THE CONTEXTS AND SOUND OF THE SQUEAKING VOCALIZATION OF WOLVES (Canis lupus)

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ABSTRACT

Little is known about squeaking, the most frequent close-range vocalization of wolves. This study was designed to determine diurnal patterns, frequency of occurrence, and range of social contexts of squeaking and to assess the individual and contextual variation in the squeaking vocalization. Squeaking events were identified from the 1995-1997 videotapes of the social behavior of captive wolves at the Canadian Center for Wolf Research (Shubenacadie, Nova Scotia); additional data were obtained from seven 24-hr watches. Wolves squeaked most frequently during dawn and dusk hours, corresponding to the times when they were most often visible in the clearing. Wolves squeaked in seven social contexts, but most frequently when approaching or orienting toward other wolves in prosocial and food contexts. Some individuals squeaked more often than others and in more social contexts, but there was no significant sex or social status difference. Acoustic analysis of squeaking vocalizations revealed that wolves have signature squeaks that vary in form as the context changes. Although a number of acoustic variables were measured at each level of the squeaking vocalization (squeak, phrase, vocalization), a combination of squeak frequency variables was most useful for distinguishing among individuals and among social contexts. The diversity and complexity of this vocalization suggest that it may play an important role in controlling and coordinating social interactions within the pack.

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Communication requires that one individual (the sender) shares information with at least one other individual (the receiver). Sharing information, by signaling, enables one individual to influence another individual's behavior (Smith, 1990). Central to communication are the concepts of message and meaning. The message is the information contained in the signal. Receivers use the signal and context-related information (location, proximity of participants, sender identity, and size) to interpret the meaning of the signal. The meaning refers to the response made to the signal by the receivers as well as the response the senders intended to elicit by providing the signal (Smith, 1977, 1990; Phillips & Austad, 1990).

Classical ethologists (Smith, 1977, 1990; Phillips & Austad, 1990) describe the signal as being "fixed" (i.e. only carrying information that has been selected through evolution). Others view the signal as being "open" (i.e., signals permit variation to provide for individual variation, subtlety of meaning, location, etc.). According to Hauser (1996), information is a feature of the interaction between the sender and perceiver. Signals carry certain kinds of information, which can be manipulated by the sender and differentially acted upon by the perceiver. Signals can be differentiated from cues. Both represent potential sources of information, but signals are more plastic and are produced in response to sociologically relevant and temporally varying changes in the environment. Cues, however, typically correspond to an individual's or species' phenotype and are essentially permanent or fixed (Hauser, 1996). Therefore, the expression of cues does not carry an immediate cost. Because signals are more variable, they are costly to produce and therefore have been designed to be informative. To determine the meaning or function of a signal requires one to look closely at its defining features (Hauser, 1996).

Wolves (*Canis lupus*) are highly social animals that live in packs consisting mostly of family members (parents, pups, aunts, uncles, etc.). They cooperate in virtually all aspects of daily living such as hunting, raising young, and travelling; all are activities that demand effective communication. Wolves have a very extensive and elaborate communication system. They have the same five senses for gathering information as humans except that the efficiency of their sense organs differs from ours. Olfaction is perhaps the most acute of the wolf's senses. The sensitivity of the wolf's nose is unknown; however, we do know that dogs are 100 to 10, 000 times more sensitive to detecting odorants than are humans (Asa & Mech, 1995). The sensitivity of olfaction highlights its importance for wolves for hunting and for social communication.

Similarly, visual communication is important in hunting and in social communication. Schenkel (1947) illustrated the importance of visual displays in communication of wolves. Features of the face, ears, body, and tail are made more salient by contrasting coloration and emphasize the signal value of facial expressions and ear, body and tail positions. The position of each feature singly and in combination is assumed to express the underlying motivation of the displaying animal. Although the sensitivity of the wolf eye is no more acute than the human eye, it has been modified to enable the wolf to adapt to nocturnal hunting. (For a description of these modifications and adaptations see Asa & Mech, 1995).

Audition is important to wolves for many reasons. Wolves are likely to use auditory information for communication with conspecifics, including pack members and other neighboring packs, and for hunting. Canids have a very sensitive auditory system enabling them to hear sounds with an upper frequency limit of 80 kHz over a maximum hearing distance of 6.4-9.6 km (Harrington & Mech, 1978). Experimental research shows that they are capable of distinguishing between pitches that are one tone apart on the musical scale (Asa & Mech, 1995).

Wolves have an extensive vocal repertoire but researchers disagree on how to categorize the sounds. Schassburger (1993) described the wolf vocal repertoire as a system divided into two sound groups: (1) harmonic sounds including whines, whimpers (squeaks), yelps and howls and (2) noisy sounds including growls, barks, snarls, whine-moans, moans, and growl-moans. Others, such as Theberge and Falls (1967), Harrington and Mech (1978), and Coscia, Phillips, and Fentress (1991), suggested that wolves produce 4-6 different sounds (growl, bark, yelp, whimper [squeak], howl, and whine) and considered the others as subclasses.

Although most of the wolf vocal repertoire consists of close-range vocalizations (whines, squeaks, growls, and yelps), more is known about the long-range vocalization - howling. Much research has focused on describing the structural and functional properties of the howl (Theberge & Falls, 1967; Harrington & Mech, 1978, 1979; Klinghammer & Laidlaw, 1979; Harrington, 1987). Howling has been proposed to function in territory advertisement and maintenance, as a contact call between separated pack members, and to announce the imminent return of adults.

Although howling is the most familiar of all wolf vocalizations, squeaking is likely one of the most frequent vocalizations made by wolves. Squeaking is an affliative vocalization that occurs in a range of social contexts. Its function can be inferred from the design features of the vocalization (Hauser, 1996). Squeaking is a low-amplitude vocalization which suggests that it is not a distal, but rather is a close range signal. Relative to other wolf vocalizations, it is a high frequency vocalization (2-4 kHz), suggesting that it is friendly rather than aggressive (Morton, 1977, 1982). Furthermore, the frequency of the squeak is highly variable both within and between individuals, suggesting that information about identity, location, and social contexts may be encoded within this signal (Hauser, 1996).

Individual and group squeaking (squeaking by more than one wolf simultaneously) has been observed during play, after an aggressive encounter, before and after feeding, during greetings, to pups inside and outside of the den, during howling, and in many other situations. Its presence in a variety of behavioral contexts suggests that squeaking likely has many functions. It may aide in maternal recognition, inform pups when it is time to leave the den, provide a relaxed atmosphere after an aggressive episode, assemble wolves for play or indicate excitement and contentment.

Although squeaking is a very common wolf vocalization, very little is known about it. Squeaking in wild wolves has been documented in descriptive accounts of personal experiences (Crisler, 1958; Mech, 1970; see Chapter 2). Preliminary captive research suggests that the acoustic structure of squeaking may differ among wolves and social contexts (Field, 1979; Fentress, Field, & Parr, 1978; Goldman, Phillips, &

Fentress, 1995; see Chapter 3). Because no study has systematically examined the contextual and acoustic properties of squeaking in pack-living wolves, this study was designed to investigate variation in the squeaking vocalizations of many wolves in several different social and movement contexts. The objectives of this study were to determine diurnal patterns of squeaking, the frequency of occurrence, and the social and movement contexts in which it occurs (Chapter 2) and to provide a detailed acoustic analysis of squeaking vocalizations investigating individual and contextual variation (Chapter 3).

In this study, the social behavior of wolves at the Canadian Center for Wolf Research (CCWR) was videotaped. In Chapter 2, squeaking vocalizations were identified from these videos and the distribution of squeaking vocalizations across time of day, individual, social and movement context was determined. In Chapter 3, high-quality recordings of the squeaking vocalizations identified in Chapter 2 were selected for acoustic analysis. A variety of frequency and temporal measurements were obtained through spectrographic analysis. These acoustic parameters were compared between individuals and between contexts to determine if wolves have signature squeaks that differ between different social contexts. A summary of findings from all chapters is provided in Chapter 4.

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Chapter 2 The Contexts of Squeaking

2.1 INTRODUCTION

Social organization in the canids ranges from almost solitary to among the most highly social of all mammals (Sheldon, 1992). Species such as the wolf, *Canis lupus*, the dhole, *Cuon alpinus*, and the African wild dog, *Lycaon pictus,* are highly social and hunt in packs. Others are moderately social (e.g., coyote, *Canis latrans*, golden jackal, *Canis aureus*); the basic social unit is the mated pair and their offspring. Perhaps the least social of all canids are the foxes of the genus *Vulpes*; they usually have a temporary pair bond and the young disperse at 5-6 months of age. (Fox & Cohen, 1977; Sheldon, 1992).

The complexity of vocal communication in canids complements their social complexity. According to Fox and Cohen (1977), eight basic kinds of vocalizations occur: whines, screams, barks, growls, coos, howls, mews, and grunts. Not all of these basic sounds are included in the vocal repertoire of every canid species. In wolves, six basic vocalizations have been described: growls, barks, yelps, howls, whines, and squeaks (Theberge & Falls, 1967; Harrington & Mech, 1978; Coscia, Phillips & Fentress, 1991). Although most of the wolf vocal repertoire consists of close-range vocalizations (squeaks, whines, growls, and yelps), more is known about the long-range vocalization of howling. Much research has focused on describing the structural and functional properties of the howl (Theberge & Falls, 1967; Harrington & Mech, 1978; Klinghammer & Laidlaw, 1979; Harrington, 1987). The focus of this study is squeaking. The following sections will define squeaking, review the historical literature, and compare squeaking across canid species.

Relative to other wolf vocalizations, squeaking is a high-frequency, soft vocalization that occurs in many different behavioral contexts at close range. A squeaking vocalization is composed of one or more squeaking phrases, each of which is comprised of one or more squeaks (see Fig. 3.1, Chapter 3). Individual squeaks are brief (less than 300 ms), low-amplitude vocalizations with characteristic energy distributed between 2 and 4 kHz. Individual and group squeaking has been observed during play, after aggressive encounters, before and after feeding, during greeting, to pups inside and outside of the den, during howling, and in many other situations. Its presence in a variety of behavioral contexts suggests that squeaking may have many functions. It may aid maternal recognition, inform pups when it is time to leave the den, provide a relaxed atmosphere after an aggressive episode, or assemble wolves for play.

Because squeaks are audible only over short distances, it has been difficult to study squeaking in wild wolves. However, early researchers described a vocalization as whimpering or whining that is similar to squeaking in functional contexts and audile properties. It has been difficult to identify and compare sounds described by previous authors unambiguously because, in most accounts, the name of the vocalization also served as the description (Harrington & Mech, 1978). Furthermore, early descriptions were often based on subjective accounts rather than on spectrographic analysis, as is evident in the following accounts.

Young (1944, p. 77; cited in Mech, 1970) wrote that the whimper "is a high, though soft, and plaintive sound similar to the whine of a puppy, and is often used mostly at or near the opening of a wolf den, particularly when the young whelps are out playing around". Joslin (1966; cited in Mech, 1970) reported several observations of whimpering in wild wolves and concluded that whimpering was a submissive or friendly greeting sound that is audible at no more than 200 meters. Crisler (1958, p. 150) provided a personal account of what probably included squeaking, although she called it "talking": "The wolf talking is deeply impressive because the wolf is so emotionally stirred. His eyes are brilliant with feeling. He seeks your eyes and utters a long, fervent string of mingled crying and wowing, hovering around one pitch".

It is difficult to compare sounds described by different authors even with spectrographic analysis. Peters (1980) referred to squeaks and whines in group greeting ceremonies and described them as low in amplitude and high in frequency (2500-2800 Hz in adults, approximately 3800 Hz in pups). Harrington and Mech (1978, p. 111) defined whimpering as "vocalizations variously classified as whines, whimpers, and squeaks". These vocalizations were characterized as having energy between 400 and 800 Hz, but with most energy at approximately 3500 Hz (hence the quality of high pitch) and a duration of approximately 0.2 to several seconds. They suggested that the briefer sounds were probably what earlier researchers termed whimpers, and that the long ones were whines. Vocalizations that lacked the low-frequency components of whimpers were termed squeaks. Coscia et al. (1991) observed captive pups (inside the den) squeaking for the first time at 15 days of age. They described pup squeaking vocalizations comprised of relatively high frequency, narrow band squeaks that varied considerably in terms of the inter-squeak interval, the number of individual squeaks per vocalization and the form of individual squeaks. Fentress, Field, and Parr (1978) described squeaking broadly as high frequency, tonal sounds.

Harrington and Mech (1978) described several social contexts in which whimpering (including squeaks) occurred. These included: (1) adult to pup at the mouth of the den, to bring the pups out of the den; (2) pup to adult to solicit care from adults; (3) adult to adult during greeting, play solicitation, mutual greeting ceremony, and the quick withdraw and submissiveness of a wolf during agonistic encounters; (4) wolf to human when approaching familiar humans or when being approached; (5) sexual behavior; and (6) chorus howls. They concluded that whimpering (including squeaks) occurred when the vocalizer decreased its distance to another, either physically or socially and that the underlying message of whimpering is the friendly, non-aggressive attitude of the vocalizer.

Fentress et al. (1978) compared squeaking between three individuals in the same social context (while orienting to a neighbour's pen) and from the same individual in three social contexts (during an howling session, during an agonistic encounter, approaching an adult male wolf). Similarly, Field (1979) compared squeaking between three individuals in the same social context (approach by a human). Squeaking was highly variable among wolves and within the same wolf in different social contexts. Whether this variation was due to differences between the contexts of occurrence, age, social position, sex, or individual was not determined. Goldman, Phillips, and Fentress (1995) found circumstantial evidence to suggest that young pups can distinguish the squeaks of their mother.

Because squeaking occurs so frequently and in so many social contexts it may be very important in controlling and coordinating social interactions in wolves (Fentress et al., 1978). If so, squeaking (or a similar close-range vocalization) is likely to be present in the vocal repertoire of other social canids. In their discussion of the vocalizations of canids, Fox and Cohen (1977) classified whines as including briefer yips and yelps, and long soft whimpers. They defined whines as "wide-banded, cyclic sounds of short duration and moderate frequency variations" (p. 735) and stated that whines are common in wolves, foxes, coyotes, and domestic dogs. Whines occurred in greeting, play solicitation (dogs only), submission, defense, care or contact-seeking (neonates only), distress (neonates only), pain, and group vocalizations. Fox (1971) suggested that whining and whimpering were associated with a decrease of social distance and submission; they were observed frequently in wolves, coyotes, and dogs.

In the dhole, Fox (1984) observed the whine or whimper during friendly approach, greeting, and food solicitation. In addition, Johnsingh (1979; cited in Fox, 1984) reported squeaks or whines from dhole pups during play. Tembrock (1963) has described the whimper in the dhole, African wild dog, Corsac fox, *Vulpes corsac*, and the red fox, *Vulpes vulpes*.

Lehner (1978) reported that coyotes have 11 basic vocalizations, which include a whine, described as a short-range, low-amplitude vocalization consisting of two types. A low-frequency whine is given by subordinate individuals to more dominant ones during greeting. In this context, the whine is accompanied by "muzzle nibbling" and tail wagging with the tail held low or between the hind legs. The high frequency whine is used by subordinate animals to express passive submission in an agonistic encounter. Lehner claims the coyote's whine is the same as soft social squeak of the wolf (Mech, 1970), the squeak of the Eastern coyote (Silver & Silver, 1969) and to whines and whimpers reported for other canids (Tembrock, 1963).

Taken together, it appears that most social canids have a close-range, relatively high-frequency, friendly vocalization that is emitted in series and occurs in many social contexts. No study has systematically examined the detailed behavioral context and function of squeaking in wolves. In this study, the contextual variation in the squeaking vocalizations of many wolves in several different social and movement contexts was examined. From past research, we know that squeaking occurs in prosocial (howling, playing, greeting), agonistic, sexual, and care-giving (pups and adults) contexts. We know less about the movements of the squeaker or recipient (s) during a squeaking vocalization. Fentress et al. (1978) reported that squeaking occurs when a wolf is approaching another wolf. It is possible that wolves also squeak when leaving other wolves. This study examined the occurrence of squeaking in all of these social and movement contexts. The main goal was to determine the distribution of squeaking vocalizations by time of day, individual, and social and movement contexts. The specific objectives were: (1) to investigate the temporal pattern of the occurrence of squeaking, (2) to determine whether some wolves squeak more than others (i.e., males versus females, dominants versus sub-dominants), (3) to determine the social and movement contexts in which squeaking occurs, and (4) to determine whether wolves squeak more frequently in some contexts than in others.

The habits of wolves often require them to be separated from one another or to be in situations where olfactory and visual communication is limited. These situations occur even when wolves are in close range of one another (during night, in the forest, upwind of others). In these circumstances, auditory communication becomes especially important for maintaining group cohesion and for coordinating social interactions. Knowledge of the behavioral and functional properties of squeaking may improve our understanding of how wolves use communication to control and coordinate social activities.

2.2 METHODS

2.2.1 **Study Site**

Data were collected from January 1995 to December 1997 at the Canadian Center for Wolf Research (CCWR), a research facility located near Shubenacadie, Nova Scotia, where wolves are maintained in a 3.8 hectare forested enclosure. CCWR supports only observational, non-invasive research. No live prey is introduced into the compound. The primary diet of the wolves is a high-quality dog food supplemented whenever possible by road-killed deer. The wolves are fed in the clearing, which consists of a knoll, a pond, and an open area. Human interaction with wolves is kept to a minimum. The wolves are not approached or handled, and their activities and social interactions are observed and recorded from one of two observation structures located next to the clearing that is frequently visited by the wolves.

Each wolf is named and individually identifiable by markings; relevant information (name, age, social status) for each wolf is presented in Table 2.1. The

Table 2.1. Relevant information for each wolf.

Wolf	Sex	Birth	Death	Social Status
Celtie (C)	F	1992	-	Sub-dominant (95, 96) Omega (97)
Devilchild (D)	F	1993	Feb. 1997	Beta (95,96) Alpha (97 ~ 3 wks)
Fiona (F)	F	1992	-	Sub-dominant (95, 96) Alpha (97)
Galen (G)	M	1988	-	Alpha (95,96,97)
Homer (H)	M	1988	May 1997	Sub-dominant (95,96,97)
Jasper (J)	M	1993	-	Sub-dominant (95,96,97)
Morgaine (M)	F	1991	Feb. 1997	Sub-dominant (95,96,97)
Noah (N)	M	1990	-	Sub-dominant (95,96,97)
Pawnee (P)	F	1984	Feb. 1997	Alpha (95, 96, 97)
Tess (T)	F	1990	Feb. 1997	Sub-dominant (95, 96, 97)
Ulysses (U)	M	1995	-	Pup (1995) Yearling (1996) Sub-dominant (1997)
Voochco (V)	M	1984	Feb. 1997	Beta (95,96,97)
Xela (X)	F	1988	-	Omega (1996,1997) Sub-dominant (1997)

number of wolves in the pack changed over the course of this study. During 1995 and 1996 there were 13 wolves, including a pup born in 1995. In 1997, the size of the pack declined dramatically. In February 1997, the alpha female (Pawnee) died from complications of old age and three females died from injuries sustained through fighting for the alpha position. A little later, the beta male (Voochco) died from natural causes. In May 1997, Homer also died from natural causes, leaving seven wolves in the pack.

2.2.2 **Data Collection**

24-hr watches. From 5 June to 24 July 1997, seven 24-hour watches were conducted. For each watch, social behavior was recorded from an observation trailer located outside the compound adjacent to the clearing. Activity was videotaped using a Hi-8 Sony CCD-TR600 Video Camcorder and Fuji Hi-8 videocassettes. A Sennheiser Super Cardioid Shotgun microphone connected to a Marantz PMD 430 stereo cassette recorder [frequency response 30 Hz - 15 kHz (3 dB with a signal to noise ratio of 75 dB)] was used for the audio recordings. All squeaking vocalizations (hereafter abbreviated SV) were recorded using Ampex 472 High Bias IEC Type II Studio audiocassettes.

The wolves were not fed during the watches, but food was generally available from the previous day's feeding. Whenever the wolves were visible in the clearing, video and audio recordings were made throughout the daytime; only audio recordings were made during the nighttime. Videotaping was conducted using wide-angle viewing during periods of inactivity or for group activities to ensure that the activity of all wolves was recorded. However, when squeaking was heard, the camera was focused on the area and on wolves that appeared to be squeaking. From the seven watches, 20 hours of video recordings and 12 hours of audio recordings were collected.

The watches were conducted by experienced wolf observers and divided into eight three-hour shifts. For the first two watches, recording began at 0500 and continued until 0500 the next day. However, the schedule was changed for the subsequent watches. Wolves are very active in the clearing at dawn and it was noticed that beginning the watches at this time seemed to affect their ongoing activities. They stopped their activity and watched as I approached the observation trailer to set up the recording equipment. To avoid this, the remaining five watches began at 0700 and continued until 0700 the following day.

Feeding watches. At CCWR, ongoing wolf social behavior is routinely videotaped from the observation trailer using a Hi-8 Sony CCD-TR600 Video Camcorder for one hour after feeding (early morning or late evening), three or four times per week. After the food is placed in the clearing, the wolves are videotaped whenever they are present in the clearing during the 1-hour period. The watch is terminated if no wolves are in the clearing for 20 consecutive minutes. Video recordings of these feeding watches from 1995, 1996 and 1997 yielded 126 hours of videotape for analysis.

With the exception of the summer 1997 when I videotaped most of the feeding watches, various other wolf researchers did the videotaping. In general, all types of social behavior were recorded, although the focus differed depending on the research project at the time. From August 1996 – December 1997, the project was this study and the taping focused on squeaking.

2.2.3 **Data Analysis**

2.2.3.1 Video Dubbing

24-hr watches. Hi-8 videocassettes were dubbed onto Sony ED T-120 videocassettes and analyzed using a NEC PC SuperVHS video recorder and an Electrohome color monitor. Each tape was viewed using standard play and all occurrences of SVs in each watch were noted. This process identified 259 SVs from the 20 hours of videotape. It was impossible to identify the squeaker and/or recipient(s) for 204 (68 % squeaker, 1% recipients, 31% squeaker and recipient) of these vocalizations. For the purposes of this study, it was necessary to have SVs with both the squeaker and recipient(s) identified. Therefore, only the 55 identified SVs were coded in detail, as described below.

Feeding Watches. Hi-8 videocassettes were dubbed onto Sony SVHS videocassettes, indexed (i.e., each frame was numbered), and analyzed using a NEC PC SVHS video recorder. To preserve the quality of the SVHS copies, a second tape was dubbed, indexed, and used for the initial viewing of the material to create a squeaking map. Each tape was viewed using standard play. Whenever an SV was heard, the index number and some descriptive information (location of squeaker; identity of squeaker and recipients, and the general activity) was recorded. This process identified approximately 2000 SVs. The squeaker and recipients could be identified for 513 of these, which were coded in detail (see below).

2.2.3.2 Coding

For each SV the following variables were coded:

Date: Date of watch.

Time/Index : For 24-hr watches, the time when all SVs began (hr, min) was recorded. For feeding watches, the index number at the beginning of each SV was recorded.

Identity: The identity of the squeaker was determined in two steps. First, the movements associated with an SV were noted; these included gaping motion of the lower jaw, movement of cheek muscles, or bellowing of rib cage. Secondly, the identity of the vocalizing wolf was determined.

Other Wolves (recipients): The recipients included any wolves that were visible in the clearing at the time of the SV unless the squeaking was obviously directed to one or more wolves.

Squeaking Vocalization Type: SVs were coded as group or individual vocalizations. A group SV occurred when more than one individual was observed or heard squeaking at the same time. An individual SV was one in which only one wolf was observed or heard squeaking at any given time.

Squeak Form: This category coded whether the squeak was an open mouth squeak, often involving gaping movements of the lower jaw, or a closed mouth squeak, involving the movement of cheek muscles or the bellowing action of the rib cage.

Social Context: This was defined by the social context in which the SV occurred. The squeaker was identified as a participant or an onlooker (Weir, 1994) in prosocial (play, greeting), status, and agonistic contexts. Separate coding was done for SVs that were directed to one or two wolves versus more than two wolves for prosocial (except howling) and food context categories.

1. PROSOCIAL (PR): These activities include all social behavior that is not considered agonistic (see below).

    a. Play (P): Play behavior includes such activities as body slamming, chasing, scruff biting, tail pulling, pinning, wrestling and so on (Bekoff, 1995). Although many of these activities are observed during aggression (see below), during play, these activities are frequently preceded by paw-raising and play-bows and there is no evidence of serious aggression (e.g., yelps, injury, etc.). The squeaker can solicit play, join ongoing play, or watch others play.

    b. Greeting (G): The squeaking wolf may squeak when approaching and then lick the muzzle of another individual or may squeak and then be approached and muzzle-licked by others.

    c. Conspecific (C): The squeaking wolf is facing one or more wolves in any area excluding the food area (see below), but there is no physical contact between individuals and no obvious social interaction.

    d. Howling (H): The howl is a continuous sound from .5 to 11 sec long. It consists of a fundamental frequency between 150 and 780 Hz, and has up to 12 harmonically related overtones. The frequency is usually constant or varies smoothly, and may change direction up to four or five times. The intensity does not vary greatly throughout (Theberge & Falls 1967). The squeaker may squeak as other wolves howl and may join the chorus howl.

    e. Yawn (Y): The squeaker can be sitting, lying, or standing alone (i.e., the squeaker is not engaged in any activity or obviously oriented to other wolves) and may yawn just before or after the SV.

2. FOOD (F): The squeaking wolf is near or in the food area, an area about two wolf lengths in diameter around the food source where one or more wolves are present and may/may not be eating. There is no physical contact between the squeaker and other wolves, nor obvious social interaction. Two possible situations were coded.

    a. Food-Squeaker Outside (F_O): The squeaker is in the clearing and the recipient(s) are in the food area.

b. Food- Squeaker Inside (F_I): Both the squeaker and recipient(s) are in the food area.

3. FOOD EXCITEMENT (FEX): The squeaking wolf (wolves) is (are) facing the food supply that may or may not be inside the enclosure. Squeaking may begin as food is brought through the gates or just after the person bringing the food leaves the enclosure. Squeaking occurs before or during the first approach to the food area by the squeaker(s) or by other wolves.

4. AGONISTIC (AG): Agonistic behaviors are defined as those associated with attack and defense (Poole, 1985). Hinde (1970, p.335) defines aggressive behaviors as "those behaviors which are directed from one individual toward another which could lead to serious injury and often results in settling status, or access to some object or space between the two". Fentress, Ryon, McLeod, and Havkin (1987) identified aggressive interactions as those where the initiator was observed raising hackles, biting, chasing, pinning, circling, lunging, raising tail, and forelimb wrestling. Recipients of such actions responded by wheeling and facing, tail tucking, fleeing, or reciprocating aggression. SVs occurred during or after two types of agonistic interactions.

    a. Fight (FT): A yelp is usually heard prior to the squeaking. The squeaker can be the recipient of the aggression or an onlooker. The aggressive interaction may or may not be over when the squeaking begins.

    b. Following/Chase (F/C): These squeaks occur immediately before a wolf is aggressively followed or chased by one or more different wolves. The squeaker can be the wolf being chased or followed or an onlooker watching the activity.

5. STATUS (STAT): Squeaking occurred during interactions in which the participants signal their social status by characteristic head, tail and body postures.

    a. Positive (+): The squeaker approaches a high-ranking wolf with body crouched, tail tucked and ears back. The low-ranking wolf may lick the muzzle of the dominant wolf.

    b. Negative (-): A high-ranking wolf approaches a lower-ranking wolf with tail raised, body high, and ears forward. The recipient, the squeaking wolf, may tuck its tail, lower its body, and leave the area. There is no physical contact between the two wolves.

6. PUP-CARE (PUP): The squeaking wolf and others are engaged in care-giving activities (playing, grooming, and muzzling) with the pup. This category includes squeaks that are directed to the pup from adults. (This context occurred in 1995 only because this was the only year in which a pup was born).

7. SEXUAL (SEX): This included squeaks directed from one member of the courting pair to the other and squeaks that occurred during courtship behaviors (genital sniffing, following the alpha female) in which one or both members of the pair were engaged with other members of the pack. The squeaker can be an onlooker (may or may not join the activity) or a participant.

8. MISCELLANEOUS (MISC): This included SVs in which the social context could not be determined accurately. This occurred when (1) the context was ambiguous (i.e., it was impossible to categorize the context as either one of two types) or (2) contextual information was not available to categorize the event (e.g., if the camera zoomed in on the squeaker preventing other wolves or activities from being observed).

Movement Context: The physical movement made by the squeaker during or within 5 sec after the end of the SV was coded. The following is a list and description of the coded movements.

1. GENERAL APPROACH (APP): A decrease in physical or social distance between squeaker and recipient(s) in one of four categories.
    a. <u>Approach</u> (AP): The squeaker approached or moved toward an area where one or more wolves were present.
    b. <u>Orient</u> (OR): The squeaking wolf was looking toward or the head was turned in the direction of one or more wolves.
    c. <u>Orient- Squeaker Approach</u> (OR-SAP): The squeaking wolf was oriented to one or more wolves during the SV and approached them.
    d. <u>Orient- Others Approach</u> (OR-OAP): The squeaking wolf was oriented to one or more wolves during the SV and was approached by them.

2. GENERAL LEAVE (LVE): An increase in the physical or social distance between squeaker and recipient(s) was coded into one of two categories.

    a. Leave (LV): The squeaker left or moved away from an area where one or more wolves were present.

    b. Orient -Squeaker Leave (OR-SLV): The squeaking wolf was oriented to one or more wolves during the SV and left or moved away from them.

3. OTHER: This category included all movements not included in the previous categories.

    a. Continuous (CONT): There was horizontal movement or orientation but no change in distance between squeaker and other wolves (following, parallel walking, chasing, etc.).

    b. Stationary Response (ST-RESP): There was no horizontal movement by the squeaking wolf, but it crouched in response to behavior from one or more wolves.

    c. Non-directional (ND): The squeaker was walking around, but its movement was not directed toward a particular wolf (random).

    d. No Movement (NM): There was no detectable horizontal or vertical movement; nor was there any obvious orientation.

2.2.4 **Statistical Analysis**

S-Plus 4.5 (MathSoft, Inc., 1998) and SPSS 8.0 (SPSS, Inc., 1998) were used for statistical analyses. For 24-hr watch data, chi-square tests were used to determine if the number of SVs was randomly distributed across (1) individuals and (2) social and movement contexts. Mann-Whitney U-tests were used to determine if the number of SVs was randomly distributed across gender and social rank.

For feeding watch data, analyses of variance (ANOVA) were used to determine the compare the number of SVs between social contexts and movement contexts with years as the replication factor. Chi-square tests were used to determine if the number of SVs was randomly distributed across individuals. Mann-Whitney U-tests were used to determine if the number of SVs was randomly distributed across gender and social rank.

2.3 RESULTS

2.3.1 24-hr Watches

On average squeaking was heard most often during the one to two hours before sunrise and the late afternoon/early evening hours before sunset (Fig. 2.1). Weather conditions during the 24-hr watches may have affected the frequency and timing of squeaking (Table 2.2, Fig. 2.2). During the first four watches, the temperature at noon was relatively cool; in contrast, the noon temperatures were quite warm during the last three watches. On three of the four cooler days the wolves were often in the clearing and squeaked during late morning and early afternoon. On all three of the hotter days, the wolves squeaked mostly in the early morning and late afternoon.

Of the 55 SVs in which both squeaker and recipient(s) were identified, 53 were individual SVs and two were group prosocial-play SVs. Only the 53 individual SVs are discussed below.

Wolves squeaked during a wide range of social and movement contexts (Table 2.3). SVs were not randomly distributed across the five general social contexts [$\chi^2 (4, N = 53) = 66.34, p < .01$; Fig. 2.3]; 64 % of the SVs occurred in prosocial contexts. Nor were SVs randomly distributed across the three general movement contexts [$\chi^2 (2, N = 53) = 32.18, p < .01$; Fig. 2.3]; 70 % of the SVs occurred during approach movements. Wolves

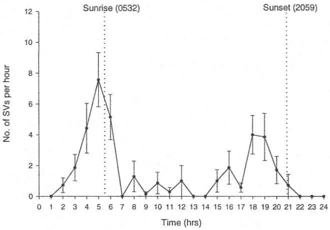


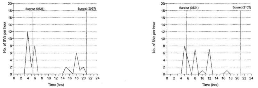
Figure 2.1 Circadian rhythm in the rate of squeaking (mean ± S.E.). The mean sunrise and sunset time is indicated (sunrise varied from 0524 to 0550; sunset varied from 2050 to 2105).

Table 2.2: A summary of the weather conditions recorded for each 24-hr watch.

Date	**Time of Watch**				
1997	**Beginning**	**Noon**	**Evening**	**Midnight**	**End**
June 5-6	Overcast, calm, 42°F	Rain, 46°F	Rain, 44°F, breezy	-	Clear, calm
June 13-14	Fog, calm, 48°F	Overcast, calm, 56°F	Overcast, calm, 56°F	Rain	Clear, calm, cool
June 19-20	Rain, calm, 57°F	Overcast, calm, 62°F	Overcast, light breeze, 62°F	Fog, calm	-
June 25-26	Fog, calm, 49°F	Sunny, light breeze, 70°F	Overcast, light breeze	Overcast, showers, calm	Overcast, breezy, cool
July 11-12	Sunny, 51°F	Sunny, breezy, 82°F	Sunny, light breeze, 74°F	Clear	Sunny, calm, cool
July 16-17	Sunny, calm, 48°F	Sunny, calm, 80°F	Overcast, calm, 70°F	-	Sunny, cool
July 24-25	Sunny, 40°F	Sunny, calm, 78°F	Sunny, calm	Clear, calm	Fog, calm, cool

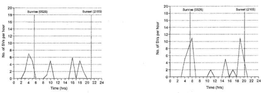
a. June 5, 1997

b. June 13, 1997



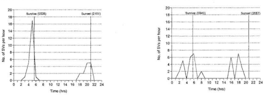
c. June 19, 1997

d. June 25, 1997



e. July 11, 1997

f. July 16,1997



g. July 24, 1997

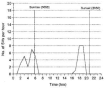


Figure 2.2 Circadian rhythm in the rate of squeaking for each 24-hr watch.

Table 2.3. 24-hr watches: The number of SVs identified in each social and movement context.

		Social Context																		
		Food				Prosocial								Agonistic		Status		FEX	Misc.	Total
		1-2 Wolves		>2 Wolves		1-2 Wolves			> 2 Wolves			Other								
Movement Context		F_I	F_O	F_I	F_O	C	P	G	C	P	G	Y	H	FT	F/C	+	-			
General	APP	0	1	0	2	3	1	2	3	0	0	0	0	0	0	1	0	0	0	13
	OR	0	2	0	1	7	1	0	4	0	0	0	0	0	0	0	0	0	4	19
	OR-SAP	0	1	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	4
	OR-OAP	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
General	LV	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3
	OR-SLV	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Other	CONT	0	0	0	0	0	2	0	0	0	0	0	0	2	2	0	0	0	0	6
	ST-RESP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
	ND	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	NM	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	3
Subtotal 1		**0**	**4**	**0**	**4**	**15**	**7**	**2**	**7**	**0**	**0**	**3**	**0**	**2**	**3**	**2**	**0**	**0**	**4**	**53**
Subtotal 2		**4**		**4**		**24**			**7**			**3**		**2**	**3**	**2**	**0**	**0**	**4**	
Total		**8**				**34**								**5**		**2**		**0**	**4**	

Note: Social Contexts: F_I - squeaker and recipients inside the food area, F_O - squeaker outside the food area and recipients inside, C - both squeaker and recipients in the clearing, G - greeting, P - play, Y - yawn, H - howl, FT - fight, F/C - follow or chase, Status + (positive), Status - (negative), FEX - food excitement, Misc. – miscellaneous. Movement Contexts: APP - approach, OR - orient, OR-SAP - orient and squeaker approach, OR-OAP - orient and others approach, LV - leave, OR-SLV - orient and squeaker leaves, CONT - continuous, ST-RESP - stationary response, ND - non-directional, NM - no movement.

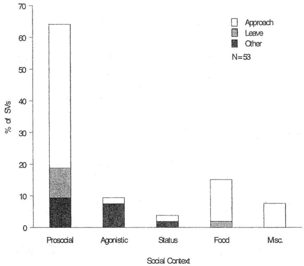


Figure 2.3. 24-hr watches: The percentage of SVs identified in each social and movement context.

squeaked most frequently when approaching other wolves in prosocial contexts. Because 45 % of the SVs occurred in the general prosocial-approach context, the distribution of SVs within the sub-categories of this classification was examined separately for prosocial activity and approach type. Overall, SVs were not randomly distributed across prosocial contexts [$\chi^2(2, N = 24) = 15.75, p < .01$;Fig. 2.4], nor across general approach contexts [$\chi^2(3, N = 24) = 10.33, p < .05$; Fig. 2.4]. Squeaking occurred more frequently as wolves approached or oriented to other wolves in the clearing than in any other prosocial-approach context.

There were differences in the frequency of squeaking among wolves (Table 2.4). Although all wolves were observed to squeak, squeaking was not randomly distributed across wolves [$\chi^2(6, N = 53) = 82.66, p < .01$]; Jasper, a sub-dominant male, squeaked more frequently than other wolves.

Some wolves squeaked in more social contexts than others (Fig. 2.5). For example, Jasper was identified as the squeaker in 57 % of the SVs in 9 of 12 social contexts, while Galen and Fiona were each identified as the squeaker in 1.9 % of the SVs and each squeaked only in one social context. Five of the seven wolves squeaked most frequently in the prosocial context. Celtie squeaked mostly in the agonistic context, whereas Galen's single SV was in the miscellaneous category.

Five of the seven wolves squeaked most frequently while approaching other wolves (Fig. 2.6). Celtie squeaked most frequently during continuous movements and 80% of those SVs were given when Celtie was the recipient of aggression. Fiona's single SV was in the yawn context as she was lying on the mound.

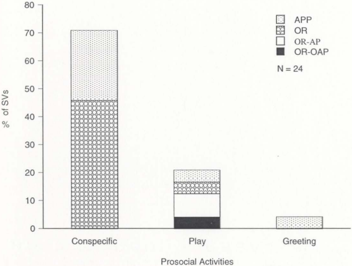


Figure 2.4. 24-hr watches: The percentage of SVs identified for each prosocial activity and type of approach.

Table 2.4. 24-hr watches: The number of SVs identified for each wolf in each social context.

	Social Context																		
	Food				Prosocial								Agonistic		Status		FEX	Misc.	Total
	1-2 Wolves		> 2 Wolves		1-2 Wolves			> 2 Wolves			Other								
	F_I	F_O	F_I	F_O	C	P	G	C	P	G	Y	H	FT	F/C	+	-			
G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	**1**
U	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	**3**
N	0	0	0	0	2	0	0	1	0	0	1	0	0	0	1	0	0	1	**6**
J	0	3	0	2	7	6	2	6	0	0	1	0	0	1	0	0	0	2	**30**
F	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	**1**
X	0	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	**4**
C	0	1	0	0	1	1	0	0	0	0	0	0	2	2	1	0	0	0	**8**
Total	**0**	**4**	**0**	**4**	**15**	**7**	**2**	**7**	**0**	**0**	**3**	**0**	**2**	**3**	**2**	**0**	**0**	4	**53**

Note: Social Contexts: F_I. squeaker and recipients inside the food area, F_O - squeaker outside the food area and recipients inside, C - both squeaker and recipients outside the food area, G - greeting, P - play, Y - yawn, H - howl, FT - fight, F/C - follow or chase, Status + (positive), Status - (negative), FEX - food excitement, and Misc. – miscellaneous. Refer to Table 2.1 for ID codes.

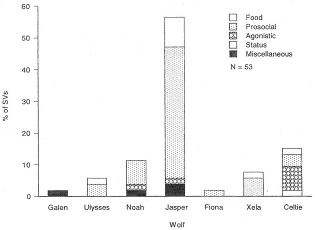


Figure 2.5 24-hr watches: The percentage of SVs identified for each wolf in each social context. Refer to Table 2.1 for wolf information.

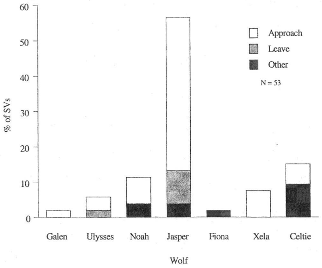


Figure 2.6. 24-hr watches: The percentage of SVs identified for each wolf in each movement context. Refer to Table 1 for wolf information.

Because Jasper squeaked substantially more than any other wolf, the observed trends may be due to Jasper. To test this possibility, the SVs of the remaining six wolves were analyzed separately. Overall, the same distribution patterns were observed. SVs were not randomly distributed across social [$\chi^2(4, N = 23) = 15.49, p < .01$] or movement contexts [$\chi^2(2, N = 23) = 11.14, p < .01$]. The highest frequency of squeaking occurred as the squeaker approached other wolves in the clearing (prosocial-conspecific). Prosocial-greeting was the only context in which Jasper was the sole squeaker (Table 2.4).

In terms of social rank, sub-dominant wolves appeared to squeak more frequently than the alpha pair. SVs were not randomly distributed across rank (dominant and sub-dominant) categories ($Z = -1.95, p < 0.05$). There was a general trend for the frequency of squeaking to increase with a decrease in the social rank of the wolves. With the exception of Jasper, there was no obvious difference in the frequency of squeaking between males and females. SVs were randomly distributed across sex ($Z = -0.18, p > .10$).

Before concluding that some wolves squeak more than others do, it is important to evaluate the role of potential artifacts. There was a possibility that some wolves were in the clearing more often than others, and therefore, were recorded squeaking more frequently. The data do not permit this question to be addressed directly. However, during 66% of the SVs, five or more of the seven wolves were present in the clearing and hence had similar opportunities to be observed squeaking.

Another potential artifact was that it may be easier to identify squeaking by some wolves. Sometimes wolves squeak with opened mouths and sometimes with closed mouths. It was much easier to identify open-mouth squeaking. If some individuals squeak more frequently with an open mouth, those wolves might be observed to squeak more frequently. An equal proportion of opened and closed mouth squeaking was observed (Table 2.5). Three wolves (Galen, Ulysses, and Xela) always squeaked with a closed mouth and one (Fiona) always squeaked with an opened mouth. The correlation between the proportion of open-mouth SVs and the total number of SVs identified for each individual was not significant [$r(5) = 0.28$, $p > .10$].

Of the 53 individual SVs, 22.6% occurred in playful or aggressive interactions. This number likely underestimates the frequency with which squeaking occurs during such social interactions. That is, play and aggression tend to involve a variety of fast-paced activities and movements, making it difficult to detect the essential movements that allow the squeaker to be identified. An estimate of the proportion of playful or aggressive interactions in which squeaking was observed versus those interactions in which no squeaking was observed should provide a better estimate of the rate of squeaking during play and aggression.

All playful and aggressive interactions from the seven watches were identified and the number in which squeaking was heard was counted (Table 2.6). In total, 50 playful interactions and 27 aggressive interactions were observed. Squeaking was heard immediately before or during 48 % of the play interactions. Six of the seven identified play SVs were from Jasper; and the other was from Celtie; the identified squeaker was a participant in six play interactions and an onlooker in the other one. Squeaking was heard during or immediately after 66.7 % of the aggressive interactions. Of the five

Table 2.5. The distribution of opened mouth, closed mouth, and opened mouth-closed mouth SVs for each wolf during the seven 24-hr watches. Refer to 2.1 for wolf codes.

Wolf	Squeak Form			
	Opened Mouth	Closed Mouth	Opened Mouth-Closed Mouth	Total
G	0	1	0	**1**
U	0	3	0	**3**
N	3	3	0	**6**
J	19	11	0	**30**
F	1	0	0	**1**
X	0	4	0	**4**
C	3	4	1	**8**
Total	**26**	**26**	**1**	**53**

Table 2.6: 24-hr Watches: The number of playful and aggressive interactions with and without SVs.

	Play	**Aggression**
Squeaking (ID)	7	5
Squeaking (No ID)	17	13
No Squeaking	26	9
Total	**50**	**27**

Note: Squeaking ID- the identity of the squeaker is known, Squeaker No ID- the identity of the squeaker is unknown, No Squeaking- no squeaks were heard.

identified SVs occurring during an aggressive interaction, four were from Celtie and one was from Jasper. In each case, the squeaker was the recipient of the aggression.

2.3.2 **Feeding Watches**

From the 126 hours of available video, approximately 2000 SVs were heard; the squeaker and recipient(s) could be identified for 513 (434 individual and 79 group SVs; Table 2.7). Initially the results were analyzed and described independently for each year. However, the same trends were observed and hence the results are presented for all three years combined. Appendices I, II, and III show the results for each year.

Of the 79 identified group SVs, 58 % were classified as food excitement squeaks, 18% occurred in prosocial contexts (of the 14 SVs, 9 were greeting; 4 conspecific; 1 howling), 15% occurred in food contexts, 7% occurred in agonistic contexts, and 1% occurred in sexual contexts. Group squeaking occurred most frequently immediately before or after the wolves were fed.

To determine whether individual SVs occurred more often in some contexts than others, the total number of SVs in each of the seven general social contexts and three general movement contexts was entered into an ANOVA with years as the replication factor. Both main effects and their interaction were statistically significant. Wolves squeaked significantly more frequently in food and prosocial contexts [F (6, 42) = 12.79, p < .001] and when approaching other wolves [F (2, 42) = 27.45, p < .001]. The significant interaction revealed that wolves squeaked most frequently when approaching other wolves during prosocial activities and at the food [F (12, 42) = 8.02, p < .001; Table

Table 2.7: A summary of the number of wolves, video data available for analysis, and the number of SVs identified for 1995, 1996, and 1997.

Year	Number of Wolves	Number of Watches	Hours of Video Available for Analysis	Number of SVs		
				Individual	Group	Total
1995 **(Jan. - Dec.)**	Jan. - April: 12 May - Dec.: 13*	92	48	144	45	189
1996 **(Jan.- Sept.)**	13	61	36	102	24	126
1997 **(Jan. – Dec.)**	Jan.: 13 Feb. - May: 8 June - Dec.: 7	83	42	188	10	198
Total	-	**236**	**126**	**434**	**79**	**513**

* A pup was born in May, but pup squeaks were not coded.

2.8, Fig. 2.7]. Because 69 % of the SVs occurred within the sub-categories prosocial-approach and food-approach, two additional analyses were performed.

To determine whether squeaking occurred during some prosocial contexts more than others, the total number of SVs identified during each of the three prosocial activities (P, G, C), directed toward either one or two wolves or a group of wolves, and four types of approach (AP, OR, OR-SAP, OR-OAP) was entered into an ANOVA with years as the replicating factor. There was no significant difference between the number of SVs directed toward one to two wolves versus a group (greater than two wolves) [F (1, 48) = 0.01, p > .05]. Wolves squeaked significantly more during conspecific activities than during play or greeting [F (2, 48) = 20.69, p < .001]. Wolves squeaked during all types of approach but significantly more frequently when they oriented to other wolves [F (3, 48) = 6.69, p < .001]. The significant interaction, shown in Figure 2.8, revealed that wolves squeaked most as they oriented to other wolves (conspecifics) in the clearing [F (6, 48) = 7.81, p < .001].

Figure 2.9 shows the number of SVs identified in each food context that was directed to one or two wolves versus a group of wolves. It was extremely rare for wolves to squeak when approaching one or two wolves at the food. Because only five SVs were identified in this situation, squeaking when approaching one or two wolves at the food was not included in the following analysis. To determine whether squeaking involving more than two wolves occurred during some food contexts more than others the total number of SVs identified during the two food contexts (F_I, F_O) and three types of approach movement (AP, OR, OR-SAP; OR-OAP did not occur in food contexts) was

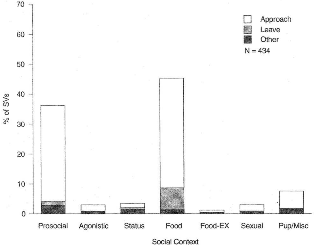


Figure 2.7. Feeding watches: The percentage of SVs identified in each social and movement context.

Table 2.8. Feeding Watches: The number of SVs identified in each social and movement context.

Movement Context		Social Context																					
		Food				Prosocial																	
		1-2 Wolves		>2 Wolves		1-2 Wolves			> 2 Wolves			Other		Agonistic		Status		FEX	SEX	Pup Care		Misc	Total
		F_I	F_O	F_I	F_O	C	P	G	C	P	G	Y	H	FT	F/C	+	-			C	P		
General Approach	APP	0	0	3	70	11	3	6	8	4	5	0	0	1	0	2	0	0	2	1	0	0	116
	OR	0	3	2	53	21	5	0	26	6	0	0	0	3	5	0	0	3	2	1	0	16	146
	OR-SAP	0	2	2	24	5	5	2	8	0	6	0	0	0	0	1	0	0	6	0	4	1	66
	OR-OAP	0	0	0	0	7	3	1	1	1	5	0	0	0	0	0	3	0	0	1	1	0	23
General Leave	LV	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3
	OR-SLV	1	2	7	21	3	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	38
Other	CONT	0	0	0	0	2	0	0	0	0	0	0	4	0	4	0	4	0	3	0	0	0	18
	ST-RESP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	1	4
	ND	0	1	2	3	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	6	14
	NM	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	6
Subtotal 1		**1**	**8**	**16**	**172**	**50**	**16**	**9**	**45**	**11**	**16**	**6**	**4**	**4**	**9**	**3**	**12**	**5**	**14**	**3**	**5**	**6**	**434**
Subtotal 2		**9**		**188**		**75**			**72**			**10**		**4**	**9**	**3**	**12**	**5**	**14**	**3**	**5**	**6**	
Total		**197**				**157**								**13**		**15**		**5**	**14**	**8**		**25**	

Note: Social Contexts: F_I - squeaker and recipients inside the food area, F_O - squeaker outside the food area and recipients inside, C - both squeaker and recipients in the clearing, G - greeting, P - play, Y - yawn, H - howl, FT - fight, F/C - follow or chase, Status + (positive), Status - (negative), FEX - food excitement, SEX - sexual, Misc. – miscellaneous. Movement Contexts: APP - approach, OR - orient, OR-SAP - orient and squeaker approach, OR-OAP - orient and others approach, LV - leave, OR-SLV - orient and squeaker leaves, CONT - continuous, ST-RESP - stationary response, ND - non-directional, NM - no movement.

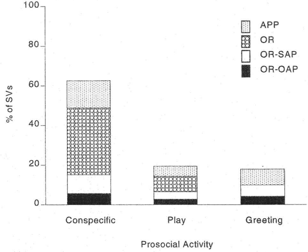


Figure 2.8. Feeding watches: The percentage of SVs identified for each type of prosocial activity and type of approach. (APP - approach, OR - orient, OR-SAP = orient and squeaker approach, OR-OAP - orient and others approach).

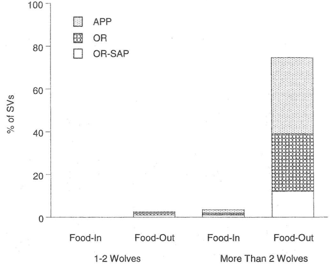


Figure 2.9. Feeding Watches: The percentage of SVs identified for each type of food activity and type of approach. (APP - approach, OR - orient, OR-SAP - orient and squeaker approaches).

entered into an ANOVA with years as the replication factor. Wolves squeaked significantly more when the squeaker was outside the food area [$F(1, 12) = 22.12$, $p < .001$]. However, there was no significant difference between the three types of approach [$F(2, 12) = 1.90$, $p > .05$].

All wolves were observed squeaking but SVs were not distributed randomly across wolves [χ^2 (12, $N = 434$) $= 1435.4$, $p < .001$; Table 2.9]. Jasper squeaked most frequently and in the greatest variety of contexts (56 % of the SVs in all social contexts). Of the 242 SVs by Jasper, 128 were directed to wolves that were at the food. In fact, 8 of 13 wolves squeaked most frequently in this context. Galen, Noah, Morgaine, and Xela squeaked most frequently in prosocial contexts. Tess squeaked most frequently as an onlooker in agonistic contexts. SVs were randomly distributed across social rank (dominant versus sub-dominant wolves) ($Z = -0.594$, $p > .05$) and sex ($Z = -1.719$, $p > .05$).

Wolves also varied in their frequency of squeaking depending on their role in social interactions (Table 2.10). The squeaker was most likely an initiator or an onlooker in playful interactions, an initiator in greeting interactions, a recipient or an onlooker in aggressive interactions, and a recipient in status interactions.

Similar patterns in the distribution of SVs across context, sex and social rank were observed when the contribution from Jasper was removed from the analysis. Squeaking occurred most frequently as wolves were approaching other wolves in prosocial and food contexts [$F(12, 42) = 5.44$, $p < .001$]. Furthermore, no significant differences were

Table 2.9: Feeding Watches: The number of SVs identified for each wolf in each social context.

ID	Social Context																				Total
	Food				Prosocial								Agonistic		Status		FEX	SEX	Pup Care		Misc.	
	1-2 Wolves		> 2 Wolves		1-2 Wolves			> 2 Wolves			Other											
	F_I	F_O	F_I	F_O	C	P	G	C	P	G	Y	H	FT	F/C	+	-			C	P		
G	0	0	2	2	2	0	0	1	2	2	0	0	0	0	0	0	0	2	0	0	2	15
V	0	0	0	7	2	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	11
H	0	1	1	9	2	0	0	3	0	0	0	0	0	1	0	0	1	2	0	0	2	22
N	0	0	0	4	6	2	0	3	0	2	1	1	0	0	1	7	1	4	0	0	5	37
U	0	1	0	7	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	13
J	0	3	13	112	22	13	8	25	9	10	5	0	1	0	2	1	2	3	1	2	10	242
P	0	0	1	7	1	0	0	1	0	0	0	0	3	0	0	0	0	0	2	1	3	19
D	0	0	0	11	4	0	0	5	0	0	0	2	0	0	0	0	0	1	0	2	0	25
M	0	0	0	1	1	1	1	1	0	1	0	0	0	0	0	2	1	1	0	0	2	12
T	0	0	0	3	0	0	0	0	0	0	0	1	0	5	0	0	0	0	0	0	0	9
F	0	1	0	4	0	0	0	2	0	1	0	0	0	2	0	1	0	0	0	0	1	12
C	1	2	0	1	3	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	8
X	0	0	0	3	3	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	9
Total	**9**		**188**		**75**			**72**			**10**		**4**	**9**	**3**	**12**	**5**	**14**	**3**	**5**	**25**	**434**

Note: Social Contexts: F_I - squeaker and recipients inside the food area, F_O - squeaker outside the food area and recipients inside, C – both squeaker and recipients in the clearing, G - greeting, P - play, Y - yawn, H - howl, FT - fight, F/C - follow or chase, Status + (positive), Status - (negative), FEX - food excitement, SEX - sexual, Misc. - miscellaneous. Refer to Table 2.1 for wolf information.

Table 2.10. Feeding Watches: The number of SVs that occurred during playful, greeting, aggressive, and status interactions in which the squeaker was a participant or onlooker in the interaction.

	Participant			Onlooker	Total
	Initiator	Recipient	Joiner		
Play	11	0	4	12	**27**
Greeting	17	2	6	0	**25**
Aggression	0	5	1	7	**13**
Status	3	12	0	0	**15**
Total	**31**	**19**	**11**	**19**	**80**

observed in the distribution of SVs across social rank ($Z = -1.385$, $p > .05$) or sex ($Z = 0.862$, $p > .05$).

2.4 DISCUSSION

Before discussing the results, it is appropriate to consider the strengths and weaknesses of captive studies such as the present one. The main weakness is that captivity typically imposes serious limitations on some behaviors of captive animals, and hence, there is great concern as to the applicability of captive data to wild populations. At CCWR, the wolves are not handled, nor are they on public display; in addition, they live in a 3.8 hectare, heavily forested area, which provides for a high degree of privacy that is absent in most other captive situations. Nonetheless, the wolves cannot hunt, nor can they leave the pack, both of which are important aspects of the lives of wild wolves (Harrington & Paquet, 1982). The strength of captive research is that one can investigate behaviors which are impossible to study in the wild, provided that conditions for normal expression of behavior exist (Klinghammer & Laidlaw, 1979). Because it is almost impossible to get close to or keep up with a pack of free-ranging wolves, much less to identify individuals and their status (Harrington & Paquet, 1982), many social behaviors can be adequately studied only in captivity where it is possible to get close enough to observe the behavior of known individuals.

Social behavior is best studied through a combination of field and captive research (Klinghammer & Laidlaw, 1979). Such an approach has been effectively used in the study of howling (Theberge & Falls, 1967; Harrington & Mech, 1978; Klinghammer & Laidlaw, 1979; Harrington, 1987). Because squeaking is a close-range vocalization that is audible over very short distances, there are no studies of squeaking on free-ranging wolves. There are only limited references to squeaking in natural history descriptions of wolf behavior (Crisler, 1958; Mech, 1970). Even our knowledge about squeaking in captivity is very minimal, being limited to a few studies on a small number of hand-reared wolves. The value of this captive study is that it provides the first extensive account of the contexts of squeaking in an intact pack over a three year period. The next step will be to use these results to guide the development of a study of squeaking in wild wolves.

From this study we can conclude that (1) some wolves squeak more frequently than others (throughout the entire study period Jasper squeaked more than all others), (2) wolves squeak in a range of social and movement contexts, but especially when approaching other wolves in prosocial (approaching any number of wolves in the clearing) and food contexts (outside the food area approaching a group of wolves), (3) there are no obvious sexual differences in the frequency of squeaking, and (4) social rank may be important; sub-dominant wolves squeaked significantly more than the alpha pair during the 24-hr watches. From the 24-hr watches, it can also be concluded that (5) wolves squeak most frequently during the dawn and late afternoon hours, corresponding to times when they were most often visible in the clearing.

Only squeaking that occurred in the clearing was recorded and analyzed in this study, yet this clearing represents only a small part of the enclosure. Little is known about the behavior and activity patterns of the wolves when they are not in the clearing. It is possible that squeaking occurs in contexts that did not occur in the clearing and that squeaking occurred at times other than those observed in this study. However, the contexts observed here do overlap with those reported by others (Harrington & Mech, 1978; Fentress et al., 1978; Field, 1979).

Over the course of this investigation there were major changes in the social structure of the pack. During the mating season of 1997, the pack was reduced from 13 wolves to seven wolves. The death of the longtime alpha female, Pawnee, lead to fighting between females for the alpha position, which resulted in the death of three females. There is no doubt that this was a very intense time for all members of the pack, particularly the subdominant wolves. It is possible that this social instability may have affected the frequency and distribution of squeaking between wolves and social contexts reported in this study. However, an examination of the results obtained separately for each year revealed the same trends as was reported for all three years combined (Appendix I – III). In each year, Jasper squeaked significantly more than any other wolf suggesting that frequent squeaking is a characteristic of Jasper's "personality" rather than a artifact of intense social discord within the pack. Similarly, in each year, wolves squeaked most frequently when approaching other wolves at the food and during prosocial activities.

The frequency of squeaking during courtship is likely to be underestimated in this study because very little courtship behavior occurred during the 1997 breeding season (Jenny Ryon, personal communication). A comparison of the number of squeaking vocalizations recorded during courtship behavior for each year of the study (SEX category of Table 1, Appendix I-III) reveals that courtship squeaks were observed more frequently in 1995 (a pup was born) than in 1996 or 1997 indicating that more courtship behavior may have occurred during the breeding season of 1995. More generally, it is important to note that the results of this study show the activities and contexts during which wolves squeak the most. It does not show the activities or contexts of which squeaking is an integral part. For example, squeaking maybe essential to courtship activities, although in this study, squeaking was seldom heard in this context, mainly because courtship seldom occurred during my observations.

Determining the importance of squeaking to different types of behaviors requires activity budgets for each wolf so that it would be possible to calculate the rate of squeaking per time at an activity. This was not possible with the current data set. However, it was possible to address the importance of squeaking during play and aggression somewhat by looking at the percentage of times wolves squeaked during these interactions for the 24-hr watches only. Squeaking was heard during 48% of the playful interactions and 67 % of the aggressive interactions suggesting that it may be an important part of these activities.

It has been suggested that information contextual to a signal (e.g., vocalization) can provide insight into the meaning or function of the signal (Smith, 1977; Dawson, 1991). Although the relationship between context and function is complex, an examination of the social and movement contexts of squeaking may aid in determining the function(s) of squeaking for wolves. Squeaking occurred predominately in friendly social and movement contexts (prosocial and food). The underlying message in all of these contexts seems to be a friendly motivation on part of the squeaker. Furthermore, it is usually accompanied by a decrease in the physical or social distance between the squeaker and recipient.

The richness and complexity of this vocalization (see Chapter 3) suggests that specific information may be encoded in the squeak signal in different social and movement contexts. In prosocial contexts, squeaking may inform others of a willingness to interact (play, greeting) or acknowledge another wolf's presence (conspecific). Squeaking while approaching or orienting to other wolves at food may function to inform other wolves that the individual is approaching the food. Squeaking in this context may also serve as a location signal. If the receivers at the food are not facing the squeaking individual, they can not see who is approaching. Even if they were facing the approaching animal, they have their heads down attending to food. Squeaking while approaching others at food thus may inform the others of the location, identity (individual, familiar/unfamiliar, pup/adult, sub-dominant/dominant) and motivation (non-aggressive, friendly) of the approaching wolf. An analysis of the acoustic structure of squeaking is needed to determine if such information is potentially available (see Chapter 3). It is also possible that, by squeaking, the approaching wolf is trying to determine if it is okay to approach the food source more closely. It was common for squeaking wolves to approach others at the food, stop, turn and walk away. This could occur several times before the squeaking wolf actually entered the food area and began eating. Perhaps, upon approach, the squeaker perceived a subtle aggressive signal from another wolf (maybe a more dominant wolf) that informed the squeaker that it was not okay to approach. The absence of an aggressive signal, or the presence of a friendly signal, may account for the squeaker proceeding to the food and eating. Although I did not notice such signals by wolves at food, there were no instances observed when wolves in the food area chased or attacked an approaching wolf that was squeaking, suggesting that wolves only approached closely when there was little threat of being attacked. A closer examination of the behavior of the other wolves at the food while the squeaker is approaching may provide insight into this hypothesis.

During agonistic and negative status contexts, the squeaker was most often the recipient of the interaction. The individual squeaked when being approached, most often by a more dominant wolf. In several interactions, the individual squeaked and attempted to increase the distance between itself and the more dominant wolf. In this context, squeaking may serve to indicate the non-aggressive motivation of the squeaker and to minimize aggression from the receivers. In many other agonistic interactions, the squeaker was an onlooker observing aggression between two or more wolves. Squeaking in this context may serve to provide a more relaxed friendly atmosphere to replace the tense aggressive one.

Although some wolves squeaked more frequently than others, it is important to note that all wolves squeaked. Young and old, dominant and sub-dominant, male and female wolves squeaked. There was a trend for sub-dominants to squeak more than the alpha pair. This observation may have led some earlier researchers to suggest that squeaking might be a submissive vocalization (Joslin, 1966, cited in Mech, 1970; Fox, 1971). A more likely interpretation is that squeaking indicates interest in interacting with the alpha wolf. That is, if squeaking signals to decrease the physical or social distance between wolves, it is understandable that sub-dominants might vocalize more often than the alpha pair. The alpha wolves are often the recipients of prosocial activity. Their presence in the group is enough to elicit excitement and activity. I have often seen a group of wolves rise from resting when the dominant male or female walked by. Without any obvious signal from the alpha member, the sub-dominants would squeak, muzzle, approach, and attempt to play with the dominant animal. The squeaking, combined with other friendly visual displays, may serve to indicate an eagerness to interact with the alpha wolf rather than to signal submission.

If squeaking truly is a submissive behavior, low-ranking wolves might be expected to squeak more frequently to higher-ranking wolves. Three observations are inconsistent with a submissive interpretation of squeaking. First, although it was often difficult to identify the specific recipient(s) because all wolves in the clearing were potential recipients, much of the squeaking was directed from one sub-dominant wolf to another, often of lower rank. Second, squeaking directed from lower-ranking wolves to higher ranking wolves, identified in status contexts, occurred less frequently than squeaking directed to other wolves, often sub-dominant wolves, in the clearing. This is evident (although to make a statistical argument would require base-rate probabilities) if we compare the number of squeaking vocalizations that occurred in status contexts and the number of squeaking vocalizations that occurred in prosocial-conspecific contexts (24-hr watches - 2 status, 21 conspecific; feeding watches- 15 status and 95 conspecific). Third, if squeaking is a submissive behavior, a change in social status should complement a change in the frequency with which an individual squeaks. In 1995 and 1996, Fiona was a low-ranking wolf and was identified as the squeaker for only 2% of the squeaking vocalizations. In 1997, she became the alpha female and was identified as the squeaker in 3.7%. These observations suggest that squeaking is a friendly, social behavior rather than a submissive behavior.

In summary, the results of this study suggest that squeaking may play an important role in the social processes of wolves. Squeaking is a part of many of the daily activities of wolves and seems to play a role in coordinating social interactions within the pack. It is involved in assembling wolves for group activities (greeting, play, howling) and maternal recognition (Goldman et al., 1995). Squeaking during agonistic and status situations may serve to prevent or minimize serious aggression, which helps maintain stability in the social hierarchy. Squeaking is a friendly vocalization that occurs in a diversity of social and movement contexts. The underlying meaning seems to be the friendly motivation of the squeakers and their willingness to interact with other members of the group. Additional information such as the identity and location of the sender is potentially available to the receivers in some contexts. An analysis of the acoustic variation in squeaking among wolves and among contexts will help determine if such information is available (See Chapter 3).

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Chapter 3 The Sound of Squeaking

3.1 INTRODUCTION

Squeaking is a soft, high frequency, affiliative vocalization that is emitted in series by wolves, *Canis lupus*. Wolves squeak most frequently during the dawn and late afternoon hours in prosocial, agonistic, food, courtship, and status contexts, but most frequently as they are approaching or orienting to other wolves during prosocial activities and to other wolves that are at the food (see Chapter 2). The underlying message of the squeaking vocalization seems to be the friendly motivation of the squeakers and their willingness to interact with others. Analysis of the acoustic structure of this vocalization may determine if information, such as the identity of the squeaker and contexts, is available.

Acoustic structure and variation are especially important in the communication of mammals (Miller & Murray, 1995). Social mammals in particular often have complex, repertoires in which different vocalizations can be merged or combined with visual and olfactory information to produce communication systems that can vary considerably both within and between individuals. Acoustic analysis has been used to determine which frequency and/or temporal variables distinguish among individuals within a species. In order for a variable to act as a potential carrier of information about individuality, the intra-individual variance should be small compared to the inter-individual variation of the same variable (Epsmark, 1975). In some species, individuals can be distinguished based on a few variables such as fundamental frequency (the howl of wolves, Tooze, Harrington, & Fentress, 1990). In other species, a combination of variables may be needed such that each individual has a unique profile of acoustic characteristics that can be distinguished from other individuals (the contact vocalization of the emperor penguin, *Aptenodytes forster* , Robisson, Aubin & Bremand, 1993; mutual display vocalization of the greater flamingo, *Phoenicopterus* ruber, Mathevon, 1997).

The acoustic structure of mammalian vocalizations can be complex, as energy is spread over a wide frequency range, and the frequency structures are often modulated within a given vocalization (Schrader & Hammerschmidt, 1997). Thus, it can be difficult to determine which variables to measure to characterize the information in a vocalization. Despite this difficulty, researchers have found individuality in the vocalizations of many mammals, including the whistles of bottlenose dolphins, *Turnips truncatus* (Caldwell & Caldwell, 1965; Tyack, 1986; Sayigh et al., 1998), the threat vocalizations of male elephant seals, *Mirounga angustirostris* (Shipley, Hines, & Buchwald, 1981), the roars of male harbour seals, *Phoca vitulina* (Hanggi & Schusterman, 1994), the pup vocalizations of grey seals, *Halichoerus grypus* (Caudron, Kondakov, & Siryanov, 1998), the screams of sea otters, *Enhydra lutris* (McShane, Estes, Riedman, & Staedler, 1995), the bleats of reindeer, *Rangifer tarandus* (Epsmark, 1975), the groans of fallow deer, *Dama dama* (Reby, Joachim, Lauga, Lek, & Aulagnier, 1998), the grunts of domestic pigs, *Sus scrofa* (Schon, Puppe, Gromyko, & Manteuffel, 1999), the short vocalization of pikas, *Ochontona princeps* (Conner, 1985), and the isolation vocalization of Mexican free-tailed bats, *Tadarida b. mexicana* (Gelfand & McGraken, 1986).

Perhaps the most extensive work on individual variation and individual recognition has been done with primate vocalizations, including the contact vocalizations of pygmy marmosets, *Cebuella pygmaeca* (Snowdon & Cleveland, 1980), the long vocalizations common marmosets, *Callithrix jacchus* (Jorgensen & French, 1998), the contact vocalizations of ringtailed lemurs, *Lemur catta* (Macedonia, 1986), the advertisement vocalizations of male mouse lemurs, *Microcebus murinus* (Zimmerman & Lerch, 1993), the coo vocalization of rhesus macaques *Macaca mulatta* (Hauser, 1991), the disturbance vocalizations of barbary macaques, *Macaca sylvanus* (Fisher, Hammerschmidt, & Todt, 1995), and the long vocalizations of red-chested tamarins, *Saquinus l. labiatus* (Maeda & Mastaka, 1987).

Information, in addition to that concerning individuality, may also be encoded in vocalizations (Struhsaker, 1967; Green, 1975). Vocalizations that were previously considered unitary in several mammalian species have been found to vary with subtle differences in social context in which the vocalizations were made (Lillehei & Snowdon, 1978). By using playback experiments, researchers have since demonstrated that these variations are detected by the animals. Contextual variation, that is subtle variation between contexts, may allow the vocalization to mean different things in different contexts.

Consider the case of vervet monkeys, *Cercopithecus aethiops*. They produce acoustically different alarm vocalizations in the presence of each of their four main predators: leopards, eagles, snakes, and baboons and respond with behaviorally appropriate escape responses (Struhsaker, 1967). In fact, even in the absence of actual predators, vervet monkeys respond appropriately to playbacks of recordings of three of these alarm vocalizations suggesting that these vocalizations may be representational or referential signals (Seyfarth, Cheney, & Marler, 1980a).

Japanese macaques, *Macaca fuscata*, have seven variants of the coo vocalization that are used in ten different contexts (Green, 1975) and they can learn to discriminate between two of the coo variants (Zoloth et al., 1979). Similar contextual variation has been found in the coo vocalization of stumptail macaques, *Macaca artoides* (Lillehei & Snowdon, 1978), the trill vocalization of pygmy marmosets (Pola & Snowdon, 1975; Snowdon & Pola, 1978), the long vocalizations and chirps of cotton-top tamarins, *Saguinus oedipus* (Cleveland & Snowdon, 1982; Snowdon, Cleveland, & French, 1983; Bauers & Snowdon, 1990), the grunts of baboons, *Pabio ursinus* (Rendell, Seyfarth, Cheney, & Owren, 1999), and the shrill barks of barbary macaques, *Macaca sylvanus* (Fisher, 1998).

The family Canidae consists of approximately 35 species categorized into 15 genera (Sheldon 1992). Social organization in canids ranges from relatively solitary to highly social. The wolf, dhole (*Cuon alpinus*), and African wild dog (*Lycaon pictus*) are highly social and hunt in packs. Others are moderately social (e.g., coyote, *Canis latrans*, golden jackal, *Canis aureus*). The basic social unit is the mated pair and their offspring. Perhaps the least social of all canids are foxes of the genus *Vulpes*; they usually have only a temporary pair bond and the young disperse at 5-6 months of age (Fox, 1971; Fox & Cohen, 1977).

Vocal individuality is likely to be important in the maintenance of pack structure and cohesion for the highly social canids. Individuality in long-range vocalizations, such as howling, can help separated members find their way back to their pack, help individuals avoid potentially dangerous interactions, and can help dispersing individuals find mates and territories without aggressive encounters by avoiding territories of alien packs and individuals (Tooze et al., 1990). Individuality in close-range vocalizations may aid in parent-offspring recognition and may help maintain pack cohesion, as well as controlling or coordinating pack dynamics. Despite the social demand for individual recognition, relatively few vocal signatures have been identified in canids. To date, vocalizations of Arctic foxes (*Alopex lagopus*), dholes, and wolves have been examined.

Within the fox-like canids, the Arctic fox seems to exhibit the most complex social system. Groups may consist of one adult male with one or more females who may live together with the young of that year. Family groups maintain territories, which are marked by scent, visual displays and vocalizations (Sheldon, 1992). One such vocalization, called territorial barking, occurs in a series and is transmitted over long distances. Frommolt, Kruchenkova, and Russig (1997) used univariate and multivariate analyses of variance and discriminate function analysis to assess individuality in the barks. They found significant differences between four individuals in 46 of 54 measured variables. Most of the differences were found in the frequency variables. The discriminant function analysis correctly assigned 91% of the barks to individual animals.

Dholes are highly social animals, comparable in the degree of their sociality to African wild dogs and wolves. They use a repetitive whistle vocalization to maintain pack cohesion in dense habitats (Fox, 1984; Sheldon, 1992). Durbin (1998) recorded 62 whistle bouts from captive dholes and used cross correlation and discriminant analysis to distinguish between five individuals. Of the various frequency and temporal variables measured, the period from the start of one syllable to the next, fundamental frequency, and maximum frequency were the important discriminatory variables.

Several researchers have investigated individual variation in the howling of wolves and agree on the presence of vocal signatures in howls (Theberge & Falls, 1967; Klinghammer & Laidlaw, 1979). Most recently, Tooze et al. (1990) found that wolves have individually distinct howls and that they discriminated between vocalizations from familiar and unfamiliar wolves. Similarly, Harrington (1986) found that adults and pups discriminated between adult and pup howls and both replied significantly more often to adult howls.

Although the number of studies of individuality in canid vocalizations is limited, individuality does appear to be coded in the long-range vocalizations of some canid species. Individuality may also be encoded in close-range vocalizations such as squeaking. The squeaking vocalization is composed of one or more squeaking phrases, each of which is comprised of one or more individual squeaks. Individual squeaks are brief (usually less than 300 msec), low-amplitude sounds with energy typically between 2 and 4 kHz. (Fig 3.1; see Methods).

Research on captive wolves has revealed a great deal of variation within the squeaking vocalization of individuals. Whether this variability is due to differences between individuals, differences between classes of individuals (e.g., age, sex, social

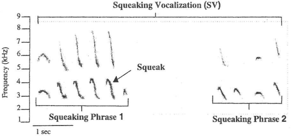

Figure 3.1. Example of a squeaking vocalization (SV) containing two squeaking phrases (SP), each of which is composed of individual squeaks. The inter-phrase interval (IPI) is measured from the end of the last squeak in the first phrase to the beginning of the first squeak in the next phrase. The inter-squeak interval (ISI) is measured from the end of one squeak to the beginning of the next squeak.

position) or the context of the vocalization has not yet been established. Fentress, Field and Parr (1978) defined squeaks loosely as high frequency (>2 kHz), tonal sounds and, based on qualitative observations, reported that squeaks from one wolf varied in form as the context changed. For example, squeaks made during group howling appeared longer in duration and appeared to have greater frequency modulation than those uttered when one wolf approached another. Within the same context, however, squeaks from several wolves appeared strikingly similar in structure.

In an attempt to define squeak variability quantitatively, Field (1979) examined squeak-type sounds that were made by an adult male, an adult female, and two pups in a single social context. The context was the reduction of distance between the vocalizing wolf and a familiar human. In comparison to the male's squeaks, the female's had higher mean frequency and duration and showed more variability in frequency. Squeaks from the two adults were grouped and compared to squeaks from the two pups. Pup squeaks had higher mean frequencies, longer mean durations, and greater mean frequency fluctuations than adult squeaks. Because squeaks from only a few wolves were compared, it is difficult to determine whether the variation reported is due to differences between individuals or between classes of individuals (e.g., sex, age).

Goldman, Phillips, and Fentress (1995) investigated the possibility of an acoustic basis for maternal recognition in wolves. They analyzed the squeaks and behavior of the mother and another adult female wolf while tending to a litter of pups during the first five postnatal weeks. They found that the two females could be identified based on the acoustic properties of their squeaks. Sound analysis revealed that the distributions of the fundamental frequencies of their squeaks were non-overlapping. In addition, they found that squeaks emitted outside the den that were associated with pups exiting the den had fundamental frequencies wholly within the mother's range. This result suggests that the pups were able to identify the mother, possibly based on the fundamental frequency of her squeaks, and that the fundamental frequency of a squeak may be an important acoustic cue available for individual recognition. This study hints that wolves may have individually identifiable squeaks that can be distinguished by their fundamental frequency.

The squeaks analyzed in previous studies were those given by only a few animals (three in Fentress et al., 1978; four in Field, 1979; and two in Goldman et al., 1995) in a maximum of three different contexts in a captive setting. Furthermore, only a few sound variables were measured (three in Field, 1979; one in Goldman et al., 1995) and, with the exception of Goldman et al. (1995), the study animals were socialized to humans. Despite these limitations, these studies provide valuable preliminary evidence to suggest that the variability in the structure of squeaks seems to follow changes in the accompanying context and hints that the squeaking vocalization may be important in individual recognition.

Individuality in such a close range vocalization could be useful to wolves, a very social species that lives in packs consisting mostly of family members. Wolves cooperate in virtually all aspects of daily living such as hunting, raising young, and traveling. Living socially demands effective communication. Individual recognition by any means (visual, auditory, or olfaction) would increase the efficiency and accuracy of communication within the pack. Individual recognition by vocal individuality may be more important in some contexts than in others. For example, it is easy to imagine why it would be important for pups inside the den to recognize the vocalization of their mother from outside the den. If squeaking does signal the time for the pup to exit the den (Goldman et al., 1995), it would be crucial for the pup to be able to distinguish between its mother's squeaking vocalizations and those of another wolf. In addition, individual recognition would be very important in situations where other visual or olfactory cues may not be available, such as when a wolf approaches other wolves from behind while they are eating, interacting in the forest, or during the night. Finally, individual recognition [through squeaking] may enable individuals to recognize potential playmates or to maintain contact with individuals who have recently been involved in affiliative social interactions (Hauser, 1991).

To summarize, there is circumstantial evidence which enables us to predict that wolves would have individually identifiable squeaking vocalizations that vary in different social contexts. Wolves are physically able to produce and perceive individual differences in vocalizations (Asa & Mech, 1995). Past research has demonstrated the presence of vocal individuality and group recognition (possibly individual recognition) in howls (Theberge & Falls, 1967; Klinghammer & Laidlaw, 1979; Tooze et al., 1990). Preliminary evidence suggests that wolves produce different squeak variants in different social contexts (Fentress et al., 1978) and there is a hint that wolves may have individually identifiable squeaks (Field, 1979; Goldman et al., 1995). Furthermore, there is evidence of individual and contextual differences in the close range vocalizations of other social animals.

To determine if the acoustic properties of the squeaking vocalization differs between individuals and contexts, a study that compares squeaking by many wolves in an intact pack in a variety of contexts is needed. The primary purpose of this study was to provide such a detailed acoustic analysis of squeaking vocalizations to address questions concerning individual and contextual variation. The specific objectives include: (1) to determine if wolves can be individually identified based on the acoustic properties of their squeaks and (2) to determine if squeaking varies as a function of social (e.g., prosocial, agonistic, food) and movement (e.g., approach, leave) contexts.

An additional goal of this study was to assess two methodological issues related to the study of acoustic variation in squeaking. The specific objectives include: (1) to determine if video recordings are adequate to detect subtle differences in the acoustic structure of squeaking vocalizations between individuals and between social and movement contexts and (2) to determine what level of analysis that is required to detect differences between individuals and contexts.

There is some question as to the sensitivity of video equipment for recording and analyzing sound (Lehner, 1996). In this study the use of video analysis was essential to identify the squeaker and recipient(s) and to determine the behavioral context in which the squeaking vocalization occurred. Although video analysis was necessary, we do not know if the sound quality of the video recordings is adequate to permit detailed investigation of the acoustic properties of squeaking. To answer this question, sonagrams of a squeaking vocalization recorded simultaneously by audio and video-recording equipment were compared. This comparison involved qualitative inspection of the sonagrams and quantitative analysis of several measurements taken from the sonagrams.

As with any vocalization or behavior that occurs in sequence or series, it is difficult to know the level (i.e., squeaking vocalization, squeaking phrase, or individual squeak) at which to analyze the squeaking vocalization. Different approaches have been taken in past research. Field (1979) measured the duration, inter-squeak interval, frequency, and fluctuation (or range) of each squeak in the squeaking phrase and then used mean values for each phrase as the unit of analysis. Goldman et al. (1995) measured the fundamental frequency of each squeak. If the fundamental frequency varied with time, the mean fundamental frequency was calculated from the fundamental at the beginning and end of each squeak. In contrast to Field (1979), they used the fundamental frequency of the individual squeaks.

The major problem with both of those approaches is that neither considered the possibility that the squeaks in the squeaking phrase may be correlated with each other such that the acoustic properties of an individual squeak may be dependent upon the properties of an adjacent squeak. In this study, the degree of correlation between squeaks within a squeaking phrase was assessed to determine whether it was appropriate to treat measurements of individual squeaks as the unit of analysis.

3.2 METHODS

3.2.1 Study Site

Detailed descriptions of the study site at the Canadian Center for Wolf Research (CCWR), Shubenacadie, Nova Scotia have been described previously (Chapter 2, Coscia, Phillips, & Fentress, 1991). Briefly, a 3.8-hectare, heavily wooded enclosure is residence to pack-reared timber wolves. The wolves are not approached or handled and their activities and social interactions are observed and recorded from one of two observation sites located next to the clearing, an area consisting of a knoll, a pond, and an open area. The wolves are provisioned in the clearing, primarily with a high quality dog food supplemented whenever possible by road-killed deer.

Each of the wolves at CCWR is named and clearly identifiable by characteristic markings. Relevant information (name, age, social status) for each wolf is presented in Table 3.1. The number of wolves in the pack changed over the course of this study. During 1995 and 1996 there were 13 wolves, including a pup that was born in 1995. In 1997, the size of the pack declined dramatically. In February 1997, the alpha female (Pawnee) died from complications of old age and three females died from injuries sustained from fighting between the females for the alpha position. A little later, the beta male (Voochco) died from natural causes. In May 1997, Homer also died from natural causes, leaving seven wolves in the pack.

3.2.2 Data Collection

At CCWR, ongoing wolf social behavior is routinely videotaped from the observation trailer using a Hi-8 Sony CCD-TR600 Video Camcorder for one hour after

Table 3.1. Relevant information for each wolf.

Wolf	Sex	Birth	Death	Social Status
Celtie (C)	F	1992	-	Sub-dominant (95, 96) Omega (97)
Devilchild (D)	F	1993	Feb. 1997	Beta (95,96) Alpha (97 ~ 3 wks)
Fiona (F)	F	1992	-	Sub-dominant (95, 96) Alpha (97)
Galen (G)	M	1988	-	Alpha (95,96,97)
Homer (H)	M	1988	May 1997	Sub-dominant (95,96,97)
Jasper (J)	M	1993	-	Sub-dominant (95,96,97)
Morgaine (M)	F	1991	Feb. 1997	Sub-dominant (95,96,97)
Noah (N)	M	1990	-	Sub-dominant (95,96,97)
Pawnee (P)	F	1984	Feb. 1997	Alpha (95, 96, 97)
Tess (T)	F	1990	Feb. 1997	Sub-dominant (95, 96, 97)
Ulysses (U)	M	1995	-	Pup (1995) Yearling (1996) Sub-dominant (1997)
Voochco (V)	M	1984	Feb. 1997	Beta (95,96,97)
Xela (X)	F	1988	-	Omega (1996,1997) Sub-dominant (1997)

feeding, three - four times per week. After the food is placed in the clearing, the wolves are videotaped whenever they are present in the clearing during the one-hour period. The watch is terminated if no wolves are in the clearing for 20 consecutive minutes. Video recordings of these feeding watches from 1995 (Jan. - Dec.), 1996 (Jan. - Sept.) and 1997(Jan.- Dec.) yielded 126 hours of videotape for analysis.

Hi-8 videocassettes were dubbed onto Sony SVHS videocassettes and indexed (i.e., each frame was numbered) using a NEC PC SVHS video recorder. In order to preserve the quality of the SVHS copies, a second tape was dubbed, indexed, and used for the initial viewing of the material to create a squeaking map. Each tape was viewed using standard play. Whenever a squeaking vocalization (SV) was heard, the index number and some descriptive information (location of squeaker[1], identity of squeaker and recipient[2], and social behavior) was recorded. This process identified approximately 2000 SVs. The squeaker and recipient(s), could only be identified for 434 of these SVs.

High-quality SVs, in which both the identity of the squeaker and recipient(s) and the social and movement context were determined, were used for acoustic analysis. Measurements were taken from 196 SVs [259 squeaking phrases (SP), 2376 squeaks] from 13 wolves in seven social contexts (13 sub-contexts) and two general movement contexts (6 sub-contexts). The following coding categories are relevant to the analysis used in this study. Other contexts were coded but not used here (see Chapter 2).

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[1] The general location of the squeaker within the compound was noted (on the mound, at the food, near the pond).

[2] Identity of the squeaker was determined by identification of the mouth and body movements associated with the SV such as gaping of the lower jaw, movement of the cheek muscles, and bellowing of rib cage. Recipients included any wolves visible in the clearing at the time of the SV unless the squeaker was obviously directed to one or more wolves.

Social Context: This was defined by the social context in which the SV occurred. Separate coding was completed for SVs that were directed to one or two wolves versus more than two wolves for prosocial (except howling) and food context categories.

1. PROSOCIAL (PR): These activities include all social behavior that is not considered agonistic (see below).
    a. Play (P): Play behavior includes such activities as body slamming, chasing, scruff biting, tail pulling, pinning, wrestling and so on (Bekoff, 1995). Many of these activities are observed during aggression (see below). However, during play these activities are frequently preceded by paw-raising and play-bows and there is no evidence of serious aggression (e.g., yelps, injury, etc). The squeaker can solicit play, can join ongoing play, or can watch others play.
    b. Greeting (G): The squeaker may squeak when approaching and then lick the muzzle of another individual or may squeak and then be approached and muzzle-licked by others.
    c. Conspecific (C): The squeaker is facing one or more wolves in any area excluding the food area (see below), but there is no physical contact between individuals and no obvious social interaction.
    d. Howling (H): The howl is a continuous sound from .5 to 11 sec long. It consists of a fundamental frequency between 150 and 780 Hz, and has up to 12 harmonically related overtones. The frequency is usually constant or varies smoothly, and may change direction up to four or five times. The intensity does not vary greatly throughout (Theberge & Falls 1967). The squeaker may squeak as other wolves howl and may join the chorus howl.

2. FOOD (F): The squeaker is near or in the food area, an area about two wolf lengths in diameter around the food source where one or more wolves are present and may/may not be eating. There is no physical contact between the squeaker and other wolves, nor obvious social interaction. Two possible situations were coded.
    a. Food-Squeaker Outside (F_0): The squeaker is in the clearing and the recipient(s) are in the food area.
    b. Food- Squeaker Inside (F_I): Both the squeaker and recipient(s) are in the food area.

3. FOOD EXCITEMENT (FEX): The squeaker(s) is (are) facing the food supply that may or may not be inside the enclosure. The SV may begin as the food is brought through the gates or just after the person bringing the food leaves the enclosure and before or during the first approach to the food area by the squeaker(s) or by other wolves.

4. AGONISTIC (AG): Agonistic behaviors are defined as those associated with attack and defense (Poole, 1985). Hinde (1970, p.335) defines aggressive behaviors as "those behaviors which are directed from one individual toward another which could lead to serious injury and often results in settling status, or access to some object or space between the two". Fentress, Ryon, McLeod, and Havkin (1987) identified aggressive interactions as those where the initiator was observed raising hackles, biting, chasing, pinning, circling, lunging, raising tail, and forelimb wrestling. Recipients of such actions responded by wheeling and facing, tail tucking, fleeing, or reciprocating aggression. SVs occurred during or after two types of agonistic interactions.

    a. Fight (FT): A yelp is usually heard prior to the SV. The squeaker can be the recipient of the aggression or an onlooker. The aggressive interaction may or may not be over when the SV begins.

    b. Following/Chase (F/C): SVs occur immediately before a wolf is aggressively followed or chased by one or more different wolves. The squeaker can be the wolf being chased or followed or an onlooker watching the activity.

5. STATUS (STAT): SVs occurred during interactions in which the participants signal their social status by characteristic head, tail and body postures.

    a. Positive (+): The squeaker approaches a high-ranking wolf with body crouched, tail tucked and ears back. The low-ranking wolf may lick the muzzle of the dominant wolf.

    b. Negative (-): A high-ranking wolf approaches (tail raised, body high, ears forward) a lower ranking wolf. The recipient, the squeaker, may tuck its tail, lower its body, and leave the area. There is no physical contact between the two wolves.

6. PUP-CARE (PUP): The squeaker and others may be engaged in care-giving activities (playing, grooming, and muzzling) with the pup. This category includes SVs that are directed to the pup from adults. (This context only occurred in 1995 only because this was the only year in which a pup was born).

7. SEXUAL (SEX): This included SVs directed from one member of the courting pair to the other and SVs that occurred during courtship behaviors (genital sniffing, following the alpha female) in which one or both members of the pair were engaged with other members of the pack. The squeaker can be an onlooker (may or may not join the activity) or a participant.

Movement Context- The physical movement made by the squeaker during or within 5 sec after the end of a SV was coded. The following is a list and description of the coded movements.

1. GENERAL APPROACH (APP): A decrease in the physical or social distance between the squeaker and the recipient(s) was coded into one of four movement categories.
    a. Approach (AP): The squeaker approached (decreased distance) an area with one or more wolves.
    b. Orient (OR): The squeaker was looking toward, or the head was turned in the direction of, one or more wolves.
    c. Orient- Squeaker Approach (OR-SAP): The squeaker was oriented (as above) to one or more wolves and approached them.
    d. Orient-Others Approach (OR-OAP): The squeaker was oriented to one or more wolves and was approached by them.
2. GENERAL LEAVE (LVE): An increase in the physical or social distance between the squeaker and the recipient(s) was coded into one of two movement categories.
    a. Leave (LV): The squeaker left or moved away from an area where one or more wolves were present.

b. Orient -Squeaker Leave (OR-SLV): The squeaker was oriented to one or more wolves and left or moved away from the area.

3.2.3 **Data Analysis**

The signal-analysis package CSL 4300 (Kay Elemetrics Co., Pine Brook, New Jersey) was used to perform detailed sound analysis. High quality SVs identified from the SVHS videotape were digitized with a 10-bit A/D converter at 20 kHz, for the frequency range 0-9 kHz. Sonagrams were produced using a 58-Hz analyzing filter bandwidth.

Preliminary analysis of the sonagrams suggested that it might be important to investigate variation in the SV at several levels. The typical duration of the inter-squeak interval (ISI), measured from the end of one squeak to the beginning of another, was less than one second (Fig. 3.2). However, sometimes there was a longer ISI (maximum ISI = 4.40 sec), but there was no corresponding change in the behavior of the vocalizing animal, suggesting that squeaks separated by a ISI greater than one second were part of the same SV, but part of a different SP. In this study, a cutoff of 1.0 seconds was used to distinguish the ISI from the inter-phrase interval (IPI), measured from the end of the last squeak in the first SP to the beginning of the first squeak in the next SP. This observation led to identification of the three levels of the SV (Fig. 3.1). The SV is the largest unit composed of one or more SPs (referred to as phrases in Fentress et al., 1978 and Field, 1979; trains in Coscia et al., 1991; sequences in Goldman et al., 1995). Each SP is composed of one or more squeaks (referred to as syllables in Fentress et al., 1978 and Field, 1979; elements in Coscia et al., 1991; squeaks in Goldman et al., 1995). Individual squeaks are brief (usually less than 300 msec), low-amplitude sounds with energy typically between 2 and 4 kHz.

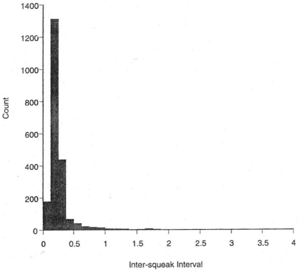


Figure 3.2. Frequency histogram of the inter-squeak interval of the SV.

I chose variables that had been previously shown to be useful in distinguishing between the squeaks of different individuals and contexts such as squeak duration, fundamental frequency, inter-squeak interval, and frequency range. Because the fundamental frequency (defined in this study as the frequency of the lowest band) can vary considerably within a squeak, I measured the start, end, maximum, and minimum frequency. Mean fundamental frequency was calculated from these four variables (comparable to fundamental frequency as measured by Goldman et al., 1995). Other variables were chosen because they appeared to vary a great deal within and between individuals and contexts.

Variables were measured directly from the sonagrams by placing cross-hairs at the target location. The accuracy of frequency measurements was ± 29 Hz and time measurements was ± 3.5 msec. The following is a description of the frequency and temporal variables measured at each level of the SV:

<u>Squeaking Vocalization (sv)</u>:

1. Duration (svdur) - the time from the start of the first squeak to the end of the last squeak in the SV.
2. Number of squeaks (svnumsq)- the total number of squeaks in the SV.
3. Mean inter-squeak interval (svisi)- the average time from the end of one squeak in the SV to the beginning of the next squeak. This measure includes the inter-phrase interval (IPI).

<u>Squeaking Phrase (sp)</u>:

4. Duration (spdur) - the time from the start of the first squeak in the phrase to the end of the last squeak in the SP.
5. Number of squeaks (spnumsq)- the total number of squeaks in the phrase.

6. Mean inter-squeak interval (spisi)- the average time from the end of one squeak in the SP to the beginning of the next squeak.

Squeak (sq):

7. Duration (sqdur) - the time from the start of the squeak to the end of the squeak.
8. Start frequency (sfreq) - the fundamental frequency at the beginning of the squeak.
9. End frequency (efreq) - the fundamental frequency at the end of the squeak.
10. Maximum frequency (mxfreq)- the peak fundamental frequency of the squeak.
11. Minimum frequency (minfreq) - the lowest fundamental frequency of the squeak.
12. Mean frequency (mnfreq) - the average of the start, end, minimum, and maximum fundamental frequency for each squeak.
13. Frequency range (range) - the difference between the maximum and minimum fundamental frequency of each squeak.
14. Onset Rise (onset) - the difference between the start frequency and the maximum frequency of each squeak.

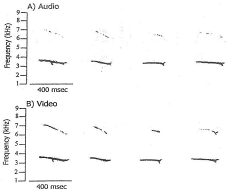
Most commonly, SVs were composed of an additional frequency component (visible on some sonagrams as second and third bands), but in recordings of distant senders energy at higher frequencies fell below the sensitivity of the recording system. This observation has led others (Schassburger, 1993; Goldman et al., 1995) to describe the SV as harmonically structured. However, some sonagrams (e.g., Fig. 3.1) indicated that the high and low components are not harmonically related (i.e., in sonagrams they are non-parallel spectral bands) which suggests they may be produced as a result of biphonation, the simultaneous generation of two audile frequencies formed by independent mechanisms (Wilden, Herzel, Peters, & Tembrock, 1998). The absence of the higher energy bands in some recordings may have been due to the limited sensitivity of the recording system; alternatively, the absence might be meaningful. Because it was impossible to distinguish between these two alternatives, the higher energy bands were not analyzed. Future research should examine the significance and function of these bands.

3.2.4 **Data Considerations**

3.2.4.1 Use of Video

In addition to the feeding watches, seven 24-hr watches were conducted between June 5, 1997 and July 24, 1997 (Chapter 2). For each watch, SVs were simultaneously recorded by video and audio equipment. A description of the video equipment is provided above. For the audio recordings, a Sennheiser Super Cardioid Shotgun microphone was connected to a Marantz PMD 430 stereo cassette recorder [frequency response 30 Hz - 15 kHz (3 dB with a signal to noise ratio of 75 dB)]. All SVs were recorded using Ampex 472 High Bias IEC Type II Studio audiocassettes. Recordings were analyzed as described above. Visual inspection of the sonagrams did not reveal any differences in the quality of the recording between the two techniques (Figure 3.3). In both examples, the variables measured were consistently higher for the video recording but the deviation was minimal (average frequency deviation = 66.8 ± 22.3 Hz, average temporal deviation = 7.5 ± 5.5 msec) with respect to the measurement error (see above), and the basic shape of the squeak has been preserved.

Example 1:



Example 2:

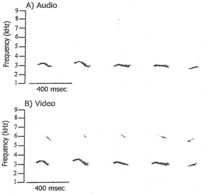


Figure 3.3. A comparison of two SP exemplars that were recorded simultaneously by video and audio recorders.

3.2.4.2 Level of Analysis (Autocorrelation)

In this study, measurements were taken of the acoustic properties of the SV, the SP, and the individual squeaks. However, before determining the appropriate method to compare squeaking between individuals and contexts, autocorrelation statistics were used to access the degree of correlation between individual squeaks within a SP. Two or three of the longest (i.e., greater number of squeaks) SP exemplars from each of eight wolves were chosen, and the correlation between squeaks for each of the frequency and temporal variables was calculated using autocorrelation function (ACF) analysis (Minitab V.10.2, Minitab Inc., 1994). The program selected a default number of lags (n/4). A t-statistic was used to determine whether the correlation between squeaks at each lag differed significantly from zero. Results are presented for lags one and two only (Table 3.2). Although there were a few significant positive correlations between adjacent squeaks (lag one) within a SP for some individuals, even within individuals there were no significant correlations between the individual squeaks in other SPs. The limited degree of correlation between squeaks within a SP suggested that it was appropriate to compare the acoustic properties of squeaks (independent of SP) between individuals and contexts as was done in Goldman et al. (1995).

3.2.5 Statistical Analysis

SPSS V 8.0 (SPSS Inc., 1998) was used for summary statistics and for all univariate and multivariate analyses. Descriptive statistics such as mean, standard deviation, range and coefficient of variation [$CV = 100 * (1 + 1/4*n) * SD/mean$, Sokal & Rohlf, 1995] were calculated for each acoustic variable measured.

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It was desirable to conduct a 3-way individual x social context x movement context analysis of variance (ANOVA) to show independent effects of individual, social context, and movement context. However, because the number of observations varied substantially across cells, the complete analysis could not be performed. Therefore, 1-way ANOVAs were used to determine the overall variation in squeaking between (1) individuals, (2) social contexts, and (3) movement contexts; sex and social rank were also examined. Additional analyses examined variation in squeaking: (1) between individuals within the same social context, thus controlling for contextual variation and (2) between social and movement contexts within the same individual, thus controlling for individual variation.

Variables that were significantly different between individuals or contexts were selected for profile analysis, a special application of multivariate analysis of variance (MANOVA). The major question addressed by profile analysis is whether the squeaking vocalization profiles of wolves/contexts differ on a set of acoustic measures. Profile analysis addresses two types of research questions important for this study: (1) Do different individuals/contexts have different acoustic profiles? This is known as the "test of parallelism" or the test of interaction. (2) Does one individual/context, on average, rate higher on a collected set of acoustic measurements than another? This is known as the "levels test". (Tabachnick & Fidell, 1996). Separate profile analyses were performed for individuals, social contexts, and movement contexts.

3.3 RESULTS

3.3.1 **General Description**

Table 3.3 provides a general description of the SV for each of the measured variables. Squeaking is a repetitive (up to 44 squeaks were observed per SV), soft, tonal sound, ranging in fundamental frequency from 1805-5974 Hz (between animals), and lasting from 0.2-22.3 seconds in duration. It is a highly variable vocalization, with coefficients of variation ranging from 8.9% to 69.7%. Much of this variation can be accounted for by differences between individuals, social contexts and movement contexts.

3.3.2 **Individual**

Visual examination of the sonagrams of different individuals squeaking in the same social and movement context revealed that individuals can be distinguished based on the acoustic properties of their squeaks (Fig. 3.4, 3.5, 3.6). Characteristic features are readily visible in the frequency and temporal components of each squeak. For example, Jasper has long squeaks with large frequency ranges whereas Noah has long squeaks with little frequency range.

Means and standard deviations for each variable are shown for each individual in Table 3.4. No significant differences between individuals were found at the SV or SP (Table 3.5). However, all measurements of the individual squeaks were significantly different between individuals, and hence were the focus of subsequent analyses.

Table 3.3: Summary statistics for each temporal and frequency variable.

Variable	Statistic			
	Mean	**Standard Deviation**	**Range**	**Coefficient of Variation (%)**
SV (N = 196)				
Duration (sec)	6.1	4.0	0.2 – 22.3	65.1
Number of Squeaks	12.1	7.4	1.0 - 44.0	60.9
Inter-squeak Interval (sec)	0.3	0.1	0.01 - 4.40	59.2
SP (N = 259)				
Duration (sec)	4.1	3.3	0.1 – 18.0	80.8
Number of Squeaks	9.3	6.9	1.0 – 44.0	74.3
Inter-squeak Interval (sec)	0.2	0.1	0.01 – 0.9	50.0
Squeak (N = 2376)				
Duration (sec)	0.20	0.10	0.03 - 2.40	63.4
Start Frequency (Hz)	3430	398.9	2180 - 5974	11.6
End frequency (Hz)	2851	369.5	1805 - 4301	13.0
Minimum Frequency (Hz)	2742	339.1	1805 - 4156	12.4
Maximum Frequency (Hz)	3676	407.3	2214 - 5974	11.1
Mean Frequency (Hz)	3175	283.8	2137 - 4352	8.9
Frequency Range (Hz)	934	503.4	0 – 3455	53.9
Onset Rise (Hz)	246	171.5	0 - 1027	69.7

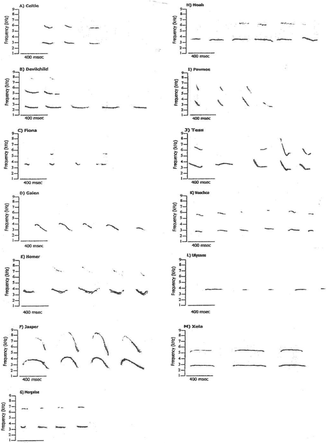

Figure 3.4. Sonagrams of squeak phrases showing differences between 13 wolves. In each case, the squeaker was approaching a group of wolves at the food.

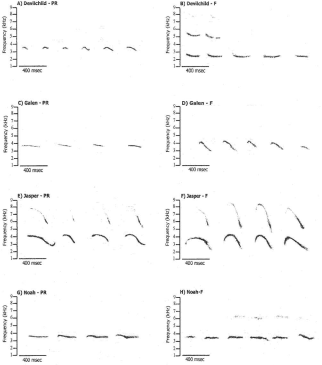

Figure 3.5. Sonagrams of four wolves squeaking in prosocial (PR) and Food (F) contexts showing differences between wolves and social contexts .

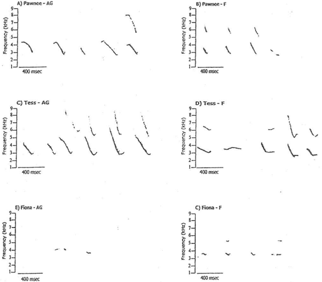

Figure 3.6. Sonagrams from three individuals squeaking in agonistic (AG) and food contexts (F). (For AG contexts, Pawnee & Tess were onlookers, Fiona was a recipient).

Table 3.4: Mean ± SD for each wolf. (n_1 = the number of SVs, n_2 = the number of SPs, n_3 = the number of squeaks). Refer to text for variable codes. Refer to Table 3.1 for wolf information.

Individual (n_1, n_2, n_3)		**Variable**															
		SV $(n_1 = 196)$			**SP** $(n_2 = 259)$			**Squeak** $(n_3 = 2376)$									
		svdur (s)	**svnumsq**	**Svisi (s)**	**spdur (s)**	**spnumsq**	**spisi (s)**	**sqdur (s)**	**sfreq (Hz)**	**efreq (Hz)**	**mxfreq (Hz)**	**minfreq (Hz)**	**mnfreq (Hz)**	**range (Hz)**	**onset (Hz)**
Female	**C** (6, 11, 69)	6.36 ± 3.47	11.5 ± 6.71	0.35 ± 0.22	2.68 ± 2.41	6.27 ± 5.18	0.19 ± 0.17	0.19 ± 0.16	3102 ± 365	2883 ± 164	3227 ± 354	2756 ± 150	2992 ± 226	471 ± 309	125 ± 101
	D (11, 16, 130)	6.45 ± 5.07	11.81 ± 6.05	0.35 ± 0.20	3.51 ± 2.53	8.87 ± 5.74	0.35 ± 0.19	0.18 ± 0.09	3291 ± 432	2968 ± 380	3435 ± 446	2863 ± 372	3140 ± 361	572 ± 367	144 ± 146
	F (8, 9, 44)	2.44 ± 2.20	5.50 ± 3.55	0.35 ± 0.19	1.87 ± 1.60	4.89 ± 3.37	0.31 ± 0.11	0.15 ± 0.10	3392 ± 320	3066 ± 314	3526 ± 274	3002 ± 289	3247 ± 258	523 ± 273	133 ± 137
	M (2, 4, 10)	3.33 ± 0.21	5.00 ± 0.0	0.69 ± 0.04	0.84 ± 0.95	2.50 ± 1.73	0.18 ± 0.25	0.12 ± 0.08	3555 ± 312	3300 ± 313	3665 ± 275	3232 ± 312	3438 ± 277	434 ± 209	111 ± 57
	P (8, 11, 96)	6.01 ± 3.29	12.00 ± 6.05	0.37 ± 0.06	3.77 ± 1.33	8.73 ± 2.90	0.31 ± 0.09	0.16 ± 0.09	3649 ± 409	2930 ± 267	3729 ± 415	2828 ± 235	3284 ± 248	900 ± 462	81 ± 76
	T (7, 8, 53)	3.80 ± 2.67	7.57 ± 3.55	0.25 ± 0.17	2.96 ± 1.68	6.63 ± 3.07	0.20 ± 0.07	0.25 ± 0.10	3976 ± 673	3257 ± 374	4152 ± 605	3010 ± 371	3599 ± 307	1142 ± 790	176 ± 161
	X (2, 2, 20)	4.12 ± 0.64	10.00 ± 2.83	0.20 ± 0.01	4.12 ± 0.64	10.00 ± 2.83	0.20 ± 0.01	0.23 ± 0.07	2921 ± 203	2807 ± 139	3096 ± 228	2691 ± 118	2879 ± 138	406 ± 185	176 ± 95
Male	**G** (9, 15, 135)	7.08 ± 3.57	15.22 ± 6.67	0.31 ± 0.11	3.49 ± 2.12	9.07 ± 5.20	0.22 ± 0.09	0.17 ± 0.08	3149 ± 250	2976 ± 194	3347 ± 261	2819 ± 165	3072 ± 122	528 ± 348	199 ± 117
	H (9, 11, 125)	6.06 ± 3.05	13.89 ± 7.04	0.28 ± 0.11	4.81 ± 3.54	11.36 ± 8.16	0.23 ± 0.10	0.22 ± 0.11	3823 ± 241	3386 ± 395	4001 ± 194	3234 ± 358	3611 ± 248	767 ± 294	177 ± 141
	J (98,128,1332)	6.87 ± 4.01	13.55 ± 8.17	0.32 ± 0.20	4.90 ± 3.79	10.37 ± 7.66	0. 25 ± 0.14	0.25 ± 0.13	3431 ± 366	2658 ± 272	3739 ± 381	2569 ± 254	3099 ± 232	1169 ± 448	307 ± 174
	N (22, 28, 218)	5.71 ± 5.08	9.91 ± 6.28	0.31± 0.23	3.87 ± 3.27	7.93 ± 5.89	0.23 ± 0.10	0.31 ± 0.26	3481 ± 325	3222 ± 248	3683 ± 316	3083 ± 227	3368 ± 228	601 ± 312	202 ± 127
	U (9, 10, 80)	4.45 ± 2.12	9.00 ± 5.38	0.28 ± 0.09	3.90 ± 2.29	8.10 ± 5.67	0.26 ± 0.07	0.27 ± 0.21	3316 ± 265	3148 ± 204	3506 ± 224	2986 ± 153	3239 ± 164	520 ± 239	190 ± 134
	V (5, 6, 64)	5.36 ± 3.75	12.8 ± 6.06	0.28 ± 0.11	3.87 ± 2.65	10.67 ± 6.05	0.23 ± 0.04	0.18 ± 0.08	3214 ± 316	2964 ± 276	3418 ± 305	2878 ± 267	3118 ± 261	540 ± 254	204 ± 115

Table 3.5. Individual differences between 13 wolves on each of the variables measured. In Tukey-Kramer HSD comparisons, brackets group those individuals that were significantly distinct from other individuals for the variable measured (significant at $p < .05$).

Variable		**F-ratio** $_{(12,183)}$	**P-value**	**Tukey-HSD**
SV	**svdur**	1.43	.155	n.s.
	svnumsq	1.81	.049	n.s.
	svisi	.952	.497	n.s.
		F-ratio $_{(12,246)}$	**P-value**	**Tukey-HSD**
SP	**spdur**	1.60	**.085**	n.s.
	spnumsq	1.49	**.125**	n.s.
	spisi	1.60	**.085**	n.s.
		F-ratio $_{(12, 2363)}$	**P-value**	**Tukey-HSD**
Squeak	**sqdur**	14.09	< .0001	(C D F G H M P V X) (N T U X) (C H J U M T X)
	sfreq	45.09	< .0001	(C V G X) (D F M U V) (F J M U) (D G U V X) (J M N) (M P)(H M) (H T)
	efreq	150.96	< .0001	(C D G P V X) (D F G P V) (M N T U) (M U F) (H M T) (J X)
	mxfreq	51.00	< .0001	(D F G M U V) (J M N P) (C G X) (C G V) (P D N) (H T) (H M)
	minfreq	140.73	< .0001	(C D G P V X) (F M N T U) (F T U V) (D F V) (J X) (H M)
	mnfreq	83.97	< .0001	(F M N P) (F M U P) (D F U V) (D G J V)(C G X) (C G V) (H M T)
	range	95.27	< .0001	(C D F G M N U V X) (H M) (H P) (J T)
	onset	43.79	< .0001	(C D F G H M N T U V X) (F G H M NT U V X) (C D F M P X) (J)

Note: Variable codes: svdur - duration of the SV, svnumsq- the number of squeaks in the SV, svisi- the interval between squeaks in the SV, spdur- duration of the SP, spnumsq-the number of squeaks in the SP, spisi-the interval between squeaks in the SP, sqdur-squeak duration, sfreq- start frequency, efreq-end frequency, mxfreq-maximum frequency, minfreq-minimum frequency, mnfreq-mean frequency, range-frequency range, onset - onset rise. Refer to Table 1 for wolf information.

Post-hoc multiway comparisons revealed that no one squeak variable was sufficient to distinguish between all individuals, but that a combination of variables was needed to distinguish between different sets of individuals (Table 3.5). In Table 3.5, letters grouped within brackets indicate those individuals that did not differ significantly from each other on the variable measured. Individuals whose measurements were significantly different are not grouped within the same set of brackets. For example, J had a significantly larger onset rise than any other wolf; however, his squeak duration was similar to six other wolves. It was also clear that some variables were better at distinguishing between some individuals than other variables (e.g., the greater number of smaller groups within brackets, the better the discrimination). In particular, frequency variables seemed most useful.

Each cell, in Table 3.6, presents the variables found to be significantly different (Tukey-HSD, p <. 05) for each pair-wise comparison of individual wolves. Note that the squeaks of 65 wolf pairs, out of possible 77 pairs, were differentiated by a set of variables. Four of the 13 wolves were distinguished from all other wolves; all wolves were distinguished from at least eight other wolves.

Although all of the examined squeak variables are potentially discriminating, some of them seem to be more important than others. Thus, in the 65 wolf-pair combinations where the individuals' squeaks were separated by one or more variables, each of the frequency variables [start (#8), end (#9), maximum (#10) and minimum

Table 3.6. Pair-wise comparisons (Tukey-HSD, p < .05) of wolves indicating which variables differed significantly between animals. (Refer to methods for variable identification, refer to Table 1 for wolf information, ND = no significant difference on any of the variables measured).

	C	**D**	**F**	**G**	**H**	**J**	**M**	**N**	**P**	**T**	**U**	**V**	**X**
C	-	8,10, 12	8,9,10, 11,12	ND	8,9,10, 11,12,13,	8, 9, 10, 11,12,13,14	8,9,10, 11,12	7,8,9, 10,11,12	8,10,12 13	7,8,9,10 11,12,13	8,9,10, 11,12	ND	ND
D		-	ND	ND	8,9,10, 11,12,13	7,8,9,10 11,13,14	9,11,12	7,8,9,10	8,12,13	7,8,9,10 11,12,13	7,9,11	ND	10,12
F			-	8,11, 12	8,9,10, 11,12,13	7,8,9,10 11,12,13,14	. ND	7,8,9,10	8,10,11 13,14	7,8,9,10 12,13	7	ND	8,9,10, 11,12
G				-	8,9,10, 11,12,13	7,8,9,10 11,13,14	9,11,12, 13,14	7,8,9, 10,11,12	8,10,12, 13,14	7,8,9,10 11,12,13	7,9,11, 12	ND	ND
H					-	8,9,10, 11,12,13,14	ND	7,8,9,10 11,12,13,14	8,9,10, 11,12,14	8,11,13	8,9,10, 11,1213	8,9,10, 11,12,13	8,9,10, 11,12,13
J						-	9,11,12, 13,14	7,9,11,12, 13,14	7,8,9,11 12,13,14	8,11,13	9,10,11, 12,13,14	7,8,9,10 11,13,14	8,10, 12,13,14
M							-	7	9,11,13 14	8,10,13	ND	9,11,12 13,14	8,9,10, 11,12
N								-	7,8,9, 13,14	8,10,12, 13	8,10, 12	7,8,9,10, 11,12	8,9,10, 11,12
P									-	7,8, 9,10, 11,12,13,14	7,8,9,10, 11,13,14	8,10,12, 13,14	7,8,10, 12,13
T										-	8,10, 12,13	7,8,9, 10,12,13	8,9,10, 11,12,13
U											-	7,9,	9,10,11, 12
V												-	10,12
X													-

(#11)] occurred in 51, 47, 49, and 46 combinations respectively while squeak duration (#7) and onset rise (#14) occurred only in 26 and 23 combinations respectively.

A profile analysis was performed on the four measurements of squeak frequency: start, end, maximum, and minimum frequency. Squeak duration was excluded because frequency variables were found to be most discriminatory (see above). Initially, range, onset rise and mean frequency were included in the analyses. However, the statistical program rejected these variables because they were redundant (i.e., they were derived from the other frequency variables). The between factor was individual; data from ten wolves were included in the analysis; individuals with a squeak sample size of less than 50 were excluded.

Using Wilk's criterion, the squeak profiles (Fig.3.7) deviated significantly from parallelism [$F(27, 6689) = 50.0$, $p < .001$, partial $\eta^2 = .16$] meaning that wolves had distinct squeak profiles. Furthermore, significant differences were found among individuals when frequency values were averaged over all variables [$F(9, 2292) = 108.14$, $p < .001$].

3.3.3 **Sex and Social Rank.**

A one-way ANOVA was used to compare the mean values for males and females on each of the measured variables. Because of the unequal contribution from some individuals (e.g., Jasper), the mean for each sex was calculated from the mean values for each individual. Squeaking differed significantly between males and females for four variables. The number of squeaks within the SV and SP, the duration of the SP, and

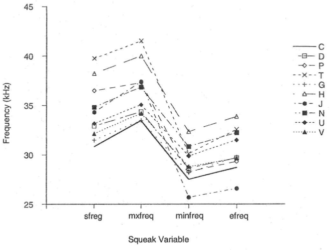

Figure 3.7. Profiles of squeak frequency variables for ten wolves.

squeak onset rise were significantly greater for males than for females [F (1, 194) = 7.04, p = .012; F (1, 257) = 6.45, p = .028; F (1, 257) = 5.25, p = .043; F (1, 2374) = 11.95, p = .005, respectively]. Although it was not possible to statistically compare variation in the acoustic structure of SVs between dominant (n = 2) and sub-dominant (n = 11) wolves, it was possible to rank order the variable means for each individual and to compare the rank scores between dominant and sub-dominant wolves. Separate ranks were assigned for males and females (Table 3.7). Pawnee, the dominant female, had the highest rank for the number of squeaks in the SV and the lowest rank for the SP duration and squeak onset rise. Pawnee also had higher ranks (a rank of six indicates that Pawnee had higher rankings than five of six sub-dominants) for start and maximum frequencies and frequency range. Galen, the dominant male, had the highest rank for the duration of the SV and the number of squeaks within the SV but the lowest rank for two of the SP variables and four of the squeak variables, including start and maximum frequency. Although Galen and Pawnee ranked oppositely, both were fairly extreme on start and maximum frequency.

3.3.4 Social Context.

Qualitative examination of the sonagrams of the same individual squeaking in different social contexts revealed subtle variations in several frequency components of the squeak (Figures 3.5, 3.6). For example, for Jasper and Galen squeaks that occurred during prosocial activities had a higher end frequency, smaller frequency range, and smaller onset rise than squeaks that occurred during food contexts.

Table 3.7. A comparison of the rank order of means for dominant (Pawnee, Galen) wolves and subdominant (SD) wolves. (The highest rank possible was 7 for P and 6 for G).

	Variable	**Female**		**Male**	
		SD	**Pawnee**	**SD**	**Galen**
SV	**Svdur**	3.83	5.00	3.00	6.00
	Svnumsq	3.50	7.00	3.00	6.00
	Svisi	3.67	4.50	4.50	3.00
SP	**Spdur**	3.67	1.00	4.00	1.00
	Spnumsq	3.83	3.00	3.00	3.60
	Spisi	5.50	3.75	4.00	1.00
Squeak	**Sqdur**	4.17	3.00	4.00	1.00
	Sfreq	3.67	6.00	4.00	1.00
	Efreq	4.17	3.00	3.60	3.00
	Mxfreq	3.67	6.00	4.00	1.00
	Minfreq	4.17	3.00	3.80	2.00
	Mnfreq	3.83	5.00	4.00	1.00
	Range	3.67	6.00	3.80	2.00
	Onset	4.50	1.00	3.60	3.00

Note: Variable codes: svdur - duration of the SV, svnumsq- the number of squeaks in the SV, svisi- the interval between squeaks in the SV, spdur- duration of the SP, spnumsq-the number of squeaks in the SP, spisi-the interval between squeaks in the SP, sqdur-squeak duration, sfreq- start frequency, efreq-end frequency, mxfreq-maximum frequency, minfreq-minimum frequency, mnfreq-mean frequency, range-frequency range, onset - onset rise. Refer to Table 1 for wolf information.

Means and standard deviations for all variables are shown for each social context in Table 3.8. Results of single-factor ANOVA showed that the inter-squeak interval of the SP was the only variable measured from the SV and SP that significantly differed between social contexts (Table 3.9). However, all variables measured from squeaks were significantly different between social contexts.

Post-hoc multiway comparisons revealed that no one variable was sufficient to distinguish between all social contexts but that a combination of variables was needed (Table 3.9). Pairwise comparisons showed that the squeaks in all but one pair of social contexts, out of a possible 21 pairs, were differentiated by some of the acoustic variables (Table 3.10). Six of the seven social contexts were distinguished from all other contexts; food excitement squeaks were not significantly different from pup squeaks on any of the acoustic variables. As with individuals, some variables seem to be more important than others. Minimum frequency (11) and onset rise (14) occurred in 15 and 11 combinations, while squeak duration, start frequency, maximum frequency, and range occurred in only 5, 6, 6, and 7 combinations, respectively.

A profile analysis was performed on four measurements of squeak frequency: start, end, maximum, and minimum. The between factor was social context; data from five contexts were included in the analysis. Data for squeaks occurring in food excitement and pup-care contexts were excluded because of small sample sizes (i.e., less than 50 squeaks). Using Wilk's criterion, the squeak profiles of the social contexts were significantly different [F (12, 6017) = 20.49, $p < .001$, partial $\eta^2 = .04$; Fig. 3.8]. Furthermore, significant differences were found among social contexts when frequency

Table 3.8. Mean ± SD for all social contexts (n_1 = the number of SVs, n_2 = the number of SPs, n_3 = the number of squeaks).

Social Context (n_1, n_2, n_3)	**Variable**													
	SV (n_1 = 196)			**SP (n_2 = 259)**			**Squeak (n_3 = 2376)**							
	svdur (s)	**svnumsq**	**svisi (s)**	**Spdur (s)**	**spnumsq**	**spisi (s)**	**sqdur (s)**	**sfreq (Hz)**	**efreq (Hz)**	**mxfreq (Hz)**	**minfreq (Hz)**	**mnfreq (Hz)**	**range (Hz)**	**onset (Hz)**
PR (71, 91, 771)	6.03 ± 3.58	11.38 ± 6.52	0.35 ± 0.22	4.26 ± 3.22	8.93 ± 6.81	0.26 ± 0.14	0.26 ± 0.18	3444 ± 383	2842 ± 3349	3683 ± 394	2751 ± 319	3180 ± 267	931 ± 481	239 ± 170
AG (8, 11, 73)	4.92 ± 4.06	9.12 ± 7.12	0.25 ± 0.19	2.88 ± 1.88	6.64 ± 4.08	0.19 ± 0.09	0.24 ± 0.17	3903 ± 631	3098 ± 373	4017 ± 616	2913 ± 356	3483 ± 359	1104 ± 716	114 ± 128
F (91,122,1230)	6.31 ± 4.04	13.10 ± 7.66	0.29 ± 0.13	4.23 ± 3.37	9.76 ± 6.93	0.22 ± 0.09	0.23 ± 0.13	3398 ± 373	2819 ± 363	3658 ± 393	2700 ± 328	3144 ± 268	958 ± 494	261 ± 170
FEX (3, 3, 50)	5.51 ± 3.32	16.67 ± 9.29	0.19 ± 0.06	5.52 ± 3.32	16.67 ± 9.29	0.19 ± 0.06	0.20 ± 0.06	3538 ± 421	2981 ± 542	3723 ± 336	2897 ± 462	3285 ± 429	827 ±211	185 ± 140
STAT (10, 12, 111)	6.49 ± 5.73	11.10 ± 10.14	0.41 ± 0.34	5.74 ± 5.59	9.25 ± 8.09	0.34 ± 0.29	0.27 ± 0.13	3359 ± 371	2750 ± 336	3709 ± 456	2621 ± 340	3110 ± 259	1087 ± 599	349 ± 195
PUP (6, 10, 45)	3.71 ± 3.16	7.50 ± 4.18	0.33 ± 0.12	2.67 ± 1.14	5.70 ± 2.45	0.35 ± 0.18	0.18 ± 0.10	3466 ± 410	2963 ± 243	3642 ± 384	2880 ± 215	3238 ± 230	762 ± 441	176 ± 118
SEX (7, 10, 96)	8.12 ± 5.46	13.71 ± 7.76	0.32 ± 0.19	3.24 ± 1.52	9.60 ± 4.95	0.31 ± 0.18	0.18 ± 0.11	3390 ± 394	3140 ± 368	3562 ± 354	3065 ± 335	3289 ± 316	497 ± 328	172 ± 122

Note: Variable codes: svdur - duration of the SV, svnumsq- the number of squeaks in the SV, svisi- the interval between squeaks in the SV, spdur- duration of the SP, spnumsq-the number of squeaks in the SP, spisi-the interval between squeaks in the SP, sqdur-squeak duration, sfreq- start frequency, efreq-end frequency, mxfreq-maximum frequency, minfreq-minimum frequency, mnfreq-mean frequency, range- frequency range, onset - onset rise. Social context codes: PR-prosocial, AG-agonistic, F - food, FEX- food excitement, STAT-status.

Table 3.9. Contextual differences between seven social contexts for each of the variables measured. In Tukey-Kramer HSD comparisons, brackets group those social contexts that are significantly ($p < .05$) distinct from other social contexts for the variable measured.

Variable		**F-ratio** $_{(6, 189)}$	**P-value**	**Tukey-HSD**
SV	**svdur**	0.84	.542	n.s.
	svnumsq	1.29	.264	n.s.
	svisi	1.83	.095	n.s.
		F-ratio $_{(6, 252)}$	**P-value**	**Tukey-HSD**
SP	**spdur**	1.09	.370	n.s.
	spnumsq	1.52	.172	n.s.
	spisi	3.864	.001	(PR AG F FEX SEX) (PR AG F FEX PUP)
		F-ratio $_{(6, 2369)}$	**P-value**	**Tukey-HSD**
Squeak	**sqdur**	7.75	< .0001	(AG F FEX PUP SEX) (PR AG FEX STAT) (F FEX STAT)
	sfreq	21.03	< .0001	(AG) (PR F FEX STAT PUP SEX)
	efreq	20.99	< .0001	(AG FEX PUP SEX) (PR F STAT) (PR SEX) (PR FEX)
	mxfreq	10.74	< .0001	(AG) (PR F FEX STAT PUP SEX)
	minfreq	21.89	< .0001	(AG FEX PUP) (PR PUP) (STAT SEX) (F STAT)
	mnfreq	23.24	< .0001	(PR F STAT PUP) (PR FEX PUP) (FEX PUP SEX) (AG)
	range	17.01	< .0001	(SEX) (PR FD STAT PUP) (AG F STAT) (PR AG F)
	onset	22.03	< .0001	(STAT) (AG FEX PUP SEX) (PR F) (PR FEX PUP)

Note: Variable codes: svdur - duration of the SV, svnumsq- the number of squeaks in the SV, svisi- the interval between squeaks in the SV, spdur- duration of the SP, spnumsq-the number of squeaks in the SP, spisi-the interval between squeaks in the SP, sqdur-squeak duration, sfreq- start frequency, efreq-end frequency, mxfreq-maximum frequency, minfreq-minimum frequency, mnfreq-mean frequency, range- frequency range, onset - onset rise

Table 3.10. Pairwise comparisons (Tukey-HSD, $p < .05$) of social contexts indicating which variables differed significantly between contexts. (Refer to methods for variable identification. ND = no significant difference on any of the variables measured).

	PR	**AG**	**F**	**FEX**	**STAT**	**PUP**	**SEX**
PR	-	8,9,10,11,12,14	7, 11	11	11,14	7,9	7,11,12 13,14
AG		-	8,9,10,11,12,14	8,10,12	8,9,10,11,12,14	8,10,12,13	8,10,11,12,13
F			-	9,11,12,14	14	9,11,14	11,12,13,14
FEX				-	9,11,12,14	ND	11,13
STAT					-	7,9,11,14	7,9,12,13
PUP						-	11,13
SEX							-

Note: Social context codes: PR - prosocial, AG - agonistic, F - food, FEX - food excitement, STAT - status, PUP - pup-care, SEX sexual.

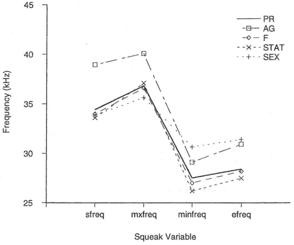

Figure 3.8. Profiles of squeak frequency variables for five social contexts. (PR-prosocial, AG-agonistic, F-food, STAT-status, SEX-sexual).

values were averaged over all variables [F (4, 2276) = 31.76, p < .001].

3.3.5 **Movement Context.**

Means and standard deviations for all variables are shown for each movement context in **Table** 3.11. ANOVA revealed that no variables measured on the SV or SP were significantly different between movement contexts. In contrast to individual and social context analyses, only minimum and end squeak frequencies and onset rise were significantly different between movement contexts [F (1, 2234) = 9.41, p = .002; F (1, 2234) = 7.46, p = .006; F (1, 2234) = 3.92, p = .048, respectively]. Comparison of the mean values for each movement context revealed that squeaks that occurred when the squeaker approached other wolves had significantly lower end and minimum frequencies, but a greater onset rise, than squeaks that occurred when the squeaker left other wolves. A profile analysis was performed on four measurements of squeak frequency: start, end, maximum, and minimum frequency. The between factor was movement context; data from two movement contexts were included in the analysis. Using Wilk's criterion, the squeak profiles for the two movements (Fig. 3.9) did not differ significantly [F (3, 2232) = 1.596, p = .189]. However, significant differences were found among movement contexts when frequency values were averaged over all variables [F (1, 2234) = 6.10, p = .014].

Table 3.11: Mean ± SD for all variables for each movement context (n_1 = the number of SVs, n_2 = number of squeaking phrases, n_3 = the number of squeaks).

Movement Context	**Variable**													
	SP ($n_1 = 196$)			**SP** ($n_2 = 259$)			**Squeak** ($n_3 = 2376$)							
(n_1, n_2, n_3)	**svdur** (s)	**svnumsq**	**svisi** (s)	**spdur** (s)	**spnumsq**	**spisi** (s)	**sqdur** (s)	**sfreq** (Hz)	**efreq** (Hz)	**mxfreq** (Hz)	**minfreq** (Hz)	**mnfreq** (Hz)	**range** (Hz)	**onset** (Hz)
APP (165, 219,1967)	6.11 ± 3.75	12.12 ± 7.26	0.32 ± 0.18	4.11 ± 3.30	9.24 ± 6.86	0.24 ± 0.12	0.23 ± 0.13	3426 ± 384	2839 ± 363	3677 ± 400	2728 ± 334	3166 ± 268	949 ± 515	252 ± 74
LVE (27, 21, 269)	6.03 ± 5.00	12.82 ± 9.10	0.27 ± 0.16	4.61 ± 3.08	10.38 ± 6.12	0.26 ± 0.14	0.23 ± 0.14	3459 ± 432	2904 ± 393	3689 ± 420	2795 ± 349	3211 ± 321	893 ± 460	229 ± 161

Note: Variable codes: svdur - duration of the SV, svnumsq- the number of squeaks in the SV, svisi- the interval between squeaks in the SV, spdur- duration of the SP, spnumsq-the number of squeaks in the SP, spisi-the interval between squeaks in the SP, sqdur-squeak duration, sfreq- start frequency, efreq-end frequency, mxfreq-maximum frequency, minfreq-minimum frequency, mnfreq-mean frequency, range- frequency range, onset - onset rise. Movement context codes: APP- general approach, LVE- general leave.

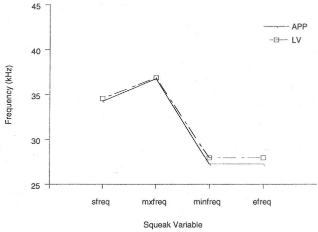

Figure 3.9. Profiles of squeak frequency variables for two movement contexts.

3.3.6 **Additional Analyses**

It was desirable to conduct a 3-way individual x social context x movement context ANOVA to determine if the acoustic structure of squeaking differed (1) between. wolves squeaking in the same social and movement contexts (2) between social contexts within the same individual and movement contexts and (3) between movement contexts within the same individual and social contexts. However, because the number of observations varied substantially across cells, the complete analysis could not be performed. Therefore, the following analyses approximate the full design as data availability permits

3.3.6.1 Individual Variation Within the Same Social-Movement Context

In an attempt to further test individuality in vocalizations, two sets of analyses compared squeaking between wolves in the same social-movement context, thereby controlling for contextual variation. Sufficient data were available to compare squeaking between (a) eight wolves approaching other wolves at food (F) and (b) five wolves approaching other wolves in the clearing (PR-C). The inter-squeak interval of the SV, duration of the SP, and eight measures of the squeak were significantly differently between wolves when approaching other wolves at food (Table 3.12). No significant differences were found at the level of the SV or SP between wolves approaching a group of wolves in the clearing (Table 3.13). However, all eight measures of the squeak differed significantly between wolves. These two analyses indicated that when the variation due to contexts was removed, squeak variables were better at discriminating between individuals (i.e., indicated by the greater number of smaller groups within brackets for the

Table 3.12. Individual differences between eight wolves approaching wolves at food. The squeaking wolves were outside the food area. In Tukey-Kramer-HSD comparisons, brackets group those individuals that are significantly distinct from other individuals for the variable measured (significant at $p < .05$).

Variable		**F-ratio** $_{(7, 67)}$	**P-value**	**Tukey-HSD**
SV	**svdur**	0.94	.478	n.s.
	svnumsq	0.97	.458	n.s.
	svisi	2.2	.044	(C D G H T) (D G H T U J N)
		F-ratio $_{(7, 84)}$	**P-value**	**Tukey-HSD**
SP	**spdur**	2.29	.035	n.s.
	spnumsq	2.01	.063	n.s.
	spisi	0.53	.081	n.s.
		F-ratio $_{(7, 840)}$	**P-value**	**Tukey-HSD**
Squeak	**sqdur**	5.86	< .0001	(C D G H T) (D H J T U) (H J N T U)
	sfreq	36.94	< .0001	(C D) (D G) (G U) (H T) (J N T) (N U)
	efreq	132.19	< .0001	(C D) (C G) (T U) (H) (J) (N)
	mxfreq	58.42	< .0001	(C D) (D G) (G U) (H T) (J N T)
	minfreq	133.17	< .0001	(H) (J D) (N T) (T U) (C D G)
	mnfreq	77.53	< .0001	(C D) (G J) (H) (N) (T) (U)
	range	86.44	< .0001	((D G N T U) (J N T U) (H D G) (C U N)
	onset	25.89	< .0001	(C D H T U) (H J N T U) (G H)

Note: Variable codes: svdur - duration of the SV, svnumsq- the number of squeaks in the SV, svisi- the interval between squeaks in the SV, spdur- duration of the SP, spnumsq-the number of squeaks in the SP, spisi-the interval between squeaks in the SP, sqdur-squeak duration, sfreq- start frequency, efreq-end frequency, mxfreq-maximum frequency, minfreq-minimum frequency, mnfreq-mean frequency, range-frequency range, onset - onset rise. Refer to Table 1 for wolf information.

Table 3.13. Individual differences between five wolves approaching conspecific wolves in the clearing. The squeaking wolves were also in the clearing. In Tukey-Kramer-HSD comparisons, brackets group those individuals that are significantly distinct from other individuals for the variable measured (significant at $p < .05$).

Variable		**F-ratio $_{(3, 18)}$**	**P-value**	**Tukey-HSD**
SV	**svdur**	1.87	.170	n.s.
	svnumsq	1.25	.320	n.s.
	svisi	0.45	.717	n.s.
		F-ratio $_{(2, 25)}$	**P-value**	**Tukey-HSD**
SP	**spdur**	0.44	.651	n.s.
	spnumsq	0.29	.749	n.s.
	spisi	0.95	.399	n.s.
		F-ratio $_{(7, 840)}$	**P-value**	**Tukey-HSD**
Squeak	**sqdur**	8.68	< .0001	(N) (C D F J)
	sfreq	7.57	< .0001	(C D F) (F J N)
	efreq	83.00	< .0001	(J) (N) (C D F)
	mxfreq	15.51	< .0001	(J N) (C D F)
	minfreq	71.14	< .0001	(J) (N) (C D F)
	mnfreq	21.37	< .0001	(N) (C D F J)
	range	51.20	< .0001	(J) (C D F N)
	onset	15.71	< .0001	(J) (N D) (C F D)

Note: Variable codes: svdur - duration of the SV, svnumsq- the number of squeaks in the SV, svisi- the interval between squeaks in the SV, spdur- duration of the SP, spnumsq-the number of squeaks in the SP, spisi-the interval between squeaks in the SP, sqdur-squeak duration, sfreq- start frequency, efreq-end frequency, mxfreq-maximum frequency, minfreq-minimum frequency, mnfreq-mean frequency, range-frequency range, onset - onset rise. Refer to Table 1 for wolf information.

Tukey-HSD comparisons) than they were in the ANOVA comparing all individuals in many social and movement contexts (Table 3.5). Squeaking differed significantly between individuals within the same context.

3.3.6.2 Contextual Variation Within the Same Individual

In an attempt to further test whether different squeak variants occurred in different social and movement contexts, squeaking was compared between different social contexts within the same individual. More explicitly, one-way ANOVAs were used to compare squeaking during prosocial (all six combined) and food (all four combined) contexts separately for Devilchild, Galen, Jasper, and Noah. In addition, squeaking that occurred during prosocial (all six) - approach and food (to a group of wolves at the food with the squeaker outside the food area) - approach contexts was compared for the same individuals.

For each of the four wolves, there were significant differences between squeaks in food and prosocial contexts (Table 3.14, Fig. 3.5). Although not significant for all individuals, a directional trend was observed. Three of the four wolves produced food squeaks with significantly lower end, minimum, and mean frequencies than prosocial squeaks. For Jasper and Galen, food squeaks had significantly greater onset rise. For Jasper, food squeaks had a significantly greater frequency range than prosocial squeaks, while the reverse was true for Noah.

There was sufficient data from three wolves to compare squeaking on various prosocial-approach contexts, thereby controlling for individual and movement contextual

Table 3.14. Contextual differences between food (F) and prosocial (PR) contexts within individual wolves. Each wolf initial is followed by the degrees of freedom for that analysis. (n_p= the number of SVs / SPs / squeaks that occurred during prosocial contexts, n_f= the number of SVs / squeaking phrases/ squeaks that occurred during food contexts, * significant at $p < .05$, ** significant at $p < .001$).

Variable		**Individual**			
		D $_{(1, 7)}$ N_p= 4 n_f= 5	**G** $_{(1, 6)}$ n_p= 4 n_f= 4	**J** ($_{1, 89)}$ n_p= 40 n_f= 51	**N** $_{(1, 11)}$ n_p= 10 n_f= 3
SV	**svdur**	0.21	0.95	1.16	0.39
	svnumsq	0.31	0.37	2.47	**6.52*** (F > P)
	svisi	0.25	0.09	**5.42*** (F > P)	0.94
		Individual			
		D $_{(1, 9)}$ N_p= 5 n_f= 6	**G** $_{(1, 11)}$ n_p= 4 n_f= 9	**J** $_{(1, 118)}$ n_p= 53 n_f= 67	**N** $_{(1, 14)}$ n_p= 13 n_f= 3
SP	**spdur**	0.36	**10.25*** (F < P)	1.03	3.99
	spnumsq	0.44	**5.10*** (F < P)	2.26	**11.55*** (F > P)
	spisi	1.36	**6.20*** (F < P)	1.02	0.18
		Individual			
		D $_{(1, 102)}$ n_p= 46 n_f= 58	**G** $_{(1, 105)}$ n_p= 49 n_f= 58	**J** $_{(1, 1218)}$ n_p= 461 n_f= 759	**N** $_{(1, 147)}$ n_p= 91 n_f= 58
Squeak	**sqdur**	1.23	0.99	2.28	**6.78*** (F < P)
	sfreq	**18.24**** (F < P)	3.60	0.62	**7.81*** (F < P)
	efreq	**33.59**** (F < P)	**21.80**** (F < P)	**9.29*** (F < P)	2.91
	mxfreq	**20.18**** (F < P)	0.39	0.18	**6.29*** (F < P)
	minfreq	**60.65**** (F < P)	**34.17**** (F < P)	**31.07**** (F < P)	2.74
	mnfreq	**41.85**** (F < P)	**24.72**** (F < P)	**6.39*** (F < P)	1.70
	range	0.64	3.32	**12.40**** (F > P)	**8.77*** (F < P)
	onset	1.37	**7.64*** (F > P)	**6.78*** (F > P)	0.878

Note: Variable codes: svdur - duration of the SV, svnumsq- the number of squeaks in the SV, svisi- the interval between squeaks in the SV, spdur- duration of the SP, spnumsq-the number of squeaks in the SP, spisi-the interval between squeaks in the SP, sqdur-squeak duration, sfreq- start frequency, efreq-end frequency, mxfreq-maximum frequency, minfreq-minimum frequency, mnfreq-mean frequency, range-frequency range, onset - onset rise. Refer to Table 1 for wolf information.

variation (Table 3.15). Only two prosocial-approach contexts could be compared for Devilchild and Galen. For Devilchild, squeaks that occurred as the squeaker was approaching either one to two wolves (C1) or a group of wolves (CG) in the clearing were compared. The squeak onset rise was the only variable that differed significantly between these two conspecific approaches. For Galen, squeaks that occurred during group play (PG) and group greeting (GG) activities were compared. Play squeaks were significantly longer with a higher start, end, maximum, and minimum frequency and a greater frequency range. Sufficient data allowed all six prosocial activities to be compared for Jasper at all levels of the SV. With the exception of the inter-squeak interval of the SV, only squeak variables differed between these activities. In fact, start and end frequency were the only variables not significantly different between at least two of the activities. Similar to D, onset rise differed significantly between the two conspecific approaches (C1, CG). Unlike G, there was no significant difference between squeaks that occurred during group play (PG) and group greeting (GG). However, the mean inter-squeak interval of the SV that occurred during group greeting was significantly longer than for SVs that occurred during all other prosocial activities.

There was also sufficient data from two wolves to perform a one-way ANOVA on four prosocial-approach movements (AP, OR, OR-SAP, O-OAP), thereby controlling for individual and social contextual variation (Table 3.16). For Galen, it was possible to compare prosocial squeaks that occurred either as he oriented (OR) or oriented as other

Table 3.15. Contextual differences between prosocial contexts within individual wolves. Each wolf initial is followed by the degrees of freedom for that ANOVA. (* significant at p < .05, ** significant at p < .001).

Variable		**Individual**		
		D $n_{C1} = 3$ $n_{CG} = 1$	**G** $n_{PG} = 1$ $n_{GG} = 2$	**J** $_{(5, 29)}$ $n_{C1} = 7$ $n_{P1} = 5$ $n_{G1} = 3$ $n_{CG} = 11$ $n_{PG} = 5$ $n_{GG} = 4$
SV	**svdur**	-	-	1.43
	svnumsq	-	-	0.80
	svisi	-	-	**5.11*** (GG) (C1,P1,G1,CG,PG)
		Individual		
		D $n_{C1} = 3$ $n_{CG} = 1$	**G** $n_{PG} = 1$ $n_{GG} = 2$	**J** $_{(5, 41)}$ $n_{C1} = 7$ $n_{P1} = 6$ $n_{G1} = 7$ $n_{CG} = 17$ $n_{PG} = 6$ $n_{GG} = 4$
Squeaking Phrase	**spdur**	-	-	0.75
	spnumsq	-	-	0.73
	spisi	-	-	0.09
		Individual		
		D $_{(1, 34)}$ $n_{C1} = 22$ $n_{CG} = 14$	**G** $_{(1, 47)}$ $n_{PG} = 18$ $n_{GG} = 31$	**J** $_{(5, 421)}$ $n_{C1} = 81$ $n_{P1} = 47$ $n_{G1} = 29$ $n_{CG} = 173$ $n_{PG} = 62$ $n_{GG} = 35$
Squeak	**sqdur**	0.629	**5.43*** (PG > GG)	**3.15*** (C1,P1,G1,CG,PG) (P1,G1,CG,GG,PG)
	sfreq	2.47	**15.23**** (PG > GG)	1.98
	efreq	1.05	**44.00**** (PG > GG)	1.99
	mxfreq	0.40	**9.37*** (PG > GG)	**5.64**** (P1,G1) (C1,G1,CG,PG,GG)
	minfreq	1.57	**29.00**** (PG > GG)	**2.64*** (C1,P1,G1,CG,PG,GG)
	mnfreq	1.67	0.07	**2.45*** (C1,G1,PG,GG) (G1,CG,PG,GG)(C1,P1,G1)
	range	0.02	**23.81**** (PG > GG)	**6.87**** (C1,G1,PG,GG) (P1,CG)
	onset	**5.41*** (C1 > CG)	0.03	**10.01**** (C1,P1,G1) (CG,PG,GG)

Note: Variable codes: svdur - duration of the SV, svnumsq- the number of squeaks in the SV, svisi- the interval between squeaks in the SV, spdur- duration of the SP, spnumsq-the number of squeaks in the SP, spisi-the interval between squeaks in the SP, sqdur-squeak duration, sfreq- start frequency, efreq-end frequency, mxfreq-maximum frequency, minfreq-minimum frequency, mnfreq-mean frequency, range- frequency range, onset - onset rise. Prosocial context codes: C1-conspecific, 1-2 wolves; CG-conspecific, group of wolves; P1-play, 1-2 wolves, PG-play, group of wolves; G1-greeting, 1-2 wolves, GG-greeting, group of wolves. Refer to Table 1 for wolf information.

Table 3.16. Contextual differences between prosocial-approach movements within individuals. Each wolf initial is followed by the degrees of freedom for that analysis. (* significant at p <.05, ** significant at p < .001).

Variable		Individual	
		G $n_{or} = 1$, $n_{or\text{-}oap} = 2$	**J** $_{(3,31)}$ $n_{ap} = 16$, $n_{or} = 6$, $n_{or\text{-}sap} = 9$, $n_{or\text{-}oap} = 4$
Squeaking Vocalization	**svdur**	-	0.54
	svnumsq	-	1.80
	svisi	-	0.53
		Individual	
		G $n_{or} = 1$ $n_{or\text{-}oap} = 2$	**J** $_{(3, 43)}$ $n_{ap} = 27$, $n_{or} = 6$, $n_{or\text{-}sap} = 10$, $n_{or\text{-}oap} = 4$
Squeaking Phrase	**spdur**	-	**5.71*** (AP,OR-0AP) (OR,OR-SAP,OR-0AP)
	spnumsq	-	**6.17*** (AP,OR-0AP) (OR,OR-SAP,OR-0AP)
	spisi	-	0.60
		Individual	
		G $_{(1, 47)}$ $n_{or} = 11$ $n_{or\text{-}oap} = 38$	**J** $_{(3, 423)}$ $n_{ap} = 141$, $n_{or} = 102$, $n_{or\text{-}sap} = 130$, $n_{or\text{-}oap} = 53$
Squeak	**sqdur**	**8.50*** (OR > OR-OAP)	**3.66*** (AP,OR,OR-OAP) (OR,OR-SAP,OR-OAP)
	sfreq	**64.64**** (OR > OR-OAP)	0.06
	efreq	**24.43**** (OR-OAP > OR)	**3.83*** (AP,OR,OR-OAP) (OR,OR-SAP,OR-OAP)
	mxfreq	**40.90**** (OR > OR-OAP)	1.06
	minfreq	**58.79**** (OR-OAP > OR)	**5.27*** (AP,OR-SAP) (OR,OR-SAP,OR-OAP)
	mnfreq	**6.23*** (OR > OR-OAP)	1.12
	range	**118.03**** (OR > OR-OAP)	**3.75*** (AP,OR,OR-SAP) (AP,OR-SAP,OR-OAP)
	onset	0.59	**5.54*** (OR-OAP) (AP,OR,OR-SAP)

Note: Variable codes: svdur - duration of the SV, svnumsq- the number of squeaks in the SV, svisi- the interval between squeaks in the SV, spdur- duration of the SV, spnumsq-the number of squeaks in the SP, spisi-the interval between squeaks in the SP, sqdur-squeak duration, sfreq- start frequency, efreq-end frequency, mxfreq-maximum frequency, minfreq-minimum frequency, mnfreq-mean frequency, range-frequency range, onset - onset rise. Movement codes: AP-approach, OR-orient, OR-SAP-orient and squeaker approaches, OR-OAP-orient and others approach. Refer to Table 1 for wolf information.

wolves approached (OR-OAP). Squeaks that occurred as Galen oriented to other wolves during prosocial activities were significantly longer with higher start, maximum, and mean frequencies, lower end and minimum frequencies, and a greater frequency range. Sufficient data allowed all four prosocial-approach movements to be compared for Jasper at all levels of the SV. There were no significant differences found between movements at the level of the SV. However, duration of the SP, number of squeaks per SP, squeak duration, end and minimum frequencies, frequency range, and onset rise were significantly different between approach movements. Similar to Galen, frequency range was significantly different between prosocial squeaks that occurred when the Jasper was oriented (OR) and those that occurred when he was oriented as other wolves approached (OR-OAP).

There was sufficient data from three wolves to perform a one-way ANOVA on three food-approach movements (AP, OR, OR-SAP) (Table 17). No significant differences were found at the level of the SV or SP for any of the three wolves. For Devilchild and Galen, it was possible to compare squeaks that occurred as they oriented (OR) and oriented and approached (OR-SAP) a group of wolves at the food (the squeaker was outside the food area). Sufficient data allowed all three food approach movements to be compared for Jasper. Although squeak variables different significantly between food approach movements for each individual, there did not appear to be any consistency across wolves for any comparison.

Table 3.17. Contextual differences between food-approach movements within individuals. Each wolf initial is followed by the degrees of freedom for that analysis. (* significant at $p < .05$, ** significant at $p < .001$).

Variable		**Individual**		
		$D_{(1, 2)}$ **$n_{or} = 2, n_{or\text{-}sap} = 2$**	**G** **$n_{or} = 3, n_{or\text{-}sap} = 1$**	**$J_{(2, 36)}$** **$n_{ap} = 23, n_{or} = 15, n_{or\text{-}sap} = 1$**
Squeaking Vocalization	**svdur**	0.24	-	1.98
	svnumsq	0.05	-	1.85
	svisi	6.49	-	2.03
		Individual		
		$D_{(1, 3)}$ **$n_{or} = 3, n_{or\text{-}sap} = 2$**	**$G_{(1, 7)}$** **$n_{or} = 3, n_{or\text{-}sap} = 1$**	**$J_{(2, 48)}$** **$n_{ap} = 31, n_{or} = 18, n_{or\text{-}sap} = 2$**
Squeaking Phrase	**spdur**	0.20	0.80	0.29
	spnumsq	0.23	0.72	0.27
	spisi	1.20	0.11	0.56
		Individual		
		$D_{(1, 56)}$ **$n_{or} = 31, n_{or\text{-}sap} = 27$**	**$G_{(1, 56)}$** **$n_{or} = 38, n_{or\text{-}sap} = 20$**	**$J_{(2, 548)}$** **$n_{ap} = 318, n_{or} = 205, n_{or\text{-}sap} = 28$**
Squeak	**sqdur**	**6.61*** (OR < OR-SAP)	2.14	**4.10*** (AP,OR-SAP) (OR,OR-SAP)
	sfreq	0.41	**8.04*** (OR > OR-SAP)	0.77
	efreq	**4.30*** (OR > OR-SAP)	2.75	**13.04**** (AP) (OR,OR-SAP)
	mxfreq	2.77	**8.63*** (OR > OR-SAP)	0.15
	minfreq	3.81	**5.81*** (OR < OR-SAP)	**38.05**** (AP) (OR,OR-SAP)
	mnfreq	0.04	0.09	**10.58**** (AP,OR-SAP) (OR, OR-SAP)
	range	**6.25*** (OR > OR-SAP)	**11.38**** (OR > OR-SAP)	**7.14*** (AP,OR-SAP) (OR, OR-SAP)
	onset	**7.60*** (OR > OR-SAP)	0.094	0.912

Note: Variable codes: svdur - duration of the SV, svnumsq- the number of squeaks in the SV, svisi- the interval between squeaks in the SV, spdur- duration of the SP, spnumsq-the number of squeaks in the SP, spisi-the interval between squeaks in the SP, sqdur-squeak duration, sfreq- start frequency, efreq-end frequency, mxfreq-maximum frequency, minfreq-minimum frequency, mnfreq-mean frequency, range-frequency range, onset - onset rise. Movement codes: AP-approach, OR-orient, OR-SAP-orient and squeaker approaches. Refer to Table 1 for wolf information.

3.4 DISCUSSION

3.4.1 Vocal Individuality in Wolves

There is solid evidence to support the notion of individuality in the squeaking vocalizations of wolves. A comparison of squeaking between wolves collapsed across all social and movement contexts, and comparison of individuals squeaking in the same social-movement contexts revealed that wolves have signature squeaks. No one variable was successful at discriminating between all individuals. Multivariate profile analysis demonstrated that each individual had a unique profile of squeak frequency characteristics. The combination of various frequency variables permits discrimination between the wolves. The necessity of many variables for individual distinctiveness has been found in studies of other birds and mammals (Epsmark, 1975; Lillehei & Snowdon, 1978; Robisson et al., 1993; Mathevon, 1997).

Although there was a great deal of variation within the variables measured at the three levels of analysis, very little of the variation in squeak vocalization and phrase variables was accounted for by inter-individual differences. With the exception of the number of squeaks within a squeaking vocalization, only squeak variables differed between individuals, suggesting that the level of analysis needed to detect individuality is at the individual squeaks that compose the vocalization.

Frequency variables were most useful for distinguish squeaking between individuals. Goldman et al. (1995) found similar results; fundamental frequency was useful in distinguishing between the squeaks of the mother and another female tending to pups inside the den. Frequency characteristics may be individually distinctive because they are largely determined by the dimensions of an animal's vocal apparatus (glottal width and vocal tract length), which is linked to its unique genetic code (Michelson, 1983). The importance of frequency characteristics in individuality has been previously identified in the vocalizations of wolves (howling, Tooze et al., 1990) and other canid species (territorial barking in Arctic foxes, Frommolt et al., 1997; whistling in dholes, Durbin, 1998).

In this study, onset rise was the only squeak variable that differed significantly between males and females. In contrast, Field (1979) reported that the female had significantly higher mean squeak frequency and duration and greater frequency range than the male. Because they compared squeaks of only one male and one female, it is likely that their findings reflected individual differences, not sex differences. In this study, squeak frequency, duration and range significantly differed between individual wolves.

Vocal individuality has been established in wolf squeaks and howls, permitting discrimination between wolves in long-range and friendly close-range situations. The presence of vocal individuality does not mean that the wolves use this information for individual recognition. However, this coupled with the ability of the wolf to detect subtle differences in sound (Asa & Mech, 1995) suggests that specific information about the identity of the vocalizing animal could be communicated through squeaking and howling. The behavioral ecological perspective highlights the utility of acoustically-based individual recognition in wolves. Wolves are highly social and occupy fairly distinct territories. In order to function as a group, communication among individuals is necessary. The lifestyle of wolves require members of the pack to be visually separated at times so that they may need to rely on olfactory and auditory modes of communication (Theberge & Falls, 1967). It is during these occasions that individual recognition by vocal communication may be most important.

3.4.2 Contextual Variation in Squeaking

There is evidence to support the notion that subtle variations in the acoustic properties of the squeaking vocalization are used in different social contexts. When squeaking was compared between contexts collapsed across all individuals, and within individuals, squeaks differed significantly across social contexts. Although the mean inter-squeak interval of the SP was significant, the most successful unit of analysis for discriminating between contexts was the squeak. A combination of variables was needed to distinguish squeaking in each social context. Multivariate profile analysis revealed that social contexts (prosocial, food, agonistic, status, sexual) had distinct squeak profiles. These results strengthen the findings of Fentress et al. (1978) and Field (1979) who reported that squeaking differed within individuals squeaking in different contexts.

Although each social context had defining squeak characteristics, squeaks occurring during agonistic interactions were the most distinct. These squeaks had higher start, maximum, and mean fundamental frequency than squeaks occurring in any other social context. In agonistic contexts, the squeaker was either the recipient of the aggression or an onlooker watching the interaction from a distance. The function of squeaking in agonistic contexts may be to provide a "relaxed" atmosphere to an otherwise tense situation (i.e., reconciliation) or to minimize aggression from the receivers, preventing an agonistic episode from escalating to a more serious aggressive interaction.

The use of squeaking in non-friendly aggressive situations seems consistent with Morton's (1977, 1982) proposed motivational-structural rules for linking the motivational state of senders to the acoustic structure of their vocalization. Morton suggests that animals use tonal high-frequency sounds when frightened, appeasing, or affiliative. In this situation, the recipient (squeaker) would be highly motivated to prevent the aggression from becoming more serious, thus lowering the risk of serious injury. An onlooker may also be motivated to minimize aggression if there was a risk of becoming involved in the aggression and getting injured.

Squeaking occurred in all of the social contexts examined, but most frequently as wolves were approaching other wolves at food or during prosocial activities. For this reason, the variation in squeaking between food and prosocial contexts could be examined within different individuals, thus controlling for individual variation (Lillehei & Snowdon, 1978). Although different variables were significant for different individuals, there was a general trend in which squeaks in prosocial contexts had higher squeak frequencies than those in food contexts. However, squeaks occurring in food contexts had greater frequency range and onset rise. This finding may reflect the design features for effective transmission of signals. Squeaking is a relatively high frequency sound within the wolf vocal repertoire. High frequency sounds travel for shorter distances than do low frequency sounds of the same amplitude (Snowdon & Hodun, 1981). Although squeaking occurs in close-range contexts, the distance between squeaker and recipient(s) does vary. For example, wolves are generally closer to one another, within a few wolf lengths, when soliciting nearby wolves to play, when greeting other wolves and in other conspecific situations than they were in food contexts. When approaching other wolves at the food, they usually began squeaking while they were some distance away, either as they were leaving the mound or approaching from the forest. Higher frequency squeaks were used in close situations (prosocial), whereas lower-frequency squeaks were used in more distant situations (food).

Another signal design feature that may be important here is sound localization. Signals that are easy to localize often have sharp onsets and wide frequency ranges (Snowdon & Hodun, 1981). This suggests that squeaks occurring as the squeaker approaches other wolves at the food may provide information about the location of the squeaker. Location might be more important in this context than in other contexts. That is, in most prosocial contexts, the squeaker and potential recipients are already engaged in an activity or are at least visually aware of each other's presence. Visual and olfactory signals are available to aid in individual recognition. However, the situation is different for squeaking that occurs in food contexts. The recipients are already at the food source with their heads down, often with their backs to the approaching wolf. Visual and olfactory cues are less available to the potential recipients. Squeaking in this context may enable the receivers to know that another wolf is approaching the food source. By squeaking, the vocalizer may announce its identity, location, and motivation.

Additional support for this notion was found by comparing the acoustic properties of food squeaks that occurred when the squeaker was inside and outside the food area.

Squeaks that occurred when the squeaker was outside the food area had significantly greater frequency ranges and onset rises, and would therefore be easier to locate, than squeaks that occurred when the squeaker was inside the food area, near other wolves [F (1, 188) = 50.21, p < .001, and F (1, 188) = 22.47, p < .001, respectively]. These results suggest that information about the location of the squeaker may be more important when wolves are at a distance and when information from other modalities is not as readily available.

There is evidence to support the notion that subtle variations of squeaking occur in different movement contexts. When collapsed across all individuals, the two movement contexts did not differ at the level of the squeaking vocalization or the phrase. However, squeaks that occurred as wolves approached other wolves had lower minimum and end frequencies and a greater onset rise than squeaks that occurred when the squeaker was leaving other wolves. Again, this points to the possibility that the location of the squeaker may be more important in some contexts than in others. Multivariate profile analysis revealed that the profiles of each movement were not distinct, but there was a significant difference between approach and leave squeaks when frequency variables were averaged.

This study suggests that wolves have signature squeaks that vary in form as the context changes. Each individual had a unique profile of squeak frequency characteristics. In general, the minimum and end frequency and onset rise were most useful for distinguishing between social and movement contexts. This suggests individual signature squeaks are modified slightly by varying the end and minimum frequencies, or onset rise in different social and movement contexts.

An additional goal of this study was to assess two methodological issues: use of video and the appropriate unit of analysis. With respect to video, there was some question as to the appropriateness of using video recordings for sound analysis. The quality of the sonagrams of squeaks simultaneously recorded by video and audio recorders were comparable. This suggests, at least for this vocalization and under the recording conditions experienced in this study, that video is an appropriate means of recording sound and can enable investigation of subtle variation in the acoustic structure of a close-range vocalization.

Variation in the acoustic properties of squeaking was investigated at three levels of the squeaking vocalization. With the exception of one or two analyses, most of the differences between individuals and contexts occurred at the level of the individual squeaks comprising the squeaking vocalization, not at the higher levels. Results of autocorrelation function analysis (ACF) revealed that it was appropriate to analyze at this level.

Although the level of autocorrelation between squeaks within a phrase was minimal, the adjacent squeaks in some squeaking phrases for some individuals were significantly correlated. We need to know when this occurs. Also visual inspection of the squeaks reveals variation in the shape of the individual squeaks [e.g., Fig. 3.1, Fig. 3.5 (E), Fig. 3.6 (D)], which leads to additional questions: Do individual wolves have characteristic squeak shapes? Are certain squeak shapes used in certain contexts? Squeak shapes are currently being coded to investigate the variability and sequencing of squeak shapes within a squeaking phrase to determine if patterns exist across individuals or contexts.

Although prior studies (Fentress et al., 1978; Field, 1979; Goldman et al., 1995) documented extensive variability in squeaking, the explanation for the variability (i.e., individual, context, age, sex, social rank) was mostly unknown. This study compared squeaking between 13 individuals in seven social contexts (13 sub-contexts) and two movement contexts (6 sub-contexts) on 14 frequency and temporal variables at three levels of the squeaking vocalization. Results showed that individual wolves have acoustically distinct squeaks that vary across social and movement contexts. To determine whether wolves can decode this information, and if so, how they use it will require playback experiments and detailed behavioral observations. Investigation of the behavioral responses of individual wolves to playbacks and an investigation of squeaking in wild wolves will further enhance our understanding of the importance of squeaking for wolves.

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Chapter 4 Conclusions

This study investigated the individual and contextual variation in the squeaking vocalization of pack-living wolves. Squeaking occurred most frequently during early morning and late afternoon hours. All wolves were observed squeaking but some squeaked more than others. There was no difference in the frequency of squeaking between males and females, but sub-dominant wolves did squeak more than the dominant pair in the24-hr watches only. Squeaking occurred in a range of social contexts but most frequently as the wolves approached other wolves in prosocial and food contexts. Specifically, wolves squeaked most when approaching or orienting (1) to other wolves in the clearing and (2) to a group of wolves at the food. The social contexts of squeaking observed in this study were similar to those reported by other researchers (Mech, 1970; Fentress, Field, & Parr, 1978; Harrington & Mech, 1978; Peters, 1980). They are also similar to the contexts reported for high-frequency, presumably friendly vocalizations, of other social canids, including the whines of coyotes *Canis latrans* (Lehner, 1978), squeaks/whimpers of dholes *Cuon alpinus* (Tembrock, 1963; Fox, 1984), and the whines and whimpers of other canids (Tembrock, 1963; Fox, 1971).

Previous research (Fentress et al., 1978; Field, 1979; Goldman, Phillips & Fentress, 1995) hinted that the audile properties of squeaking differed between individuals and social contexts. In this study, visual assessment of squeak sonagrams and quantitative (univariate and multivariate) analyses led to the conclusion that wolves have signature squeaks that vary in form as the social and movement context changes. Although a number of acoustic variables were measured at each level of the squeaking vocalization, a combination of squeak frequency variables was most useful for distinguishing among individuals and among social and movement contexts. For individuals, the start, end, maximum, and minimum fundamental frequencies were most useful. Generally, the end and minimum fundamental frequencies and onset rise were most useful for discriminating between social and movement contexts. This observation suggests that individuals have signature squeaks that vary (i.e., subtle variations in the end and minimum frequency, onset rise) in different social and movement contexts.

Although squeaking occurs in a variety of social and movement contexts, the underlying message seems to be the friendly motivation of the squeakers and their willingness to interact with other wolves. The acoustic richness and complexity of this vocalization provides additional information in some contexts. For example, squeaking that occurs when approaching others at food may inform the receivers of the location, identity, and motivation of the approaching wolf. This information is most valuable in situations where information from other sensory modalities is less available.

In summary, wolves are highly social animals with an extensive communication system of visual, auditory, olfactory, and tactile signals. Although these modalities are often investigated and discussed as discrete units, they seldom function alone. Squeaking is often accompanied by visual displays such as facial expressions, and ear, body and tail positions that together emphasize the identity (individual, familiar/unfamiliar, pup/adult, dominant/sub-dominant), motivation (friendly, non-aggressive) and location of the sender. Squeaking is present in many of the daily activities of wolves suggesting that it is important for controlling and coordinating the social dynamics of the pack.

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Appendix I

Results - 1995

Table 1: Feeding Watches (1995): The number of squeaking vocalizations identified in each social and movement context.

Movement Context		Social Context																					
		Food				Prosocial								Agonistic		Status		FEX	SEX	Pup Care		Misc.	Total
		1-2 Wolves		>2 Wolves		1-2 Wolves			> 2 Wolves			Other											
		F_I	F_O	F_I	F_O	C	P	G	C	P	G	Y	H	FT	F/C	+	-			C	P		
General Approach	APP	0	0	1	24	3	0	2	0	0	2	0	0	0	0	0	0	0	2	1	0	0	35
	OR	0	2	0	9	4	0	0	9	1	0	0	0	3	3	0	0	2	2	1	0	7	43
	OR-SAP	0	1	0	11	2	1	0	2	0	1	0	0	0	0	1	0	0	4	0	4	1	28
	OR-OAP	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	4
General Leave	LV	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
	OR-LV	0	1	5	9	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	16
Other	CONT	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	3
	ST-RESP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ND	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	5	10
	NM	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3
Subtotal 1		**0**	**4**	**7**	**55**	**11**	**2**	**2**	**11**	**1**	**3**	**3**	**0**	**3**	**5**	**1**	**1**	**4**	**10**	**3**	**5**	**13**	**144**
Subtotal 2		**4**		**62**		**15**			**15**			**3**		**3**	**5**	**1**	**1**	**4**	**10**	**3**	**5**	**13**	
Total		**66**				**33**								**8**		**2**		**4**	**10**	**8**		**13**	

Note: Social Contexts: F_I. squeaker and recipients inside the food area, F_O - squeaker outside the food area and recipients inside, C - both squeaker and recipients in the clearing, G - greeting, P - play, Y - yawn, H - howl, FT - fight, F/C - follow or chase, Status + (positive), Status - (negative), FEX - food excitement, SEX - sexual, Misc. – miscellaneous.
Movement Contexts: APP - approach, OR - orient, OR-SAP - orient and squeaker approach, OR-OAP - orient and others approach, LV - leave, OR-SLV - orient and squeaker leaves, CONT - continuous, ST-RESP - stationary response, ND - non-directional, NM - no movement.

Table 2: Feeding Watches (1995): The number of squeaking vocalizations identified for each wolf in each social context.

	Social Context																					
	Food				Prosocial								Agonistic		Status		FEX	SEX	Pup Care		Misc.	T
	1-2 Wolves		> 2 Wolves		1-2 Wolves			> 2 Wolves			Other											
ID & Rank	F_I	F_O	F_I	F_O	C	P	G	C	P	G	Y	H	FT	F/C	+	-			C	P		
G M-A	0	0	2	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	7
V M-B	0	0	0	6	2	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	10
H M-SD	0	0	0	7	1	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	12
N M-SD	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	1	3	0	0	2	11
J M-SD	0	3	4	24	1	0	1	5	0	3	2	0	0	0	1	0	1	3	1	2	4	55
P F-A	0	0	1	6	1	0	0	1	0	0	0	0	3	0	0	0	0	0	2	1	3	18
D F-SD	0	0	0	5	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	0	10
M F-SD	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	2	8
T F-SD	0	0	0	1	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	4
F F-SD	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3
C F-SD	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
X F-O	0	0	0	1	2	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	5
T	4		62		15			15			3		3	5	1	1	4	10	3	5	13	144

Note: Social Contexts: F_I - squeaker and recipients inside the food area, F_O - squeaker outside the food area and recipients inside, C – both squeaker and recipients in the clearing, G - greeting, P - play, Y - yawn, H - howl, FT - fight, F/C - follow or chase, Status + (positive), Status - (negative), FEX - food excitement, SEX - sexual, Misc. - miscellaneous, ID: G - Galen, V-Voocho, H - Homer, N- Noah, J -Jasper, P - Pawnee, D -Devil Child, T -Tess, F -Fiona, C -Celtie, X -Xela, M - male, F – female, A - alpha, SD - sub-dominant, and O – omega.

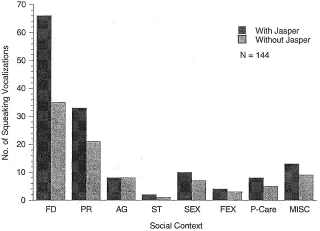

Figure 1. Feeding Watches (1995): The number of squeaking vocalizations identified in each social context (with and without Jasper). (FD = food, PR = prosocial, AG = agonistic, ST = status, SEX = sexual, FEX = food excitement, P-care = pup care, MISC = miscellaneous).

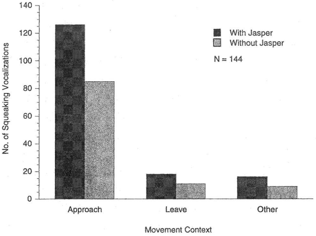

Figure 2. Feeding Watches (1995): The numberof squeaking vocalizations identified in each movement context.

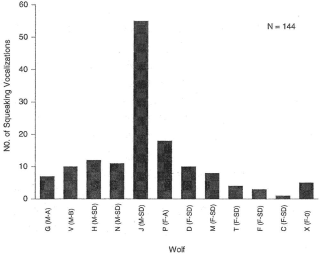

Figure 3. Feeding watches (1995): The number of squeaking vocalizations identified for each wolf. ID codes: G – Galen, V – Voochco, H – Homer, N – Noah, J – Jasper, P – Pawnee, D – Devilchild, M – Morgaine, T – Tess, F – Fiona, C – Celtie, X – Xela, F- female, M- male, A – alpha, SD – sub-dominant, O – omega.

Appendix II

Results - 1996

Table 1: Feeding Watches (1996): The number of squeaking vocalizations identified in each social and movement context.

		Social Context																			
Movement Context		Food				Prosocial								Agonistic		Status		FEX	SEX	Misc	Total
		1-2 Wolves		>2 Wolves		1-2 Wolves			> 2 Wolves			Other									
		F_I	F_O	F_I	F_O	C	P	G	C	P	G	Y	H	FT	F/C	+	-				
General Approach	APP	0	0	0	13	2	3	0	4	2	2	0	0	1	0	0	0	0	0	0	27
	OR	0	1	1	12	5	1	0	7	4	0	0	0	0	0	0	0	0	0	2	33
	OR-SAP	0	0	1	1	0	3	0	4	0	2	0	0	0	0	0	0	0	2	0	13
	OR-OAP	0	0	0	0	2	1	1	0	0	2	0	0	0	0	0	0	0	0	0	6
General Leave	LV	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	OR-LV	1	1	1	3	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	8
Other	CONT	0	0	0	0	0	0	0	1	0	0	0	3	0	2	0	2	0	1	0	9
	ST-RESP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	2
	ND	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3
	NM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T_1		1	3	4	30	10	8	1	17	6	6	0	3	1	2	0	3	0	3	4	102
T_2		4		34		19			29			3		1	2	0	3	0	3	4	
T_3		38				51								3		3		0	3	4	

Note: Social Contexts: F_I - squeaker and recipients inside the food area, F_O - squeaker outside the food area and recipients inside, C - both squeaker and recipients in the clearing, G - greeting, P - play, Y - yawn, H - howl, FT - fight, F/C - follow or chase, Status + (positive), Status - (negative), FEX - food excitement, SEX - sexual, Misc. – miscellaneous.Movement Contexts: APP - approach, OR - orient, OR-SAP - orient and squeaker approach, OR-OAP - orient and others approach, LV - leave, OR-SLV - orient and squeaker leaves, CONT - continuous, ST-RESP - stationary response, ND - non-directional, NM - no movement.

Table 2: Feeding Watches (1996): The number of BID squeaking vocalizations identified for each individual in each social context.

	Social Context																			
	Food				Prosocial								Agonistic		Status		FEX	SEX	Misc.	T
	1-2 Wolves		> 2 Wolves		1-2 Wolves			> 2 Wolves			Other									
ID & Rank	F_I	F_O	F_I	F_O	C	P	G	C	P	G	Y	H	FT	F/C	+	-				
G M-A	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	3
V M-B	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
H M-SD	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	2	7
N M-SD	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	1	0	0	2	6
J M-SD	0	0	3	20	6	8	1	10	6	4	0	0	1	0	0	0	0	0	0	59
U M - Y	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
P F-A	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
D F-SD	0	0	0	4	1	0	0	3	0	0	0	2	0	0	0	0	0	0	0	10
M F-SD	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	2	0	0	0	4
T F-SD	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	3
F F-SD	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2
C F-SD	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
T	4		34		19			29			3		1	2	0	3	0	3	4	102

Note: Social Contexts: F_I . squeaker and recipients inside the food area, F_O - squeaker outside the food area and recipients inside, C – both squeaker and recipients in the clearing, G - greeting, P - play, Y - yawn, H - howl, FT - fight, F/C - follow or chase, Status + (positive), Status - (negative), FEX - food excitement, SEX - sexual, Misc. - miscellaneous, ID: G - Galen, V- Voocho, H - Homer, N- Noah, J -Jasper, U -Ulysses, P - Pawnee, D -Devil Child, T -Tess, F -Fiona, C -Celtic, M - male, F – female, A - alpha, SD - sub-dominant, and O – omega.

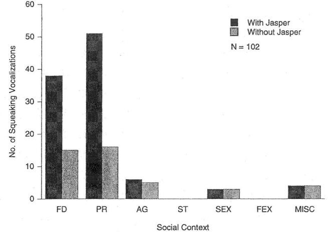

Figure 1. Feeding watches (1996): The number of squeaking vocalizations identified in each social context (with and without Jasper). Social context codes: FD - food, PR – prosocial, AG – agonistic, ST – status, SEX – sexual, FEX – food excitement, and MISC – miscellaneous.

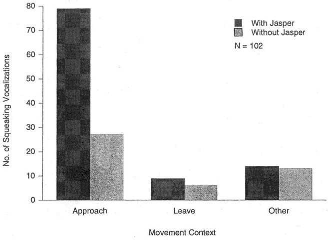

Figure 2. Feeding watches (1996): The number of squeaking vocalizations identified in each movement context (with and without Jasper).

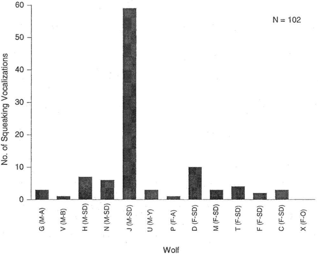

Figure 3. Feeding watches (1996): The number of squeaking vocalizations identified for each individual. ID codes: G – Galen, V – Voochco, H – Homer, N – Noah, J – Jasper, U – Ulysses, P – Pawnee, D – Devilchild, M – Morgaine, T – Tess, F – Fiona, C – Celtie, X – Xela, F- female, M – male, A – alpha, SD – sub-dominant, O – omega.

Appendix III

Results - 1997

Table 1: Feeding Watches (1997): The number of squeaking vocalizations identified in each social and movement context.

Movement Context		Social Context																			Total
		Food				Prosocial								Agonistic		Status		FEX	SEX	Misc.	
		1-2 Wolves		>2 Wolves		1-2 Wolves			> 2 Wolves			Other									
		F_I	F_O	F_I	F_O	C	P	G	C	P	G	Y	H	FT	F/C	+	-				
General Approach	APP	0	0	2	33	6	0	4	4	2	1	0	0	0	0	2	0	0	0	0	54
	OR	0	0	1	32	12	4	0	10	1	0	0	0	0	2	0	0	1	0	7	70
	OR-SAP	0	1	1	12	3	1	2	2	0	3	0	0	0	0	0	0	0	0	0	25
	OR-OAP	0	0	0	0	4	1	0	1	1	3	0	0	0	0	0	3	0	0	0	13
General Leave	LV	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	OR-LV	0	0	1	9	2	0	0	0	0	0	0	0	0	0	0	1	0	0	1	14
Other	CONT	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	2	0	1	0	6
	ST-RESP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2
	ND	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	NM	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	3
Subtotal 1		**0**	**1**	**6**	**86**	**29**	**6**	**6**	**17**	**4**	**7**	**3**	**1**	**0**	**2**	**2**	**8**	**1**	**1**	**8**	**188**
Subtotal 2		**1**		**92**		**41**			**28**			**4**		**0**	**2**	**2**	**8**	**1**	**1**	**8**	
Total		**93**				**73**								**2**		**10**		**1**	**1**	**8**	

Note: Social Contexts: F_I . squeaker and recipients inside the food area, F_O - squeaker outside the food area and recipients inside, C - both squeaker and recipients in the clearing, G - greeting, P - play, Y - yawn, H - howl, FT - fight, F/C - follow or chase, Status + (positive), Status - (negative), FEX - food excitement, SEX - sexual, Misc. – miscellaneous. Movement Contexts: APP - approach, OR - orient, OR-SAP - orient and squeaker approach, OR-OAP - orient and others approach, LV - leave, OR-SLV - orient and squeaker leaves, CONT - continuous, ST-RESP - stationary response, ND - non-directional, NM - no movement.

Table 2: Feeding Watches (1997): The number of squeaking vocalizations identified for each individual in each social context.

	Social Context																			
	Food				Prosocial								Agonistic		Status		FEX	SEX	Misc.	Total
	1-2 Wolves		> 2 Wolves		1-2 Wolves			> 2 Wolves			Other									
ID & Rank	F_I	F_O	F_I	F_O	C	P	G	C	P	G	Y	H	FT	F/C	+	-				
G M-A	0	0	0	1	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0	5
H* M-SD	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3
N M-SD	0	0	0	3	5	1	0	0	0	1	0	1	0	0	1	6	0	1	1	20
U M - Y	0	0	0	6	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	10
J M-SD	0	0	6	68	15	5	6	10	3	3	3	0	0	0	1	1	1	0	6	128
F F-A	0	0	0	3	0	0	0	2	0	1	0	0	0	0	0	0	0	0	1	7
D* F-SD	0	0	0	2	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	5
T* F-SD	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2
X F-SD	0	0	0	2	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	4
C F-SD	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	4
Total	1		92		41			28			4		0	2	2	8	1	1	8	188

* These wolves died between January and May, 1997. (P, M, and V also died during this period).

Note: Social Contexts: F_I. squeaker and recipients inside the food area, F_O - squeaker outside the food area and recipients inside, C – both squeaker and recipients in the clearing, G - greeting, P - play, Y - yawn, H - howl, FT - fight, F/C - follow or chase, Status + (positive), Status - (negative), FEX - food excitement, SEX - sexual, Misc. - miscellaneous, ID: G - Galen, H - Homer, N- Noah, J -Jasper, U -Ulysses, D -Devil Child, T -Tess, F -Fiona, C - Celtie, X -Xela, M - male, F – female, A - alpha, SD - sub-dominant, and O – omega.

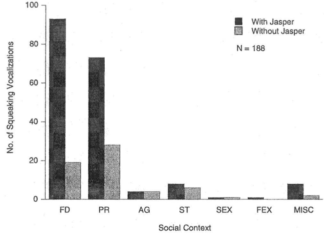

Figure 1. Feeding watches (1997): The number of squeaking vocalizations identified in each social context (with and without Jasper). Social context codes: FD – food, PR – prosocial, AG – agonistic, ST – status, SEX – sexual. FEX - food excitement, MISC – miscellaneous.

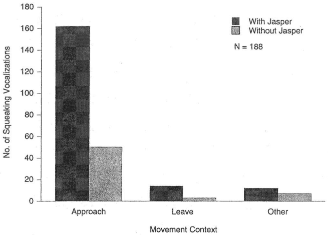

Figure 2. Feeding watches (1997): The number of squeaking vocalizations identified in each movement context (with and without Jasper).

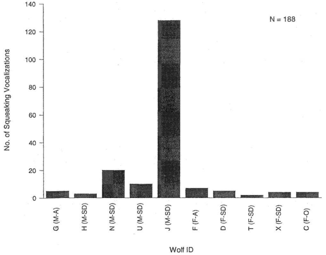

Figure 3: Feeding watches (1997): The number of squeaking vocalizations identified for each individual. ID codes: G – Galen, H – Homer, N – Noah, U – Ulysses, J – Jasper, F – Fiona, D – Devilchild, T – Tess, X – Xela, C – Celtie, F – female, M – male, A – alpha, SD – sub – dominant, O – omega.