains both short distance and long distance vocal types indicating that a large portion of the information is meant for intra-pack communication rather than to a neighboring pack.

## Vocal Composition of Choruses

The choruses of wolves have been described as long distance vocalizations, which play a significant role in interpack communication, primarily functioning in territory defense. The chorus may provide information on pack identity, location, motivation and, potentially, pack size. It's been suggested that the frequency and the frequency modulations contained within the howls are the primary structural components that carry this information. I propose that the combination of the associated vocal types also assists in conveying the information to neighboring packs.

The vocal type known as the howl was the most numerous in the choruses, with a mean of 56% of the total number of vocalizations counted. In this study, three forms of the howl were identified. These three forms were the solo howl, the breaking howl and the woa-woa howl. The form described as the solo howl made up the largest number of the howls in the choruses (96%). These howls were relatively flat (CoFM=3.2%), low frequency (512 Hz) and long duration (1.78 s). When the solo howls were compared structurally to both the breaking howls and woa-woa howls, they were found to be higher frequency and longer duration. According to Morton's motivational-structural rules, this would indicate that the solo howl is not as aggressive a sound as either the breaking howl or the woa-woa howl. This is not consistent with findings by Harrington and Mech (1978a) who observed that the mean fundamental frequency for solo howls was lower than that for breaking howls. However, the sample size for this present study was only n=1 breaking howl, which was not representative of the vocalization. Morton (1977) suggested that animal sounds follow a graded continuum whereby lower frequency sounds are more aggressive and high frequency sounds, at the opposite end of the continuum are more 'friendly'.

Woa-woa howls were not much lower in frequency than the solo howls, yet their structure was very different. Rather than a flat howl, these howls

consisted of short chevron shaped howls in sequence with virtually no temporal separation. They tended to occur near the middle of the chorus and added to the overall modulation of the chorus. Woa-woa howls were described by Tooze (1987) in conjunction with an animal that had been isolated from its pack mates. This study shows it in another context, the chorus. It's been suggested that these howls contribute to a form of Beau Geste effect as proposed by Krebs (1977), whereby animals exaggerate their apparent numbers to rivals, in this case, to other wolf packs (Harrington, 1989). Overall, the howls in the study were somewhat shorter than those previously reported. It's been reported that the howls of adult wolves last at least 3 s (Theberge & Falls, 1967; Harrington & Mech, 1978a), however the data from this study showed that the mean duration of howls was less than 2 s. This is consistent with previous work, indicating that howls uttered in chorus are shorter than howls uttered alone (Joslin, 1967; Harrington & Mech, 1978a; Tooze, 1987).

Squeaks were a large part of all choruses recorded during this study. They accounted for 36±11% of all chorus vocalizations. Squeaks are high frequency, short duration vocalizations that function in communication between pack members. In this study the squeaks were not heard at distances of 300 m so the theory that they function as short distance vocalizations is well founded. If this were correct, why would this vocal type be so prevalent in choruses, vocalizations that are heard over distances up to 10Km (Joslin, 1967; Harrington & Mech, 1978a)? Squeaks serve to communicate between pack members and operate in many contexts; from adult to pup (Fox, 1971; Coscia et. al. 1991; Goldman et. al. 1995), pup to adult (Fox, 1971; Peterson, 1974), adult to adult (Harrington & Mech, 1978a). In all cases, these contexts are non-aggressive. It has also been observed that during choruses, young, or subordinate animals will often squeak and try to lick the face of more dominant animals (Harrington & Mech, 1978a). This was observed in this study also. Choruses were typically accompanied by squeaking, face nuzzling, tail wagging, which sometimes lasted throughout the entire chorus, although these behaviors were most often observed at the beginning of choruses and after the chorus had ended. This vocal type may serve to rally the wolves together and involve the whole pack in the chorus.

Barks were uttered in 10 of the 17 choruses recorded during the study. Behaviorally the bark is considered an aggressive sound that may serve to attract attention toward the vocalizing animal (Bekoff, 1974), who is often visually conspicuous (Harrington & Mech, 1978a). Structurally barks bear the physical characteristics that make them localizable (Harrington & Mech, 1978a). These vocalizations are short duration, low frequency with a sharp onset and a broad spectrum. Konishi (1973) indicated that short bursts of energy covering a broad spectrum should be easy to localize. If barks are easily localizable their inclusion in choruses could indicate the general area of their territory to neighboring packs and lone, dispersing wolves, thereby lessening the chances of an encounter. This would be beneficial since most encounters between wolf packs result in interpack strife (Mech, 1994). It is of

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interest to note that barks were not uttered in the spontaneous choruses. In the two spontaneous choruses recorded during the study, only howls and squeaks were heard. This would be consistent with the previous theory on the importance of localizability of the chorus. A spontaneous chorus occurs without any apparent stimuli and is therefore not necessarily directed toward any particular listener, thereby removing the necessity of including information on location. Many more natural choruses would have to be analyzed for vocal composition to make any concrete conclusions however.

Growls were uttered in 8 of the 17 choruses recorded during the study. Growls were only heard in choruses that also contained barks. This vocal type has been described as a deep, course sound (Harrington & Mech, 1978a) which functions primarily in the contexts of warning, threat, defense, attack and dominance (Fentress, 1967; Fox, 1971; Field, 1978; Harrington & Mech, 1978a; Schassburger, 1987, 1993). These are the same contexts that are associated with the bark vocal type. It would be logical therefore for growls to be heard in choruses that also contain barks. However, growls are not heard at distances that normally separate wolf packs in the wild. In this study, growls were not heard from the 300 m that separated the pack from the audio recording equipment. The growls were only accurately recorded on the video recordings made within several meters from the pack. If this is the case, and growls are not heard by neighboring wolf packs, what is their role during a chorus? They are likely used to communicate between pack members during the chorus and may serve to communicate the state of arousal of the

dominant animals to the rest of the pack. Morton (1977) suggested that animal vocalizations follow motivational-structural rules whereby low frequency sounds convey aggressive motivations while higher frequency sounds convey more 'friendly' motivations. The growls may serve to provide an internal (within pack) stimulus which motivates the pack to respond more aggressively (with lower frequency howls and barks) to neighboring packs if they are perceived as a threat. Morton (1977) also suggested that longdistance vocal signals might communicate subtle changes in the motivational state of social, group-living animals that communicate between groups. In this way the growl may affect the overall state of arousal within the pack and this change in motivation may be conveyed to neighboring packs in the chorus.

The combination of vocal types within a chorus could potentially carry information. This has been proposed for coyotes (*Canis latrans*) whereby the combination of two or several sound types would carry specific information over long distances (McCarley, 1978). It has been suggested that the frequency, duration, and overall frequency modulation of choruses carry the relevant information, but perhaps the vocal composition of choruses is equally important.

# Effectiveness of Stimuli

The stimuli for this study were successful at eliciting vocal responses from the study packs. These stimuli were artificially created from human howl imitations and manipulated to create stimuli that varied on a graded

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continuum of duration, frequency modulation and the number of individuals participating in the stimuli. In this study however, two of the stimuli were less successful at eliciting vocal responses than the rest. Stimulus 1 and Stimulus 2, both representing one wolf, failed to elicit responses in 3 of 6 presentations. Several studies have utilized live human howling representing one wolf howling (recent examples include Harrington & Mech, 1979, 1983; Harrington, 1987, 1989; Tooze, 1987; Fuller & Sampson, 1988). The stimuli in some of these studies had variable success in eliciting responses.

Fuller and Sampson (1988) used human howls (after Harrington & Mech, 1982) to elicit vocal responses from wolves to conduct a census of wolf density in a given area. The stimuli, which consisted of one person emitting a sequence of three howls, were presented to wolves on 22 nights, at a mean of 7.5-sites/ night, for a total of 165 presentations. Vocal responses were elicited for 11 of these presentations. In this case, this method was not highly effective at estimating the number of wolves in the area. Harrington and Mech (1982) had more success with their study yet found that stimuli that represented two wolves howling, rather than stimuli that represented one wolf, were better at eliciting responses. It was suggested however that stimuli of single howlers be utilized to census wolf numbers because small wolf packs responded less to stimuli representing two animals than they did to single howls. The use of single howler stimuli would thereby lessen the difference in reply rate between small and large packs (there was no data on the number of animals in a small pack versus a large pack). The present

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study showed that stimuli representing 2 or 5 wolves were more effective at eliciting responses than stimuli representing 1 wolf, even for the smallest pack in the study, the pack at the International Wolf Center, that consisted of four animals. Depending on the nature of the studies, perhaps the use of pack stimuli would be more successful at eliciting responses than the previously used single animal stimuli.

### Vocal Mimicry

Vocal mimicry is reportedly a common occurrence in animal signaling systems (Zahavi & Zahavi, 1997). Jays (*Garrulus glandarius*), for example, are able to mimic a telephone ring, sending unsuspecting people to answer it. Also, many have heard the parrot (*Psittacidae* sp.) mimic human speech in seemingly appropriate contexts (or people mimicking the parrot mimicking them). One suggested function of mimicking is to convince a listener that the vocal communication is being addressed to it specifically (Hultsch & Todt, 1986 in Zahavi & Zahavi, 1997). In many bird species, such as indigo buntings (*Passerina cyanea*), it was observed that the birds mimic the songs (called song-matching) of their neighbors (Payne, 1983). Perhaps wolves, when responding to the vocalizations of conspecifics, mimic some aspects of the chorus.

The data from this study were mildly suggestive of vocal mimicry, in terms of overall duration and frequency modulation of the chorus. As the duration and CoFM of the stimuli increased, there was a trend toward increased duration and frequency modulation of the elicited choruses. This could indicate that wolves respond with choruses that closely match that of the stimulus, perhaps to indicate to the stimulus pack that it is responding directly to them and not to another pack (or a spontaneous chorus). Further studies on this should concentrate more on the frequency modulation because wolf packs frequently begin their responses to choruses before the stimulus chorus is terminated which suggests that they do not attend specifically to the overall duration of the stimulus.

It would be interesting to discover whether or not wolves mimic the choruses of their conspecific neighbors and if so, it would be equally interesting to discover whether they also mimic the choruses of sympatric species such as coyotes. Birds frequently mimic the songs of sympatric species. One theory is that by mimicking the territorial or aggressive vocalizations of competing species, birds can deter their competitors from shared resources (Harcus, 1977). Both wolves and coyotes are territorial and both employ characteristic vocalization used in the defense of these territories (wolves chorus and coyotes group yip-howl (McCarley, 1975; Lehner, 1978; Lehner, 1982). Where the species are sympatric coyotes typically inhabit the areas that are at the boundaries of resident wolf pack territories (Fuller & Keith, 1981). Coyotes inhabit these areas, known as 'buffer zones', because wolves are rare there, and wolves often kill coyotes they catch. Perhaps coyotes are considered rivals for space and food resources, and by mimicking

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the coyote group yip-howl, wolves can deter them from occupying a certain area.

### Conclusions

The wolf group vocalization referred to as the chorus howl has historically been described as a form of howl, one which is uttered by two or more pack members vocalizing together. While this group vocalization does contain howls, it also contains squeaks, barks, growls and bark-howls. For this reason the vocalization should not be classified as a howl. The chorus howl should be referred to simply as the "chorus" in the future and be given its own category as a separate vocal type. The data also provided evidence that the vocal types contained in the chorus corresponded to the vocal types previously described for the wolf, suggesting that the combination of these vocal types within the chorus may provide the information that the chorus carries both within the pack and between packs. The combination of vocal types within a chorus might also be a function of vocal mimicry. Data was mildly suggestive vocal mimicry, or vocal imitation, whereby wolves mimic the duration and frequency modulation of the stimulus chorus.

# **Directions for Future Research**

This study provided evidence that the chorus vocalizations of wolves contain several of the vocal types previously described for the species. The data was also mildly suggestive of vocal mimicking, whereby chorus responses mimic the duration and frequency modulation of the stimulus. The

evidence however does not elucidate the kind of information carried in the chorus. It has been hypothesized that choruses may provide information about pack size to neighboring packs and dispersing wolves looking to settle new territories (Mech, 1970). A study by Harrington (1989) suggested that choruses might not carry such information on pack size. He observed that during the course of his study, that involved human howling at wolf packs and recording responses, that humans could not accurately count the number of wolves participating in a chorus, even between groups of two to three wolves. Spectrographically, larger groups (4 to 12 wolves) were indistinguishable from one another. These findings would suggest that wolves howl to exaggerate the apparent number of individuals howling. This would be particularly useful for smaller packs. There is evidence that pack encounters are influenced by pack size, with larger packs prevailing (Mech, 1966; Mech & Freznel, 1971; Harrington, 1989). Any information about pack size contained within the chorus could therefore determine the outcome of the encounter. Because encounters between wolf packs seldom occur, it was predicted that the chorus might facilitate the avoidance. In this way, Harrington (1989) suggested that the chorus of wolves might provide the first mammalian example of Krebs' (1977) Beau Geste effect. This effect was suggested for birds, whereby resident birds on a territory had large song repertoires to exaggerate the number of birds in an area and discourage nonresident birds from settling. A study similar to that conducted here could be undertaken to see if wolves exaggerate their numbers in the chorus to ward off potential

intruders or if they mimic the chorus of the intruder to acknowledge its presence. In such a study, particular emphasis should be placed on further analyzing the woa-woa howl and its effect on the overall frequency modulation of choruses.

Observations from this study suggested that at distances that typically separate wolf packs in the wild, squeaks and growls contained within the chorus are not heard. A study in which the position of the recording equipment was taken into account could provide information on the distances at which the vocal types can be heard. This would ascertain what vocal types in the chorus are used to carry information to other packs (between packs) and which vocal types provide information within the pack during a chorus. This information could potentially lead to better understanding intra-pack interactions during a chorus. The more information available about the physical parameters of the chorus, the more will be understood about the functions of these vocalizations, which will give us a better understanding of the wolf vocal communication system, and subsequently about wolf behavior. Appendix 1. Formula used to calculate the coefficient of frequency modulation (CoFM).

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f(t)= fundamental frequency at time t

n= number of sample points

Appendix 1.

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IMAGE EVALUATION TEST TARGET (QA-3)







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