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Ontogeny of Timber Wolf Vocalizations:
Acoustic Properties and Behavioural Contexts

by

Elizabeth Maria Coscia

Submitted in partial fulfilment of the requirements for the Ph.D. degree

at

Dalhousie University
Halifax, Nova Scotia



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ABSTRACT

This thesis concerns the ontogeny of vocal patterns in wolves, including their acoustic properties, contexts of expression and apparent functions. While it has long been recognized that wolves are among the most complex terrestrial social mammals and that their vocal behaviour contributes significantly to their social organization, objective and quantitative assessments of wolf vocal ontogeny have been lacking. In this study I have provided the first systematic evaluation of neonatal wolf vocalization patterns. Recordings were obtained from three litters of pups in a semi-natural, undisturbed den. The development of vocal behaviour during the pups' first six weeks of age was quantified using a multidimensional classification scheme. I catalogued 3396 sounds and 800 behavioural events and subjected them to detailed analyses. Vocalizations were divided into 11 classes based on their spectrographic structure. Properties used to distinguish vocal classes included: gross spectral type, duration and three frequency variables. Measures of frequency variation, inter-element-interval duration of sound series and relative amplitude were also taken for selected sounds. Eight vocal classes were quantified. Vocal classes were subdivided into three groups: early-appearing neonate-specific, early-appearing adult-structured and late-appearing adult-structured. Ontogenetic trends included changes in the relative proportion of specific vocal classes, decreases in fundamental frequency and combinations of specific sounds into patterns of non-random series. The behavioural context of vocal classes was examined with descriptive and statistical analyses of the relations between selected vocal classes and three behavioural categories: pup and adult behaviour at onset of pup vocal activity, and subsequent adult responses to vocalizations. The context of vocal classes distinguished as neonate-specific did not vary significantly with maturation, whereas the context of the adult-structured classes varied with changes in social and physical development. Interpretations of the expressive content and the function of pup vocal behaviour were based on the objective criteria used to describe behavioural changes in development.

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CHAPTER ONE

INTRODUCTION: VOCAL COMMUNICATION AND WOLVES

The production and significance of vocalizations can change dramatically with age, yet there are few quantitative studies of the development of vocal behaviour for non-human mammals. Timber wolves, *Canis lupus*, have an elaborate vocal repertoire composed of long-range and short-range vocalizations. Detailed developmental studies of acoustic communication in this social species are lacking. This thesis concerns the ontogeny of vocal behaviour in timber wolves.

General Introduction on Vocal Communication

Communication is traditionally defined as involving events where the actions of one individual (the sender) alters the behavioural patterns of another (the receiver) in a manner that benefits the sender and/or receiver (Busnel, 1963; Wilson, 1975). Effective communication can be achieved through a variety of visual, tactile, olfactory and vocal signals (Sebeok, 1977). Visual and tactile communicative behaviours convey detailed information to a recipient immediately and directly. An assortment of postures, facial expressions, movements or direct physical contacts can inform the receiver of the sender's physical and/or motivational state and possibly alert the receiver to the sender's likely subsequent actions (e.g. Schenkel, 1947; Hinde and Rowell, 1962). This

process, however, is limited to individuals within clear view of each other and is ineffective for species which inhabit large or densely vegetated habitats. Olfactory communication is used by many species, and in this case the receiver need not be nearby. For example, information concerning an individual's presence within an area, their territorial boundaries, or their sexual status is commonly mediated through olfactory means (e.g. Peters and Mech, 1975; Müller-Schwarze and Heckman, 1980). One limitation with chemical forms of communication is that they sometimes require direct scrutiny, and thus may remain undetected for a considerable time. When messages need to be conveyed quickly across distances, vocal communication can be the most reliable form of regulating social behaviour in group-living species (Sebeok, 1977).

Research into Vocal Communication In Mammals

Acoustic properties of sounds

The study of vocal communication in social mammals is of particular interest because of the diversity and complex nature of their vocal utterances. In mammals, vocalizations are produced by means of the larynx and a supralaryngeal vocal tract. Vocal cords in the larynx allow airstreams, produced by the lungs during exhalation, into the vocal tract. The vocal tract serves as a filter. Sounds of varying spectral content can be produced depending on the shape and the size of the vocal tract. The resulting vocalizations tend to take

one of three acoustic forms: pure tone, harmonic and noisy, each of which may have separable developmental chronologies. Pure tone vocalizations are composed of single frequencies. Harmonic vocalizations are composed of a mixture of associated frequencies: the "primary" or "fundamental frequency", and the "harmonic series", which are integral multiples of the fundamental frequency. Typically the fundamental frequency is the "dominant frequency", in that it often has the greatest amplitude, and sets the pitch perceived by the listener. Noisy sounds are aperiodic and have continuous, often broad, spectra. Vocalizations may be structured with one or more of these gross spectral types. Vocalizations may also vary on other acoustic dimensions including duration, amplitude, presence or absence of frequency modulation and rate of frequency modulation (Fry, 1979).

Structure of the repertoire

Studies of mammalian acoustic and behavioural repertoires are numerous and the approaches for analysis have been diverse, thus rendering inter- and intra-specific comparisons difficult. Most of the problems arise as a result of differences in taxonomic criteria applied to vocal and behavioural repertoires. Some vocal taxonomists prefer to delineate only a few vocal categories with a broad list of either acoustic or behavioural traits for each category. Typically, these repertoires have large amounts of variation within each category. Other taxonomists tend to create numerous categories with a narrow range of traits,

which results in minimal variation within groups. Deciding where to draw the line between "lumping" and "splitting" in category formation is often a difficult process. The dilemma is not knowing which acoustic traits to measure. This decision ideally should be based on categories which are meaningful to the species in question (Marler, 1982). In practice, determining these categories is difficult and, quite often, they cannot be delineated comprehensively without controlled manipulation of vocal stimuli.

Vocalizations are often classified by the human observer/receiver based on the behavioural contexts and implied functions (Peters, 1980). This procedure, however, can be biased and anthropomorphic, and can lead to confusion in defining the vocal repertoire for cross-study comparisons. A more objective process of vocal classification involves delineation of the sound's acoustic structure through spectrographic analyses (Hopkins et al., 1974). Spectrographic analyses enable quantitative assessments of the acoustic properties of vocalizations which comprise an animal's repertoire. This method avoids misclassification (e.g. lumping) of acoustically-distinct sounds which are not distinguishable by perception alone. Recently, Kanwal et al. (1994) classified the acoustic repertoire of bats (*Pteronotus parnellii*) through spectrographic analysis. Categorization of calls was based on a quantitative scheme which classified sounds using multiple acoustic parameters. The authors stressed the importance of applying a consistent, unbiased classification scheme (i.e., the categorization of sounds based on their physical structure) to

facilitate cross-study comparisons of sound forms. Following the categorization of sounds within the repertoire, studies of these perceived categories can determine whether the species makes similar divisions using the same parameters. One method to examine the categorization of sound classes based on their acoustic properties is to observe how the various sound classes are emitted under specific behavioural contexts. Understanding which behavioural actions elicit specific vocalizations and which behavioural responses recipients show toward each vocalization, can lead to guarded interpretations of the function(s) of specific sounds and/or sound combinations.

In their analyses of vocal communication systems investigators often seek to determine how vocalizations within repertoires are patterned (Marler, 1965). Vocal repertoires may be composed of graded signal structures in which the acoustic structures of sounds vary along a continuum (Rowell, 1962). Vocal repertoires may also be composed of discrete categories of sounds; "discrete" in the sense that vocal units within the repertoire are structurally-distinct (Gouzoules et al., 1984).

Communicative value of the repertoire

Researchers have also focused on the communicative information that vocal signals transfer. The expression of the emotional state of animals has been emphasized since Darwin's 1872 classic essay on communication. Darwin theorized that non-human animals used signals, including vocalizations, to

express their emotions (e.g. hunger, fear, affiliation, aggression). The presumption was, however, that all non-human animal signals were simply expressions of the caller's motivational state. The evidence that vocal signals express the emotional state of mammals has been presented for many non-human primate species (Green, 1975; Jürgens, 1979). Green's (1975) spectrographic analysis of the vocal repertoire of free-ranging Japanese macaques (*Macaca fuscata*) showed how vocalizations, similar in sound structure, were produced in similar behavioural contexts. He also found a graded relationship between the acoustic properties of sounds and the social context in which the sounds were emitted. Graded changes in the arousal state of the animal were associated with graded changes in the properties of the vocalization. For example, long vocal series from infants who were being weaned were composed of intergraded vocalizations: as the arousal state of the infant increased, the variability and the associated noise of the vocalizations increased. Jürgens (1979) experimentally manipulated the emotional state of squirrel monkeys through the use of electrical brain stimulation. Certain monkey calls were evoked through neural stimulation. He showed how call morphology was related to the caller's "hedonic" state: the aversiveness of the call was positively correlated with both the sound's frequency range and irregular patterns of frequency modulation.

Evidence that vocal signals are expressions of the sender's motivational state has been described for other non-primate species (See Tembrock (1976)

and Morton (1977) for review). Both Tembrock and Morton analyzed the acoustic properties of sounds from a variety of mammalian species through spectrographic analysis. Both authors showed how the acoustic characteristics of the sound were related to the physical production of the sound, which in turn is a probable reflection of the emotional state of the animal. Similarities of the changes in the acoustic features across different species adds support to these generalities.

Other studies, however, have shown how some vocalizations may also encode more specific information than simply the internal state of the animal. The specific information encoded in vocalizations can be of at least two broad classes. One class is "representational" in which the acoustic signal provides information about a specific object or event (Gouzoules et al., 1984). Representational signals have been described as a form of semantic communication in which distinct signals are used to reference a specific object or event (Altmann, 1967). For example, Seyfarth et al. (1980) identified three acoustically distinguishable alarm calls (both by ear and spectrographically) of vervet monkeys (*Cercopithecus aethiops*) in the wild. These three call types were produced by vervets differentially in the presence of three classes of predators. The vervets also responded to these calls with three distinct escape reactions.

A second class of information which acoustic signals may encode is "signature information" in which vocalizations of similar structure contain variants

which are consistent for an individual and allow for individual recognition (Kaplan et al., 1978; Symmes et al., 1979). Vocal signatures enable members within a group to differentiate each other and are potentially beneficial for species which use long-range communication. Vocal signatures have been identified in the contact calls of spider monkeys, *Ateles geoffroyi* (Chapman and Weary, 1990) and in the separation calls of young microchiropteran bats, *Pipistrellus pipistrellus* (Jones et al., 1991).

Vocal repertoires may be composed of signals which may reflect the internal state or motivation of the caller and/or of signals representing referential information (i.e., objects in the environment or individual identity). These two classes of information are not, however, mutually exclusive. Green's (1975) documented repertoire of macaque sounds had graded acoustic morphologies and functionally-discrete subclasses were likely perceived (by the species) within the repertoire. In support of this claim, recently Marler et al. (1992) proposed that referential signals are not devoid of motivational information and motivational signals are not devoid of referential information. They argued that the traditional dichotomy of signals as either motivational or referential in content is misleading because it masks the complexity of vocal repertoires. For example, the alarm calls of vervet monkeys, which reference different types of predators, likely encode motivational information (e.g. the arousal state of the caller) which is reflected in the call morphology. More detailed acoustical analyses are required to examine subtle differences in call morphology (e.g.

changes in amplitude or call rate). Although the argument presented by Marler et al. was speculative, they cautioned researchers to avoid the characterization of animal signals as being one mode of communication or the other. Detailed examination of the structure and usage of acoustic communication within a natural setting and through controlled experimental analyses is required to elucidate the relationships between motivational and referential signals.

Research into the Development of Vocal Communication

Nature versus nurture

By far, studies of vocal development are few in comparison to studies of adult vocal repertoires. A common concern in early developmental studies of mammalian acoustic communication has been the issue of whether vocal processes are innate or learned (Newman and Symmes, 1982; Snowdon et al., 1986). Early studies of infant separation calls of non-human primates, reared in isolation, suggest that acoustic signals resembled adult calls at birth (Winter et al., 1973; Newman and Symmes, 1982). Other evidence suggests that mammalian young of some species do not produce all of the sounds present in their adult repertoire (see review in Ehret, 1980). From this, one might infer that the adult-structured sounds are differentiated based on learning. Vocal learning can take place at a number of different levels. First, individuals may learn when is the appropriate time to vocalize. Second, individuals may learn how to fine-tune the acoustic structure of their emitted sound. Third, individuals

could learn to whom vocal production should be directed. Learning, however, is not the only explanation for the emergence of new vocalizations as young mature. Another plausible reason is that young individuals do not possess the necessary vocal/motor capabilities to produce these vocalizations or that maturational processes are involved, so that the neural/motor hardware may be either absent or present but inhibited. Finally, young may also require exposure to the appropriate context in which to express the vocalization.

Among mammals, reports of vocal learning are uncommon. Evidence for vocal learning has been shown for specific sound types of various gregarious primates with large vocal repertoires. For example, Seyfarth and Cheney (1980, 1986) demonstrated that young vervet monkeys learn when to produce appropriate predator alarm calls. When alarm calls were given, infants that were closer in proximity to their mothers were more likely to show the correct strategic response (e.g. look up and run into the bushes when an eagle flies overhead). In addition, as vervets matured, the number of alarm calls produced in the presence of a nonpredatory species decreased, as well as the number of inappropriate alarm calls produced in response to a predator species. The authors suggest that learning plays a critical role in the ontogeny of alarm calling behaviour.

Hauser (1989) investigated the ontogeny of species-specific calling in vervet monkeys. He selected a unique call of the vervet monkey, the "intergroup wrt", and measured the development of its duration, frequency

(including mean fundamental, dominant, and modulation) and amplitude modulation. He noted significant developmental changes in all parameters measured. Hauser states that the gradual developmental changes found in the intergroup sounds of young vervets include a variety of physical/maturational changes combined with social experiences. His conclusion that multiple ontogenetic processes affect vocal development of animals in nature was similar to the inferences made by Romand and Ehret (1984) of the vocalizations produced by normal, isolated and deafened kittens (*Felis catus*).

The degree to which mammalian vocalizations are fixed at birth and/or change with time (due to maturational and/or experiential factors) obviously varies across species and perhaps even across sound measures. Behavioural phenotypes are the result of diverse contributions from both genetic (nature) and experiential (nurture) sources (West and King, 1987; Johnston, 1988).

Communicative value of the neonate vocal repertoire

Aside from the questions generated from the nature versus nurture issue in vocal development are questions pertaining to the function of the neonate vocal repertoire. What is the communicative function of neonate vocalizations? The majority of studies on vocal development which have discussed the communicative function of vocal signals focus on specific classes of calls such as distress or separation calls. Most mammalian young are dependent upon their mother or care-giver for their basic nutritional, protective and

thermoregulatory needs. When young are separated from their mother or caregiver, or a mother is in search of her young, acoustic signalling is an effective contact mechanism for the expression of their internal state. Tembrock (1963) divides these distress sounds into two groups based on their function, "care calls" and "contact calls".

Care calls are the first form of acoustic signalling in neonates (Tembrock, 1963). These calls serve to elicit care-giving behaviours and to attract attention when isolated. The majority of these types of calls are indicators of the internal state of the young (Tembrock, 1963). Masataka and Symmes (1986) examined the isolation or distress calls of separated infant squirrel monkeys (*Saimiri sciureus*). These authors measured eight different call parameters including the duration of the call and seven frequency-related measures. Only call duration varied significantly: call length was a direct function of the separation distance between young and their natal groups; the greater the distance between the caller and the receiver, the longer the call duration. These changes in duration were, likely, related to changes in the motivational state of the caller (i.e., the longer calls were associated with an elevated state of arousal).

Contact calls, sounds associated with the time later in development when the young are mobile, are produced by both young and adults and serve to unite group members who have been temporarily separated (Tembrock, 1963). Most of the developmental studies of contact calls have explored issues of acoustic recognition found in mammalian colonial breeders and den/cave

dwelling species. The presence of vocal signatures in contact calls of young has been found in primates (e.g. squirrel monkeys: Lieblich et al., 1980), ungulates (e.g. reindeer, *Rangifer tarandus*: Espmark, 1975), bats (e.g. microchiropteran: Jones et al., 1991) and seals (e.g. Northern elephant seals, *Mirounga angustirostris*: Petronovich, 1974). A primary acoustic feature in these studies, which differentiated individual calls, was fundamental frequency.

Not all infant vocalizations appear to be care-soliciting or contact seeking expressions. Snowdon et al. (1986) described what they term "babbling" in marmosets and tamarins (family Callitrichidae). When young were separated from their care-givers, they emitted a series of isolation vocalizations. Within their vocalizations, individual vocal elements resembled adult vocal forms although they were not produced in the proper adult context, nor were the elements combined in an adult-like manner. These vocal utterances have been regarded as vocal practice which function to exercise the vocal organs or develop coordination between a mental representation of the sound and the neural/muscular activity required to create it.

Vocal Repertoire of the Wolf

Social species with diverse, rich vocal repertoires are well suited for the analysis of vocal production and its ontogeny. It is for this reason that the majority of vocal studies have concentrated on gregarious and territorial primate species. Few studies have analyzed vocal ontogeny in other highly social

mammals with complex repertoires of communicative behaviours. One such species is the timber wolf, *Canis lupus*, a pack-living carnivore that depends on cooperative interactions for the maintenance of social structure, successful rearing of young, territorial defense and prey acquisition (Mech, 1970; Peterson, 1977; Fentress and Ryon, 1982; Harrington and Mech, 1982).

The adult wolf's vocal repertoire is composed of both long-range and short-range vocalization types. The vocal complexity of this repertoire is reflected in the lack of consensus among researchers of the number of discrete sounds in the repertoire. Schassburger (1987, 1993) delineated 11 major vocal types which he reported were acoustically distinct both perceptually and based on spectrographic analyses of various acoustic dimensions. These vocal categories were called the howl, whine, whimper, yelp, growl, snarl, woof, bark, moan, whine-moan and growl-moan. In addition to these major sound classes, Schassburger subclassified vocalizations that appeared to be intermediate in form between the major classes. Also, Juxtaposed sounds (different sounds which were produced in rapid succession) were classified separately with a new name. The repertoire described by Schassburger consisted of nearly 50 classes and subclasses of vocalizations. Schassburger also, however, divided the repertoire of the wolf into two basic sound classes based on call morphology, harmonic and noisy. All of the classes and subclasses of sounds he identified could be partitioned into one of these two structural categories. Within each category, the sounds formed a graded continuum of acoustic units.

Other researchers (Joslin, 1966; Harrington and Mech, 1978) divide the vocal repertoire of the wolf into four basic sound classes based on their presumed functions: howl, whimper, bark and growl. Whether the wolf's vocal repertoire consists of four or 50 basic sound units is an open question. The number of vocal classes within the wolves' acoustic repertoire reflects the level of analysis (i.e., how classes are divided and then subdivided) which each researcher chooses to employ.

The structure of the wolf's vocal repertoire is often misinterpreted because certain sounds, which are spectrally similar, have been labelled with different names by various authors. For example, whimpers, whines and squeaks are all terms used to describe the high-pitched sounds which occur in a series of short-duration elements (Joslin, 1966; Fentress, 1967; Fentress et al., 1978; Harrington and Mech, 1978; Schassburger, 1987, 1993; and Coscia et al., 1991). When different acoustic labels are used for the same sounds, cross-study comparisons are confusing. Thus, a strategy is needed to examine and distinguish vocal properties to facilitate cross-study comparisons. An objective means to distinguish vocal properties is to quantify and categorize sounds based on their acoustic structure (Coscia et al., 1991).

Despite confusion about the number of distinguishable vocalization classes and their labels, all wolf researchers have recognized the complex nature of wolf vocal behaviour. One question that remains is whether distinct vocalizations result in discrete communicative messages. Here the focus

switches from sound form to its function. Schassburger (1987, 1993) proposed that the wolf's repertoire could be grouped into two main categories based on sound form, harmonic and noisy. He also described general functions for each of these sound forms: all harmonic vocalizations (including howls) were associated with approach/friendly behaviour and all noisy vocalizations were associated with aggressive behaviour. This dichotomy was also used by Harrington and Mech (1978) to describe whimpers (harmonic sounds) and growls (noisy sounds) respectively. The dichotomy of the total repertoire as proposed by Schassburger is, likely, an oversimplification of wolf communication because the variety of vocalizations found within each of these sound-form categories probably encodes a variety of messages.

Individual vocal classes within the wolf's repertoire are reported to appear under different behavioural contexts. Some of the acoustic parameters which delineate these vocal classes, as well as the situations in which they have been observed, will be reviewed for the four major classes initially identified by Joslin (1966): the howl, the whimper (which will also be referred to as the squeak for consistency with later reports: Field, 1978; Coscia et al., 1991), the bark and the growl. Joslin's categories of vocal types will be used since all analyses of the wolf's vocal repertoire in both wild and captive animals have recognized these sound classes.

The howl

The wolf howl is harmonically structured. This vocalization is long in duration (ranging from 0.5 to 11 seconds) and varies in fundamental frequency (from 150 to 780 Hz) (Theberge and Falls, 1967; Harrington and Mech, 1978). The howl may be produced as one vocalization or as a series of vocalizations by an individual. These howls have been labelled "solo" or "lone" howls (Zimen, 1971). More typically, howls are emitted as a series by several individuals, and are called "chorus" or "group" howls (Zimen, 1971).

The howl has been the primary focus of the majority of wolf vocal communication studies. Its long-distance sound transmission enables clear recordings both in the wild and in captivity. Howls from one wolf within a pack are followed by approach and subsequent howling from other pack members. If a wolf separated from its pack howls, pack members approach the howling wolf. In contrast to howling within a pack, howling between neighbouring packs leads to subsequent avoidance. It is for this reason researchers assert that the howl serves as a form of communication to decrease distance between pack members and maintain distance between neighbouring packs (Mech, 1970; Harrington and Mech, 1979).

Evidence for individual identity in the wolf howl, proposed initially by Theberge and Falls (1967), has been found in the solo howls of captive wolves (Tooze et al., 1990). Group members separated from their pack-mates produced series of Howls. Tooze et al. selected two "modifier" variables, four

"pitch" variables, and seven "shape" variables to measure from these howls. All variables, from a sample of 308 howls from seven wolves, were subjected to multivariate statistical analyses. These analyses were employed to determine if there were significant acoustic differences between the howls of identified animals and whether individual wolves could be discriminated on the basis of specific acoustic variables. Tooze et al. found that the howls of individual wolves were significantly different. The critical variables which provided information on individual identity were the fundamental frequency of the howl, and frequency modulation within each howl.

Harrington (1987) used the acoustic variable, frequency, to analyze aggressive howling in wolves. He followed Morton's (1977) hypothesis that sounds follow motivational-structural rules. Morton suggested that low pitched sounds were associated with aggression and increasingly high pitched sounds were associated with friendliness. Harrington analyzed howls from single adult wolves as they related to the distance between the "howler" (either a human simulation or the play-back of a tape-recorded wolf howl) and the suspected "receiver". Harrington proposed that wolves approaching an unfamiliar howl were acting aggressively because encounters with foreign wolves often result in aggressive interactions (Mech, 1970; Harrington and Mech, 1979). He found lower frequency howls from wolves that approached the stimulus howl while higher pitched howls were produced by individuals that kept their distance.

Examinations of chorus howling in captive wolves reveal that howls may

also serve as an affiliative contact mechanism. Chorus howls were commonly preceded and/or succeeded by a ritualized greeting display. The chorus howl display involved animals with wagging tails aggregating to rub heads and nuzzle faces. This ritualized behaviour was also associated with squeaks (Mech, 1970; Klinghammer and Laidlaw, 1979; Schassburger, 1987, 1993). The expression of howls within this context may indicate the use of the howl as a short-range form of communication.

The whine/squeak

Whines or squeaks are perceived as a high-pitched sound with spectral energy averaging around 3500 Hz (Joslin, 1966; Harrington and Mech, 1978; Schassburger 1987, 1993). Lower-pitched spectral energy components (between 400 and 800 Hz) are also sometimes present. Squeaks occur typically in series of pure-tone or harmonic elements (Field, 1978). The duration of these elements is relatively brief, ranging between 0.2 seconds up to several seconds. The longer duration elements have been labelled whines, and the shorter elements, whimpers or squeaks (Harrington and Mech, 1978).

Crisler (1958) referred to the high-pitched vocalizations of wolves as "conversational whimpers", "protesting whines", "social squeaks" and "puppy calls". Squeaks are primarily associated with care-giving or affiliative behaviours (Field, 1978, 1979; Harrington and Mech, 1978). Adults squeak at pups during approach and interactive contact, and to elicit pup emergence from the den

(Fox, 1971; Coscia et al., 1991; Goldman et al., 1995). Pups also squeak to adults in these same contexts. Squeaks are associated with the ceremonial actions of wolves, particularly emitted by subdominants, during chorus howls (Harrington and Mech, 1978; Schassburger, 1987, 1993).

Squeaks have been observed to vary in acoustic structure among individuals (Fentress et al., 1978; Field, 1979). That acoustic variants of squeaks may be salient to wolves has been proposed by Goldman et al. (1995), who suggested that vocal signatures were based on differences in fundamental frequency. Squeaks produced by one female (the mother) were lower in pitch than squeaks produced by a second female care-giver, a subdominant pack member. In addition, pups responded to the squeaks within the lower mean fundamental frequency range of the mother with approach, whereas pups did not approach squeaks outside of the upper mean frequency range of the mother.

The bark

The wolf bark is both a harmonic and noisy, explosive sound with a frequency range of 320 to 904 Hz (Tembrock, 1963). The bark is typically short in duration, occurring singly or in patterned and/or irregularly-timed series of elements (Joslin, 1966; Harrington and Mech, 1978).

The bark is observed in predominantly agonistic contexts (Harrington and Mech, 1978; Schassburger, 1987, 1993). Most accounts describing the

behavioural context of barks are anecdotal. Joslin (1966) described temporal differences between barks categorized as alarm calls and those classified as threat gestures: alarm barks were shorter in duration and produced singly in comparison to threat barks which were longer in duration and produced in series. Joslin, however, did not have quantitative data to support his observations.

Barks have also been observed in association with howls, either as a separate preceding or succeeding vocal outburst (Mech, 1966), or as a component combined with the howl, forming what has been termed the "bark-howl". Bark-howls are emitted by adults, particularly when intruders approach young pups (Theberge and Falls, 1967). Bekoff (1974) speculated that barks serve to draw an intruder's attention toward the vocalizer, thereby distracting their attention from vulnerable young. Barks may also be used to threaten the intruder. It is also possible that barks serve as a cue to vulnerable young to be cautious. Wild and captive wolf pups were observed to run into the den in response to adult bark-howls when a human entered the area (personal observations; Ryon, personal communication). This would indicate that barks may function both as a threat and an alarm vocalization.

The growl

The acoustic structure of the growl is noisy, with a spread of spectral energy ranging from 70 to 2175 Hz (Tembrock, 1963; Harrington and Mech,

1978; Schassburger, 1987, 1993). Growl durations vary in length from less than one to several seconds (Schassburger, 1987, 1993).

The growl, like the bark, is primarily associated with agonistic interactions (Harrington and Mech, 1978; Schassburger, 1987, 1993). Few descriptions of growls are presented in the literature. This may be in part due to this sound's low amplitude and the attendant difficulty in recording it in the wild (Harrington and Mech, 1978). Accounts of growls as threats or forms of warning have been found in both captive and wild animals (Joslin, 1966; Fentress, 1967; Fox, 1971; Schassburger, 1987, 1993).

In summary, various functions for these four structurally distinct sounds of the adult wolf have been suggested. The majority of these vocalizations appear to be reflections of the internal state of the animal (e.g. growls are motivated by agonistic behaviour and squeaks are motivated by affiliative behaviour). This thesis will examine the acoustic properties and the behavioural contexts of these four vocalization classes to characterize the vocal repertoire of young wolves. Five other classes of vocalizations, which have also been identified in a few other studies, will also be described. These other sound classes are: moans, whines (different from Joslin's (1966) definition), screams, squeals and woofs. These classes were judged to be discrete categories based upon their spectrographic structures (Schassburger, 1987, 1993; Frommolt et al., 1988; Coscia et al., 1991). It was not apparent that these vocalizations were simple variations of either howls, squeaks, barks or growls.

Ontogeny of Wolf Vocal Communication

Research into wolf development, including pup social development, is limited. Several investigations into the ontogeny of social behaviour in domestic dogs (*Canis familiaris*) provide comparative data that are useful because of the genetic similarities between these species (Mech, 1970; Wayne, 1993). Although canid communication systems may differ slightly due to genetic diversity as well as a wide range of social systems, underlying physiology and early neonate behaviour share many similarities (Scott and Fuller, 1965; Mech, 1970; Fox, 1971). There are a few studies which provide qualitative and quantitative information on vocal ontogeny (Fox and Cohen, 1977; Field, 1978; Schassburger, 1987, 1993; Coscia et al., 1991).

Pregnant wolves bear their young in dens following a gestation period of approximately 63 days. A litter comprises of four to seven young on average, each weighing roughly 0.5 kilograms (Rutter and Pimlott, 1968; Mech, 1970). Pups reside within the den for the first two to three weeks of life. Between three and six weeks of age, pups may venture from the den to explore their environments. During these short escapades, pups begin to interact with and integrate with pack members other than their mother or in-den care-giver (Ryon, 1977). After approximately six weeks of age pups vacate the den and reside with the pack (Young, 1944; Ryon, 1977).

Before two weeks of age, wolf pups (like domestic dogs) are blind and deaf, and lack coordinated motor skills, yet they are highly vocal (Scott and

Fuller, 1965; Mech, 1970; Frommolt et al., 1988; Coscia et al., 1991). Their activities during this period consist primarily of nursing, sleeping and seeking physical contact. The directional crawling movements of newborn wolves are presumably to maintain contact with their mother and/or siblings, perhaps for thermoregulation, as has been suggested for similar behaviours observed in domestic dogs (James, 1952).

McLeod (1987) examined the development of interactive behaviour in hand-reared wolf pups after the first postnatal week. When neonatal pups aggregate, they manipulate other pup's bodies which results in either continued body contact or facial/oral contact. This neonate huddling was viewed as an early precursor to subsequent interactive behaviour because they both involved similar motor movements. Neonatal pawing and mouthing were classified as "non-social" interactions because pups responded to their sibling in the same manner as they would to an inanimate object (McLeod, 1987).

Early vocal communication of wolves and dogs has been referred to as quiet harmonic expressions of discomfort or separation (James, 1952; Bleicher, 1963; Scott and Fuller, 1965; Fox, 1971; Fox and Cohen, 1977; Field, 1978). The majority of the pups from these studies were manipulated by their observer, thereby exposed to unnatural conditions which were perhaps stressful to them. Among the early pup sounds differentiated in these studies, the most common vocalizations are harmonic in structure. The majority of these harmonic vocalizations were not overtly responded to by the mother or the care-giver. If

pup communication is defined as an intent to elicit an overt response from the care-giver this may suggest that the expression of these sounds is ineffectual in communication. If pups vocalize because of discomfort or separation, it seems logical to assume that their vocal expressions should elicit care-giving behaviour. An alternative view is that these harmonic vocalizations may serve as comfort-state sounds which signal to the care-giver that pups are healthy and content. The rhythm of production of these harmonic sounds is identical to that of normal, silent breathing, suggesting that these vocalizations are derived directly from breathing (Coscia et al., 1991). It may be the absence of these sounds that will elicit care-giving behaviour. Deafened mother turkeys (*Meleagris gallopavo*), for example, will kill their chicks immediately after hatching (as they would an encroaching predator) suggesting that vocal activity from chicks inhibits attack behaviour (Schleidt et al., 1960).

At approximately two weeks of age, a number of physiological and behavioural transformations occur in neonates. Pup eye opening is synchronous with ear erection, onset of hearing and sound localization (Scott and Fuller, 1965; Ashmead et al., 1986). Pups ambulate in an increasingly coordinated manner, engaging first in "unsynchronized" (non-concurrent), and later coordinated (concurrent), interactions with siblings (Havkin, 1981; McLeod, 1987). Adult-like playful and agonistic postures and behaviours occur, although early forms are not necessarily exhibited in the same contexts as for adults (McLeod, 1987).

A number of changes in vocalizations occur in pups after two weeks of age. The rate of vocalizations by pups, especially the harmonic vocalizations which decrease during the first two weeks of life, continue to diminish (Scott and Fuller, 1965; Fox, 1971; McLeod, 1987; Coscia et al., 1991). A number of recognizable adult-type vocalizations (e.g. squeaks, howls) appear at this time, although they are uncommon (Fox, 1971; Schassburger, 1987, 1993; Frommolt et al., 1988; Coscia et al., 1991).

Other notable changes occurring after two weeks of age provide some evidence for physical transformations. Coscia et al. (1991) described a developmental decrease in the fundamental frequency for the harmonically structured neonate sounds (moans and whines). Harrington and Mech (1978) and Schassburger (1987, 1993) reported decreases in fundamental frequency for pup howls. These changes may reflect, in part, the physical growth of the pups. As pups mature, their vocal tract lengthens, thus supporting lower frequency sounds. Additional changes in vocal tract anatomy, for example changes in tension on the vocal chords, likely influence development of call structures. However, increased control of the laryngeal muscles has the effect of elevating the fundamental frequency of sounds. Studies of vocal development in both human infants (Sheppard and Lane, 1968) and kittens (Romand and Ehret, 1984) reported increases in fundamental frequency during the early postnatal days, which they attributed to an increase in subglottal pressure resulting from development of vocal-motor control. They also

documented subsequent and substantial decreases in call fundamental frequency, attributed to an increase in the length of vocal chords.

Reports on the behavioural context of early pup vocalizations are anecdotal. Coscia et al. (1991) report recognizably adult sounds (e.g. barks) emitted in non-adult contexts (e.g. resting). They also document some early pup vocalizations (e.g. squeaks, woofs) that were acoustically adult-like, and emitted in adult-like behavioural contexts. Some investigators state that the neonatal whine, which is said to be produced in a distress-associated context, is the progenitor to the adult howl (Harrington and Mech, 1978; Schassburger, 1987, 1993; Frommolt et al., 1988). Both pup whines and adult howls are produced in some contexts of separation.

The limited knowledge of wolf vocal development is due, in part, to the shy and elusive nature of the wild wolf, rendering close-range examination of developmental changes in wild pups virtually impossible. There are also difficulties in recording detailed observations of ontogenetic processes in captive wolf pups. Captive female wolves, if given the opportunity, dig dens for bearing and raising pups (Ryon, 1977). Most observations of pup behaviour come from animals that were removed from their den and either manipulated by their observers or were housed in an artificial manner (Schassburger, 1987, 1993; Frommolt et al., 1988). These conditions may lead to disruptions in natural behavioural patterns. Significant differences in the frequency and quality of vocal behaviour in young monkeys reared in an artificial environment, compared

to young reared in semi-natural conditions, have been described (e.g. Kawabe, 1973).

Wolf behavioural research is also plagued with the same problems as other mammalian vocal communication studies: 1) problems with categorizing vocalizations; and 2) problems with determining which and how many acoustic parameters should be measured. Neither Schassburger (1987, 1993) nor Frommolt et al. (1988) clearly describe their scheme for categorizing vocalizations. They merely report the measurements of various acoustic dimensions. While these authors do describe the age of emergence for the various vocal classes, they do not report the sample size from which their measurements were taken for each vocal class and each age category.

An unobtrusive system for monitoring the behaviour of adults and neonates in the den of a captive pack of wolves has been developed in our research lab (McLeod, 1987; Coscia et al., 1991; Goldman et al., 1995). A remote-controlled, in-den recording system permits extensive and unobstructed video and audio monitoring of activities from birth. With this system, visual and vocal behaviour may be recorded on a 24-hour basis to systematically document behavioural events. The relatively brief period of time which pups spend in their natal den is a critical time when pups develop the acoustic and behavioural repertoires required for pack integration and survival.

Coscia et al. (1991) have described the changes in the vocal behaviour of a litter of pups from birth until pup departure from the den, thus providing a

framework by which to analyze and classify the wolf vocal repertoire (Coscia et al., 1991). The physical structure of sounds was examined and a scheme for categorizing sounds was developed based on joint differences in at least two dimensions from a list of five acoustic parameters selected for analysis. The acoustic properties used to classify pup vocalizations were: 1) gross spectral type (i.e., harmonic, noisy), 2) duration, 3) absence or presence of frequency modulation, 4) rate of frequency modulation, and 5) the frequency range or spectral bandwidth. Before pups abandoned the den at six weeks of age, they produced all of the classes of primary vocalizations reported for adult animals. Since that initial examination, two more litters have been added to the existing database. These litters provide additional quantitative data to assess the generality of Coscia et al.'s (1991) findings. In addition to characterizing the acoustic properties of vocalizations, a detailed, quantitative analysis of the behaviour accompanying pup vocal production was undertaken to examine the functional role of the various vocal classes. This analysis of the development of sound communication in wolves may provide comparative data and a framework for future studies of vocal ontogeny in wolves and other social mammals.

Purpose of the Present Study

It is critical first to obtain quantitative descriptive data that traces both the sources of variation as well as the sources of stability in vocalization parameters

through development. Longitudinal studies can be useful in clarifying the process of development, including the basic question of how specific changes in one behavioural domain relate to other behavioural domains or other changes within a given domain (Golani and Fentress, 1985; Smith and Thelen, 1993). For such efforts to be successful a prerequisite is to provide objective taxonomies of behaviour that can be applied in a consistent manner across the developmental time period of interest (e.g. Adams-Curtis and Fragaszy, 1994).

There are few studies in which objective, multidimensional taxonomies have been applied to the analysis of vocal ontogeny. There have been only three studies which attempted to describe comprehensively the early vocal development of wolves. The first two of these studies lacked systematic methodologies for classification, lacked quantitative data and involved manipulation of study animals (Schassburger, 1987, 1993; Frommolt et al., 1988). The third study (Coscia et al., 1991) described neonate vocalizations in a systematic, quantitative manner from undisturbed animals within a semi-natural setting. That examination characterized the vocalization classes acoustically according to an objective classification scheme but without details about their behavioural context.

Based on data from these previous studies, it is evident that the process of vocal development in wolf pups is not clearly understood. First, wolf pups produce vocalizations that can be grouped into discrete categories. Many of these categories have been characterized solely as expressions of the young's

internal state of discomfort and/or distress. Pups also produce adult-like vocalizations early in development. Are these early-appearing adult-like sounds produced in the form of "babbling", as described for some primates (Snowdon et al., 1986)? In this case, one would expect to find that the adult-like vocalizations were not associated with adult-like contexts. Second, there are reports in the previous literature (e.g. Schassburger, 1987, 1993; Frommolt et al., 1988) that some adult-like vocalizations (barks and growls) are not present at birth, but occur at later ages in pup development. It is not known, however, in what context these adult-like vocalizations are produced and whether the context changes with maturation. Third, it is also not known if and how the relative proportion of various vocalizations change as a function of age and what happens to the acoustic structure of vocalizations with both physical and social development.

Examinations of the behavioural state of pups and their care-giver, the external stimuli which may have elicited pup vocal production and the behavioural response of their care-giver to pups' vocalizations may shed light on the communicative function of the pup vocal repertoire. It was the purpose of this study to assess quantitatively previous findings in a more detailed and rigorous manner than previously described, and to examine neonate vocalizations within their behavioural context. To achieve the goals of this study the following approach was undertaken:

1. Use of a systematic, multivariate classification scheme to categorize vocalizations from three litters of wolf pups during a critical time in their development, the first six weeks of age.
2. Analyze the acoustic structure within vocal classes to: (a) determine if the vocal repertoire can be classified into discrete categories and/or whether vocalizations were graded along a continuum, and (b) address whether these parameters were invariant across time.
3. Analyze the relative proportions of vocal classes as a function of age.
4. Analyze if and how different vocal classes are related temporally (i.e., combined in series).
5. Analyze selected behaviour associated with the more common pup vocalizations to: (a) address how selected patterns of the behavioural repertoire changed as a function of age, and (b) address whether and how the associations between selected patterns of behaviour and vocalizations changed.
6. Interpret the usage/function of elements within the vocal repertoire in pup development.

CHAPTER TWO

METHODS

Study Site

The wolves were maintained at the Canadian Centre for Wolf Research (CCWR), a secluded reserve in Shubenacadie, Nova Scotia. This heavily wooded, semi-natural enclosure housed a group of pack-reared animals within a 3.1 hectare area. The wolves were fed daily with a high quality prepared dog kibble (Eukanuba) and, on occasion, road-killed deer. The pack-reared animals had no direct physical contact with researchers at the field station but were habituated to the presence of observers outside of the fenced-in enclosure. The number of animals in the pack ranged from 9 - 14 individuals during the four year period of data collection.

Subjects

The captive wolves were descendants of North American timber wolves. "Pawnee", the alpha female, was the mother of all litters in this study. Each year Pawnee gave birth to a single litter of pups in a den. "Ursula", an adult female who had pups in previous years, would occasionally enter the den and care for the pups either when Pawnee was present or absent. The paternity of each litter was uncertain since it was not possible to observe all matings. However, copulatory ties between Pawnee and the alpha male, "Fingal", were observed

during the mating seasons in which the pups were conceived. In the past several years, subdominant males also mounted the alpha female and subdominant females. Males were never observed to enter dens during any of the pup seasons studied. Specific information regarding birth dates and number of pups within each litter follows:

1988: Five pups, four males and one female, were born May 14th. Two males were removed for hand-rearing on May 28th. Data were collected on the remaining three pups.

1989: Five pups, four males and one female, were born May 14th. Two males were removed for hand-rearing on May 23rd. Due to the poor health of one of the hand-reared pups, a third pup, a male, was removed on May 27th. The two remaining pups in the den did not survive past two-and-a-half weeks of age thereby terminating data collection. Data from this litter had to be eliminated from the study as a complete six week record of activities was not possible.

1990: Five pups were born May 10th. One pup died within the first 48 hours. Data were collected on the remaining two males and two females. At three weeks of age, pups were individually marked for identification, by carefully shaving a small section of fur dorsally.

1991: Three pups, all female, were born May 9th. No pups died and none were removed for hand-rearing.

Monitoring System

Den description

The pups were delivered in one of two modified dens (McLeod, 1987). The dens were naturally dug out by the wolves within mounds of earth and woody debris situated around the periphery of the compound. Dens have been periodically reinforced with lumber and galvanized tin to prevent natural deterioration. Additional modifications included installation of a 3.5 m long, 90 cm diameter galvanized steel conduit buried within the mound adjacent to the internal den. The conduit did not obstruct the tunnel created by the wolves for movement into and out of the den, and provided an observer access to the in-den recording equipment for unobstructed monitoring of wolf activities in the den (Figure 1). The equipment was mounted on a 76 cm cubical wooden frame for support. A removable wooden frame with a mesh metal screen was attached to the end of the conduit adjoining the den to protect the equipment from the wolves. The screen had a central 10x10 cm opening for the camera lens. The opposite end of the conduit was fitted with a wooden, hinged door to prevent wolves from entering it.

Recording equipment

A video camera was located at each of the two den sites. A Panasonic WV-1650/KT2 CCTV black-and-white surveillance camera with an 8.5 mm lens (f/1.5) and a Sony, black-and-white, TV camera were used in 1988. In 1989,

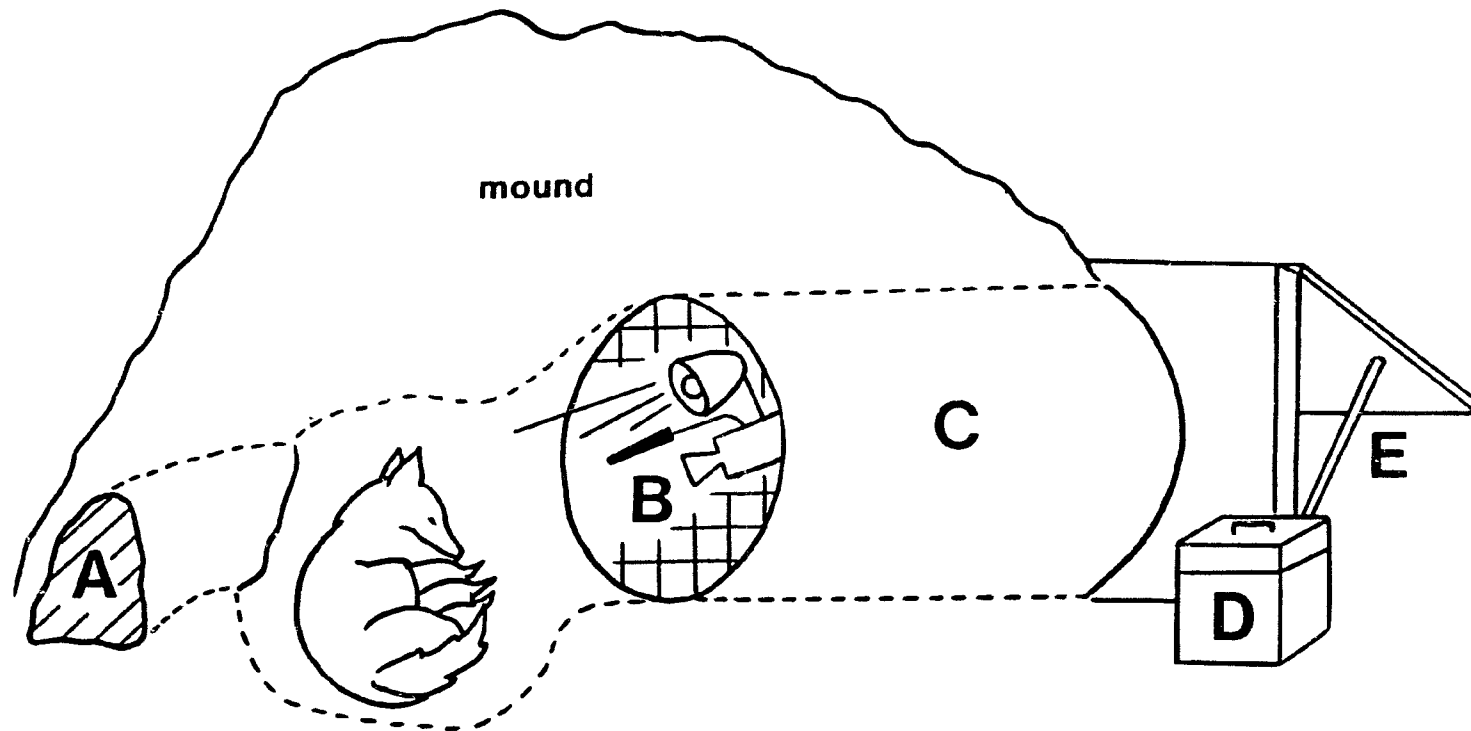


Figure 1. Schematic representation of modified wolf den (1988-1990). A: wolf entrance; B: microphones, camera, and lamp mounted to wood frame behind a protective mesh screen; C: galvanized steel culvert through which equipment and power cables are run; D: safeguard box with audio and video recorders and marine battery power source; E: observer entrance into tunnel for access to equipment.

an Hitachi VK-C150 colour video camera with an 8 mm lens (f/1.5) replaced the Sony camera. In 1991, the colour camera was fitted with a Cosmocar Zoom Lens (12.5 - 75 lens (f/1.8)) adjusted with a Vicon V3030 Pan Tilt remote-controlled unit, to increase viewing range, and a zoom/focus mechanism to adjust focal length. These features permitted close-up or wide-range monitoring and allowed individual pup or litter movements to be followed smoothly with conversion from wide-angle to telephoto viewing by means of a Vicon V1121C controller. The cameras were connected to a Panasonic NV-8420 or an AG-400 portable VHS cassette recorder. From 1988-1989, 12 volt marine batteries served as the power source at both den sites. A single 55 Watt halogen car headlight equipped with a filter was used to illuminate the dens.

In 1991 the lighting was altered in Den 1 to increase illumination, particularly in the den tunnels. Four 55 Watt halogen car headlights were installed in the den ceiling. The lights were directed to a reflector board and provided light of uniform distribution. Wooden safeguard boxes located outside the conduit protected the batteries and recording equipment, and allowed observers to change tapes and batteries with minimal disturbance to the wolves in the den. Also in 1991, electricity was wired to Den 1 and a surveillance blind was constructed outside of the enclosure nearby. Cables connected to the in-den equipment and lights were wired to the video and audio recorders and a video monitor within the blind. The purpose of this was two-fold. First, all tape changes were possible without entering the wolves' enclosure. Second, on-site

monitoring with the remote-controlled camera allowed observers to witness den activities as they occurred and adjust camera focal length and position according to pup movements and actions in the den. In addition, a Panasonic AG-7400 portable S-VHS recorder was used to record representative, high-quality video images at pre-selected times.

Two Sennheiser Super Cardioid Shotgun ME 80 microphones, each with a Sennheiser K3-U power module and MZW-415 windscreen, were used to collect audio signals. Audio recordings were made on Sony UX90 Type II cassettes with a Marantz PMD 430 stereo cassette recorder (4.75 cm/sec) simultaneous to video recordings on T120 Scotch HG VHS or T120 Pro JVX ST S-VHS video cassettes. The audio frequency response of the tape recorder was flat from 30 Hz to 15 kHz with a signal to noise ratio of 75 dB. The audio frequency response of both Panasonic video tape recorders was flat from 50 Hz to 12 kHz, with a signal to noise ratio of 43 dB for the VHS recorder, and a signal to noise ratio of 48 dB for the S-VHS recorder. The audio recorder's sensitivity level was optimized for recording vocalizations from wolves in the den.

The majority of all tapes were recorded in standard play (120 minutes per tape) but a few tapes were recorded in slow-play (360 minutes per tape). The quality of spectrographic recordings from the slow-play tapes was visually compared with standard play tape recordings and there appeared to be no anomalies in any of the frequency/time acoustic parameters measured.

Data Collection and Data Scoring

For all three years, recordings of litter activities were systematically collected to cover all times of the day every three days. Efforts were made to record on a daily basis. The schedule was occasionally interrupted because of either equipment malfunction or a den transfer. The observation period spanned from birth to postnatal week six. After six weeks of age, pups spent the majority of their time outside the den. Nearly 900 hours of video and audio recordings were collected in total from the 1988, 1990 and 1991 litters. Most video and audio recordings were made simultaneously except for the 1988 recordings in which 47% of the audio tapes were recorded without the camera and lights in operation. This was done to eliminate possible confounding influences the lights may have had upon wolf vocal production. The audio tapes from 1988 have been analyzed previously (Coscia et al., 1991). It was determined that operating the camera and lights did not obviously affect the vocal production of the pups because pups produced the same types of vocalizations under both conditions. Audio recordings in 1990 and 1991 were only collected with the camera and lights in operation.

From the library of tapes, three two-hour video tapes from three different times per day (approximately 00:00 hours, 08:00 hours and 16:00 hours) for each of the six postnatal weeks for all three litters were used. For each week, the first available tape from the pre-selected three day time period was chosen. For example, for week one, tapes were selected from each litter between

postnatal days two to five, week two between days seven to ten, etc. A total of 108 hours of video tape were selected to be analyzed, 36 hours from each of the three litters. The 1988 litter data tapes used in the Coscia et al. (1991) study were not included in the present study. The large library of audio (99 hours) and video (186 hours) tapes recorded during 1988 made this possible.

Scoring accoustical data

Figure 2 displays a schematic diagram of the behaviour/sound analysis system. Each video tape was viewed in real-time for analysis of the behavioural activities in the den. Headphones were used to listen to the audio component of each tape for detection of all sounds, including adult wolf vocalizations and environmental noise outside the den. The electrical signal from the video system was amplified and sent directly to a Data Translation 2821-F-SE analogue/digital converter board of a Dell 386 computer. Vocalizations were digitized using SIGNAL™ and RTS™ (Real-Time Analysis System). Both programs were designed by Engineering Design (1990) specifically for the spectral analysis of animal vocalizations. The programs have a 12-bit ADC, with a maximum sampling rate of 150 kHz. The digitized signal, resulting from a 512 point Fourier transform of the analogue signal, was displayed on a monitor in continuous frequency-time plots (spectrograms) generated from RTS. Spectrograms scrolled across the screen in real-time, but could be "frozen" in time for acoustic measurement. Measurements were made directly on-screen

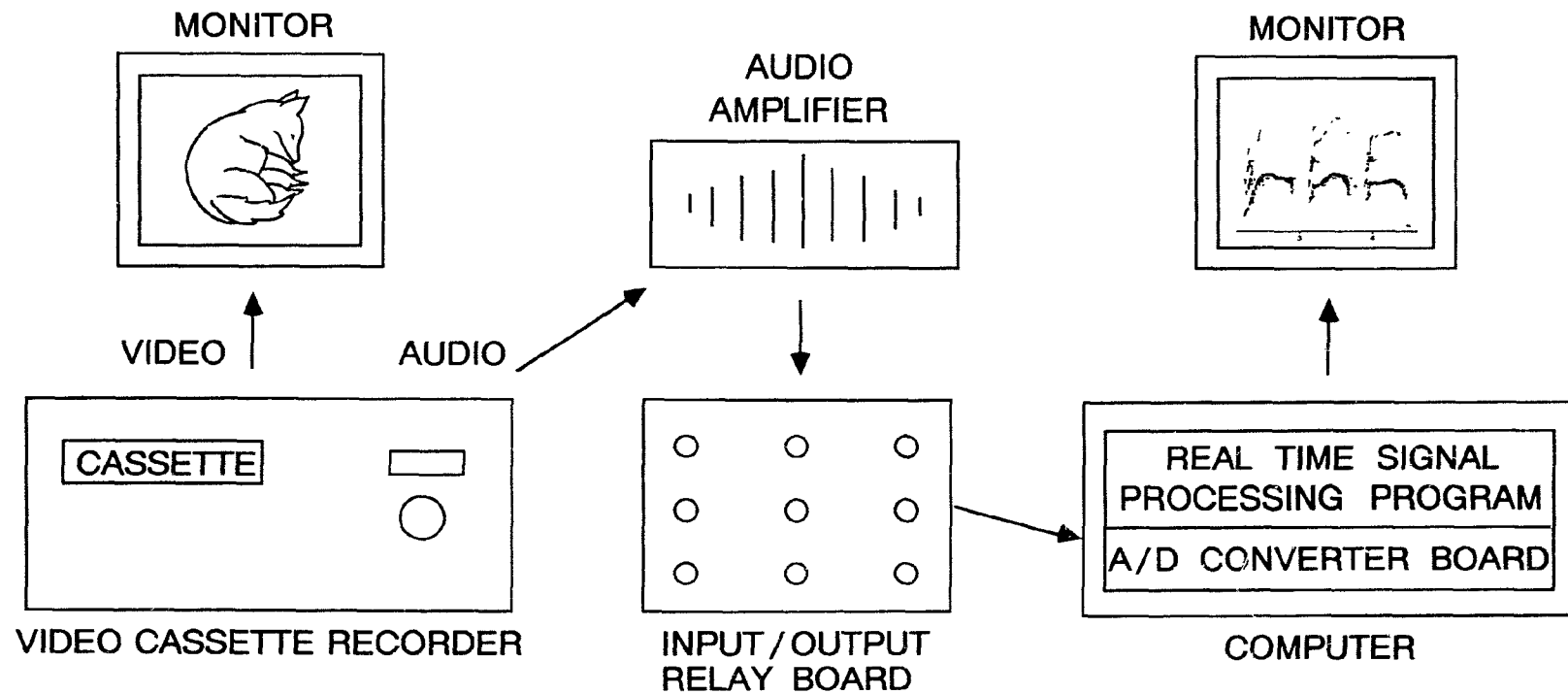


Figure 2. Schematic diagram of the system used for analyzing vocalizations and corresponding behavioral context.

with the program's time/frequency maneuverable cross-hair cursors. Time and frequency values, and differences between chosen points, were automatically displayed on-screen. The digitized wave forms for representative spectrograms were stored in separate files for transfer to SIGNAL. Hard-copies of the representative spectrograms were generated using SIGNAL and a 300-dpi Hewlett Packard LaserJet Series II printer. RTS did have hard-copy capabilities but the quality of the SIGNAL spectrographic image was preferable because the time and frequency scales were included in the printout.

RTS allows its user to adjust the number of points per second based on the fixed 512 point Fourier transform for a series of spectrographic images. The points per second yielded various bandwidths. For example, if the points per second were set at 10,000, the operative analysis bandwidth was 4000 Hz. Thus, the narrower the bandwidth, the better the spectral resolution. Wolf pup vocalizations contained spectral energy across a frequency range of 30 - 15000 Hz. Certain vocal classes, e.g. Squeaks, required a wider bandwidth than others, e.g. Growls, to capture the entire spectral image.

For each measurable pup vocalization that scrolled across the computer screen in real-time, the image was "frozen". The relevant acoustic data were measured and directly entered into a spreadsheet (Quattro Pro). When several pups vocalized simultaneously, or when other sounds or noise occluded the spectral structure of the pup sound, only the class of vocalization(s) emitted and the behavioural information related with the acoustic event were recorded.

Moans and Whines, often emitted in continuous series, were not counted or quantified. Moans and Whines were described quantitatively in Coscia et al. (1991). Representative samples of these sounds across the six week analysis period in this study were collected. Moans and Whines followed the same developmental trends as those presented in Coscia et al. (1991).

The acoustic parameters used to classify vocalizations were:

- (1) Gross spectral structure (Pure tonal, Harmonic, Noisy, or a combination of structures).
- (2) Mean sound duration (in seconds).
- (3) Mean duration (in seconds) between sounds within a series of consecutive sounds. Sounds within a series were named "elements". If the duration of the "inter-element-interval" was greater than 1.5 seconds, the sound subsequent to the pause was classified as separate from the series. Typically, the inter-element-interval varied across sound classes but did not exceed 1.0 seconds for all sound classes. Although the decision to choose an interval duration of 1.5 seconds was, in part, arbitrary, it provided a standard measure to assess different sound classes across different ages.
- (4) Frequency modulation. The presence or absence of frequency modulation was noted and described. The coefficient of frequency modulation (COFM) was quantified for Howls greater

than 0.3 seconds in duration. The COFM provides a relative measure of frequency modulation between consecutive intervals within a sound. The COFM was computed by summing the absolute differences of the fundamental frequency (Hz) between 0.1 second intervals for individual Howls. This sum was divided by the total number of intervals. These means were standardized by dividing by the mean fundamental frequency for that Howl, then multiplying by 100.

- (5) Mean fundamental frequency (Hz) of pure tonal and harmonic vocalizations. Fundamental frequency measurements were sampled at 0.1 second intervals for vocalizations longer than 0.3 seconds in total duration. In order to minimize sampling error of the low-frequency harmonic vocalizations, frequency and time measurements were taken from the second harmonic, and then divided by a factor of two.
- (6) Mean fundamental frequency variation (Hz) of pure tonal and harmonic vocalizations. The difference between the maximum frequency and the minimum frequency was calculated to obtain the frequency variation.
- (7) Mean maximum and minimum fundamental frequency (Hz). The noisy vocalizations which contained minimum frequencies below 100 Hz could not be accurately or consistently measured because

of intermittent interference with background noise. Therefore, the minimum frequencies for these sounds were not measured.

- (8) Maximum amplitude range (voltage) of Squeals and Screams. Squeals and Screams were two sound classes which had overlapping distributions of both fundamental frequency and duration. Squeals and Screams, however, differed perceptually (i.e., detected, by human observers, with the recording equipment) in sound intensity. Accurate measurements of absolute sound amplitude are difficult to obtain because it varies depending on the vocalizer's orientation to the microphone and the amount of environmental interference. To assess the relative maximum amplitude, 12 samples each of Squeals and Screams were selected from a single tape from each litter across the three week period when these two sounds were most common (weeks one to three). The frequency-time window and gain setting were fixed for the analysis. Amplitude measurements of the samples from weeks two and three from the 1991 litter were not possible without adjusting the gain so they were omitted from the amplitude analysis. Although RTS displays the time waveform on-screen, there is no scale by which to measure the voltage. Files of the digitized waveforms were generated through SIGNAL for amplitude analysis. The maximum amplitude range was defined as the point

of greatest amplitude for each waveform. This point was measured, using the on-screen frequency cursors, for 168 Squeal and Scream waveforms.

Scoring behavioural data

For each pup vocalization, or when several pups vocalized, a frame-by-frame analysis of the in-den behaviour was performed. The behavioural categories selected for analysis were chosen to describe the contextual setting of pup vocalizations in an *objective* (i.e. no implied functions were associated with each category) manner. These data were collected to assess the behavioural activity of pups, the behavioural state of the care-giver (if present) and the behavioural response of the care-giver to pup's vocal activity. In addition, any audible stimuli external to the den, which may have elicited pup vocal activity, were of interest. The following in-den behavioural information, when discernible, was hand-scored onto a spreadsheet (Quattro Pro) on a Commodore PC10 286 computer:

- (1) Vocalization class or classes (if multiple sound types were produced consecutively in the form of series). Vocalization classes included: Squeals, Screams, Yelps, Growls, Barks, Squeaks, Woofs and Howls/Bark-Howls. Sound series were either labelled as "Pure" or "Mix". Pure series contained only one

sound class, whereas Mix series (i.e., mixed series) contained multiple sound classes. In this thesis, the phrase "Mix" series was used to avoid confusion for the reader between mixed *series* and mixed *sounds* (see Chapter Three).

- (2) Number of pups present.
- (3) Pup behaviour. Behaviour categories included: 1) "contact stationary", physical contact with other pups or adult(s), includes nursing, huddling, resting; 2) "contact moving", physical contact with other pups or adult(s), includes substantial body movements such as rolling, locomoting; 3) "no contact stationary"; 4) "no contact moving"; and 5) "interactive" behaviour with littermate(s) or adult(s) includes wrestling, pawing, chewing and all forms of reciprocated and un-reciprocated (in which a pup's directed actions are not overtly responded to by the receiver) interactions.
- (4) Vocalizer's identification (1990 litter only). If it was possible to identify the vocalizer, the vocalizing posture was also recorded.
- (5) Presence/absence of mother and/or other adult.
- (6) Mother's/adult's behaviour. Adult behaviour was categorized as: 1) "stationary", contact with pups includes huddling/resting and nursing; 2) "groom", physical contact with pups in the form of licking, nuzzling and/or nibbling; and 3) "movement", repositioning and exiting/entering (both often associated with pups being

stepped on), pup carry; and 4) "vocal".

- (7) Care-giver's response to the pup's vocalizations. Responses were categorized as: 1) "no response", no overt change in the care-giver's behaviour; 2) "ears", ear movement oriented towards the pups; 3) "other", includes ear movement and/or nuzzling, grooming, repositioning, pup carry and other overt behaviours not including vocalizing; 4) "other vocal", "other" response (see 3) plus vocalizing. The class of vocalization(s) emitted by the care-giver was also noted.
- (8) External (to the den) sounds. These sounds included wolves vocalizing outside the den (in particular Howls and Squeaks), wolf movement near/in the den tunnel and environmental noise (trains, planes, automobiles, avian calls and precipitation).
- (9) Additional notes were taken to record other significant activities in the den.

On average, six hours were required to score the acoustic properties and the behavioural context for one, two-hour, video-tape. Approximately 648 hours were required to score 108 hours of tape. In total, 3,396 sounds were categorized and measured quantitatively and over 800 acoustic/behavioural events were described.

CHAPTER THREE

RESULTS: ACOUSTIC PROPERTIES OF WOLF PUP VOCALIZATIONS

General Acoustic Observations

Neonatal wolf pups emitted sounds moments after birth. Vocalizations occurred frequently during the first two postnatal weeks for all three litters, and then decreased as pups matured. An increased variety of vocalization forms emerged as pups matured, although vocal production in general was less frequent.

The acoustic database of 3,396 sounds is the largest ever obtained for wolves. This database consists of only the clearly defined vocalizations collected when a single pup was vocalizing. When more than one pup vocalized, the spectrographic image was intricate, with occluded structures, rendering quantification of single calls unreliable; therefore absolute counts of all vocalizations were not possible.

Identification of the vocalizing pup was rarely possible as the majority of pup sounds were emitted with no discernable facial or postural movements. Therefore, vocalizations were necessarily characterized for a combined litter rather than for a single pup. On a few occasions, however, the oral-facial musculature and the body posture of the pup enabled the identification of the vocalizer pup (e.g. Howls and occasionally Screams and Yelps, vocalizations in which mandible opening correlated with the vocal output). Tracking of a single

pup's development throughout the duration of the study was not possible because pups were similar in size and colour and, therefore, were difficult to distinguish. In addition, pups could not be sexed by size. Although sexual dimorphism in pup body weight exists, it reportedly does not begin until around week ten of postnatal development (Mech, 1970), several weeks after the analysis period of this study.

Quantitative Acoustic Analyses

This chapter on the acoustic properties of wolf pup vocalizations is divided into six sections. The first and second sections present descriptive quantitative data on the vocal classes emitted by three litters of pups and their development from birth to six weeks of age. The three litters were pooled for these statistical analyses. The third section presents the relative proportion of the most common vocal classes for each litter as a function of age. The fourth section is composed of statistical analyses of the acoustic properties of Squeals and Squeaks. Large samples of these vocalizations allowed for the quantitative analysis of individual litter trends. The final two sections present descriptive information on Mix series and observations of isolation Howls and mixed sounds (single vocalizations which are composed of two distinct sound classes).

Vocalization classes distinguished

Eight vocalization classes were described and quantified in this study:

Squeals, Screams, Yelps, Growls, Barks, Woofs, Squeaks, and Howls. Criteria for each sound class are outlined below. Representative spectrograms of these eight vocal classes are displayed in Figures 3-10. Three samples are provided for each vocalization depicting their spectral characteristics at various ages. Vocal categories were distinguished by joint differences in at least two acoustic dimensions following Coscia et al. (1991).

The acoustic structures for all of the vocal classes are characterized below and summarized in Table I. The mean data from all three litters were calculated for each week and then averaged across the six week period of development to provide mean profiles. In the first column of Table I (reading from left to right) the vocalization classes are listed, including the total number of vocalizations of each class that were measured for all litters. Columns two through six display the acoustic properties for each vocal class. In column two, the gross spectral type for each vocalization class is described. Column three presents the mean duration (\pm standard error) of all vocalizations within each class. In column four, the general pattern of frequency modulation is described for all of the harmonic and pure tonal sounds. Column five provides the mean fundamental frequency (\pm standard error) for the harmonic and pure-tone sound classes. In the last column, the mean highest frequency element and the mean lowest frequency element of all sounds are specified to define the extreme components of a sound's frequency range.

Table I is a revised version of the table of acoustic properties of wolf pup

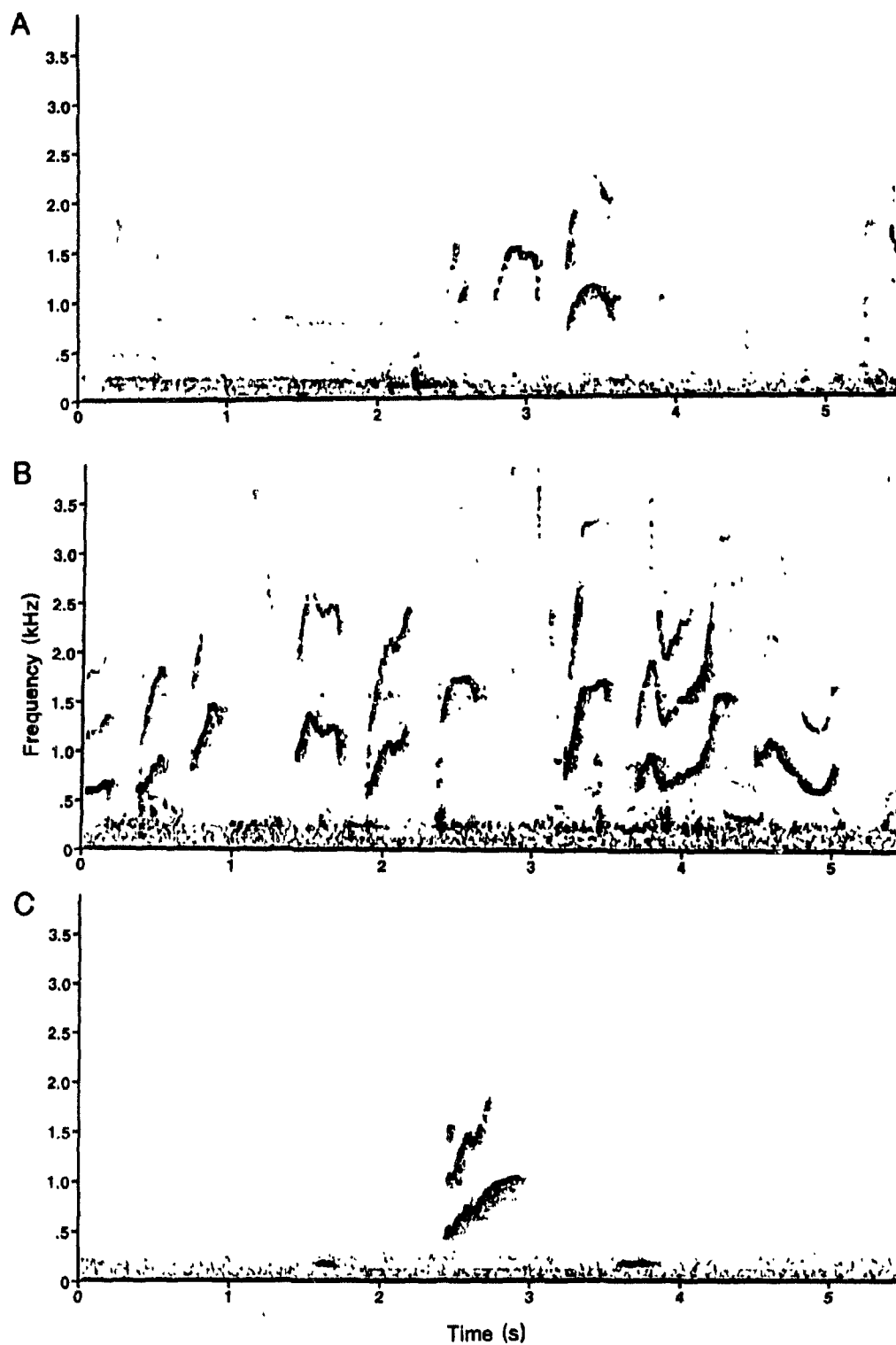


Figure 3. Squeals: week one (A), week two (B) and week four (C).

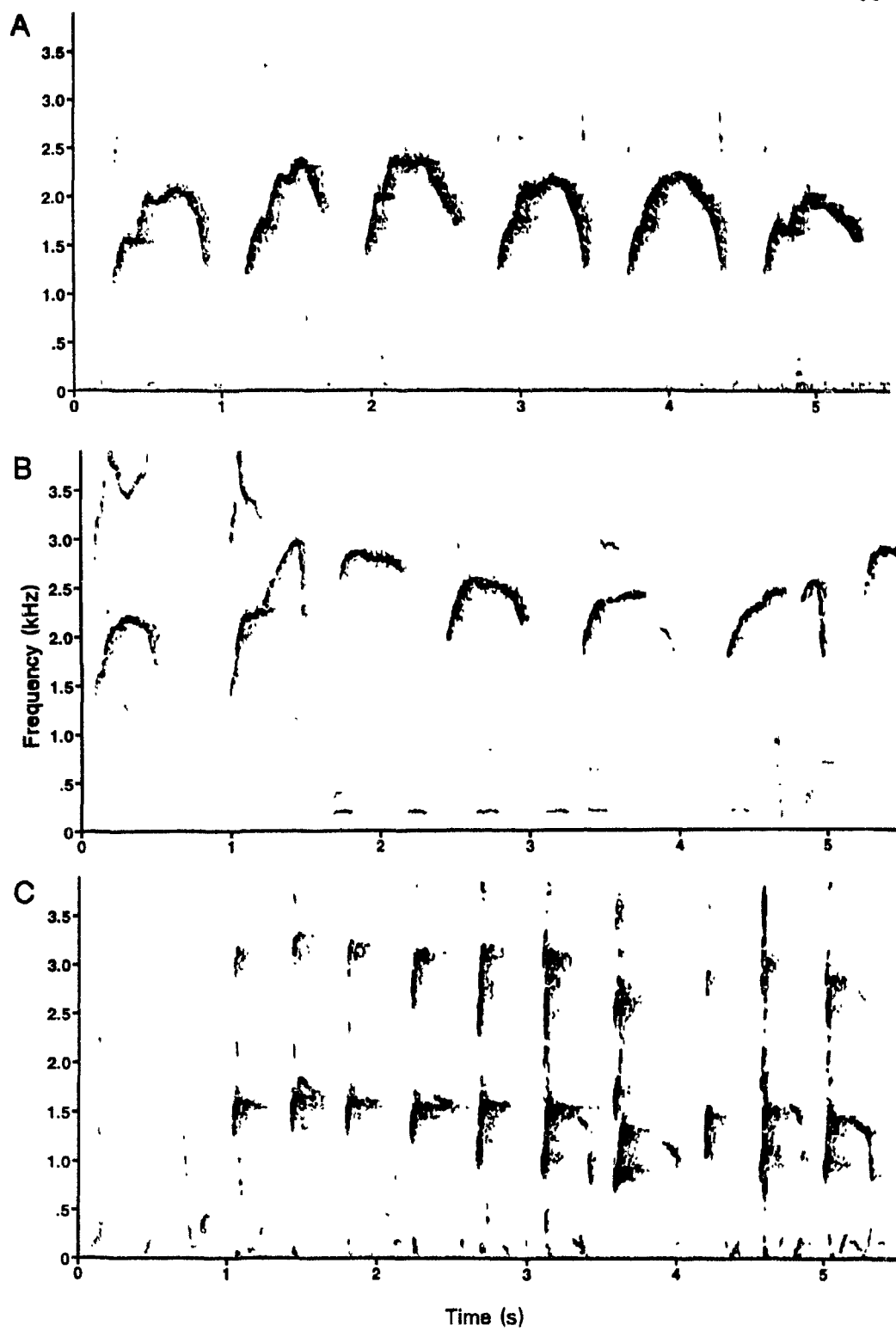


Figure 4. Screams: week one (A), week two (B) and week five (C).

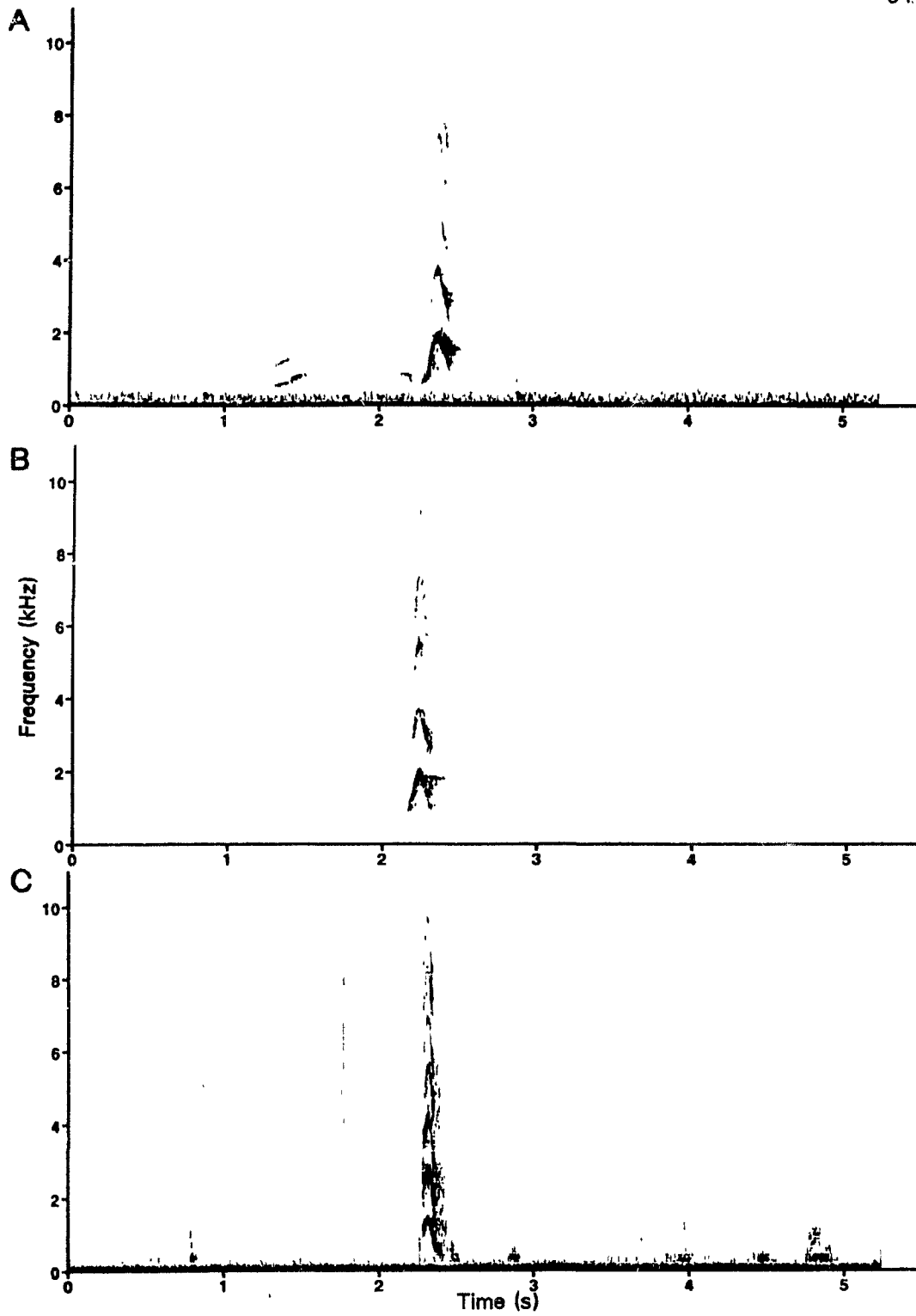


Figure 5. Yelps: week one (A), week one (B) and week two (C).

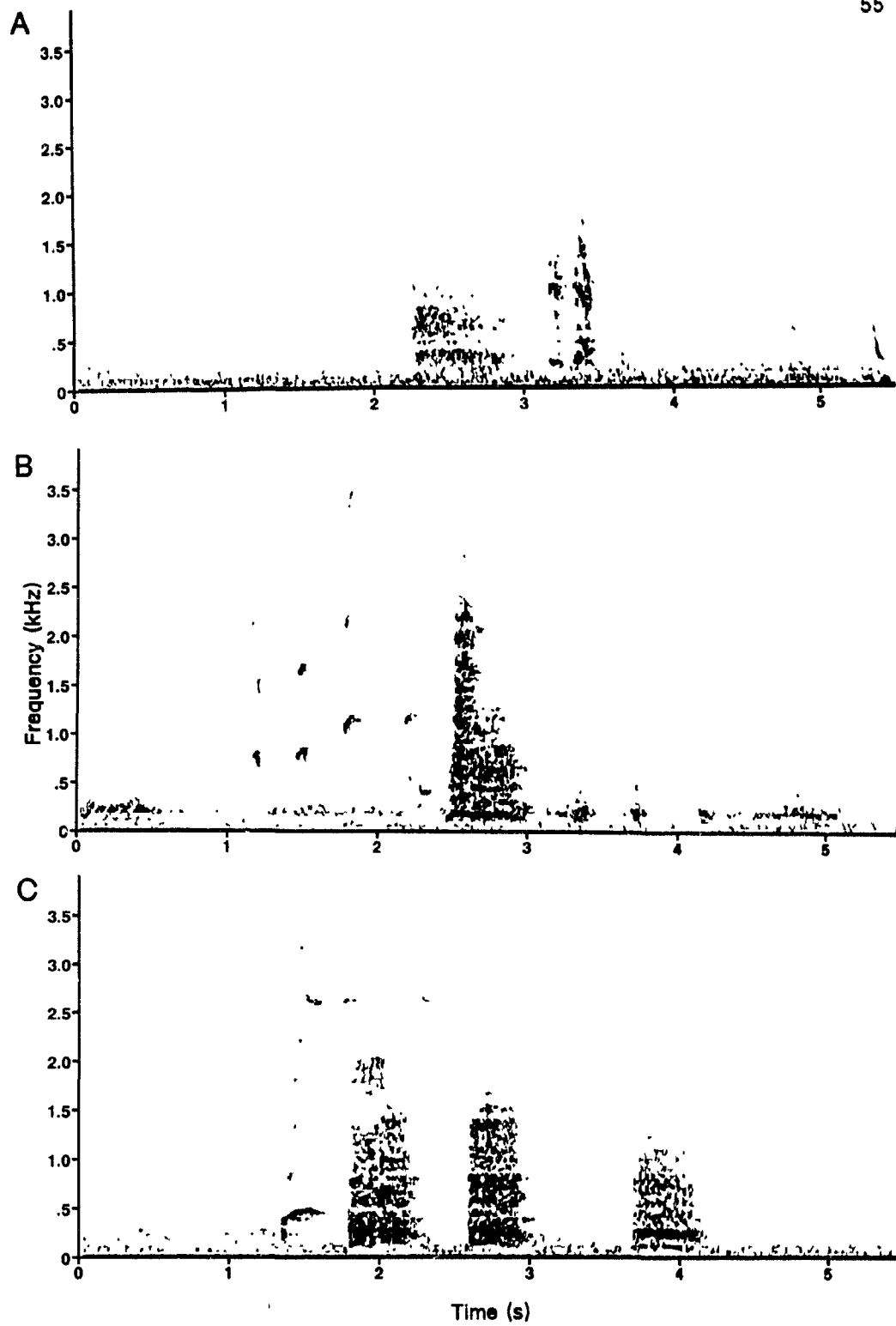


Figure 6. Growls: week one (A), week three (B) and week four (C).

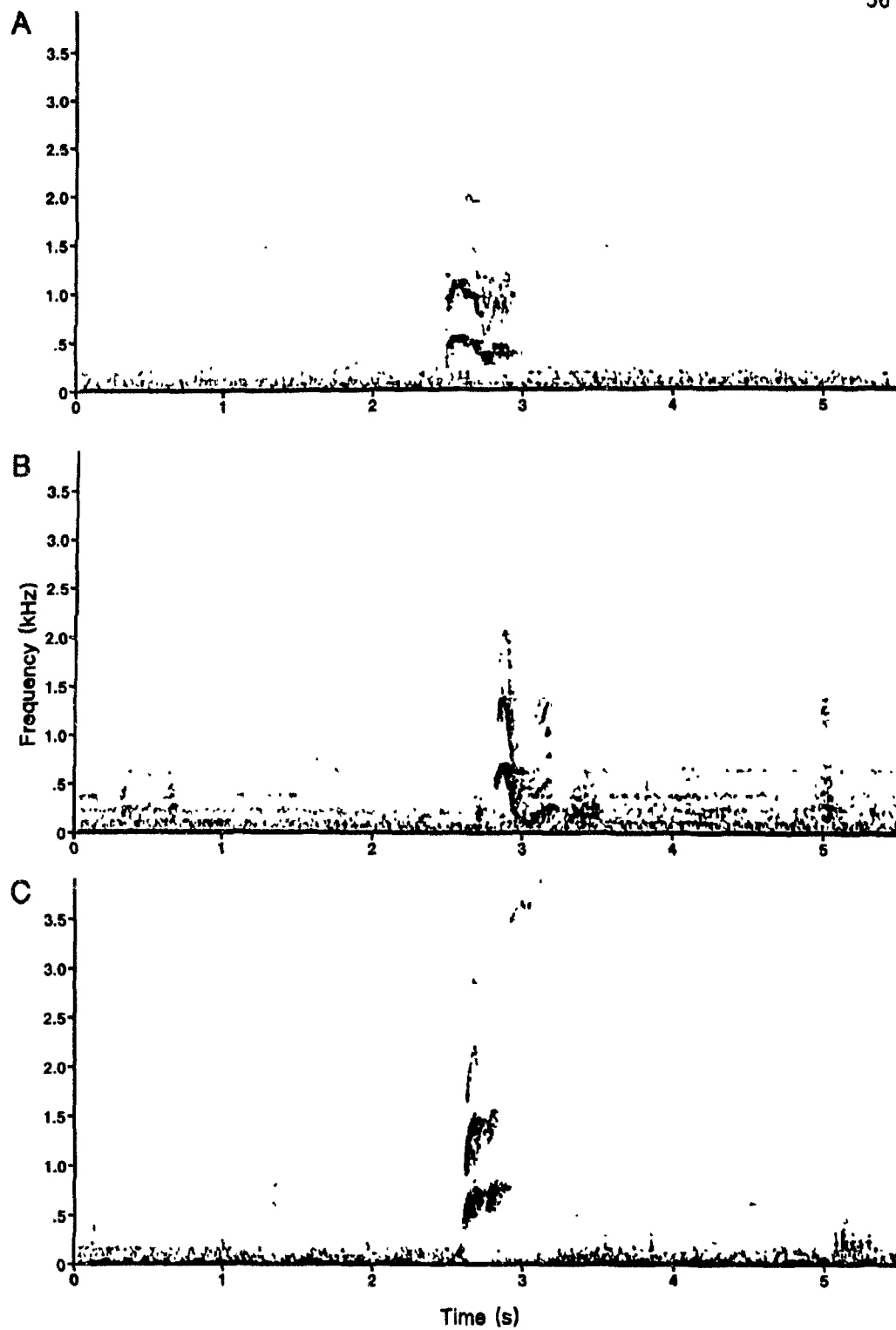


Figure 7. Barks: week one (A), week four (B) and week five (C).

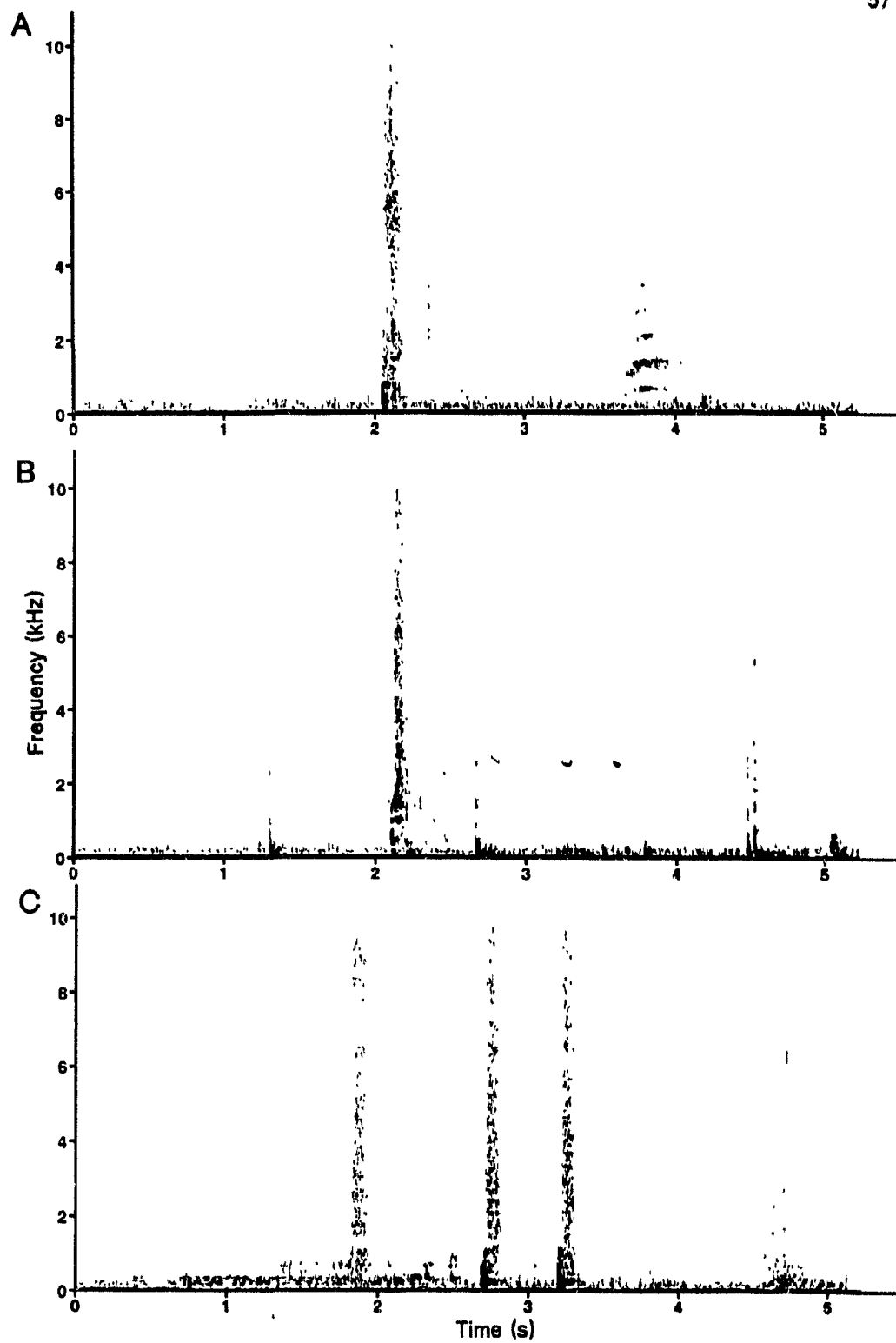


Figure 8. Woofs: week four (A), week five (B) and week six (C).

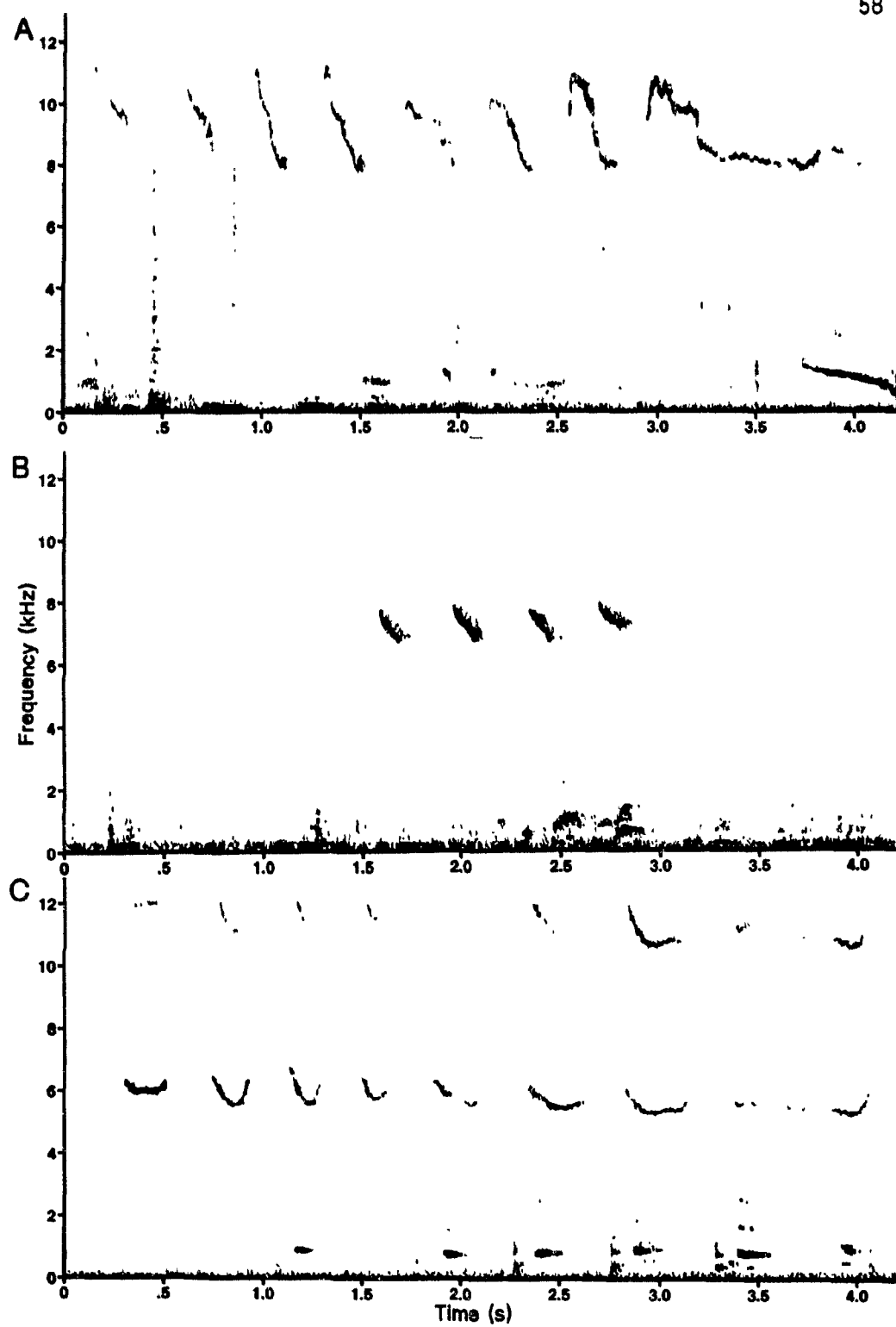


Figure 9. Squeaks: week three (A), week four (B) and week six (C).

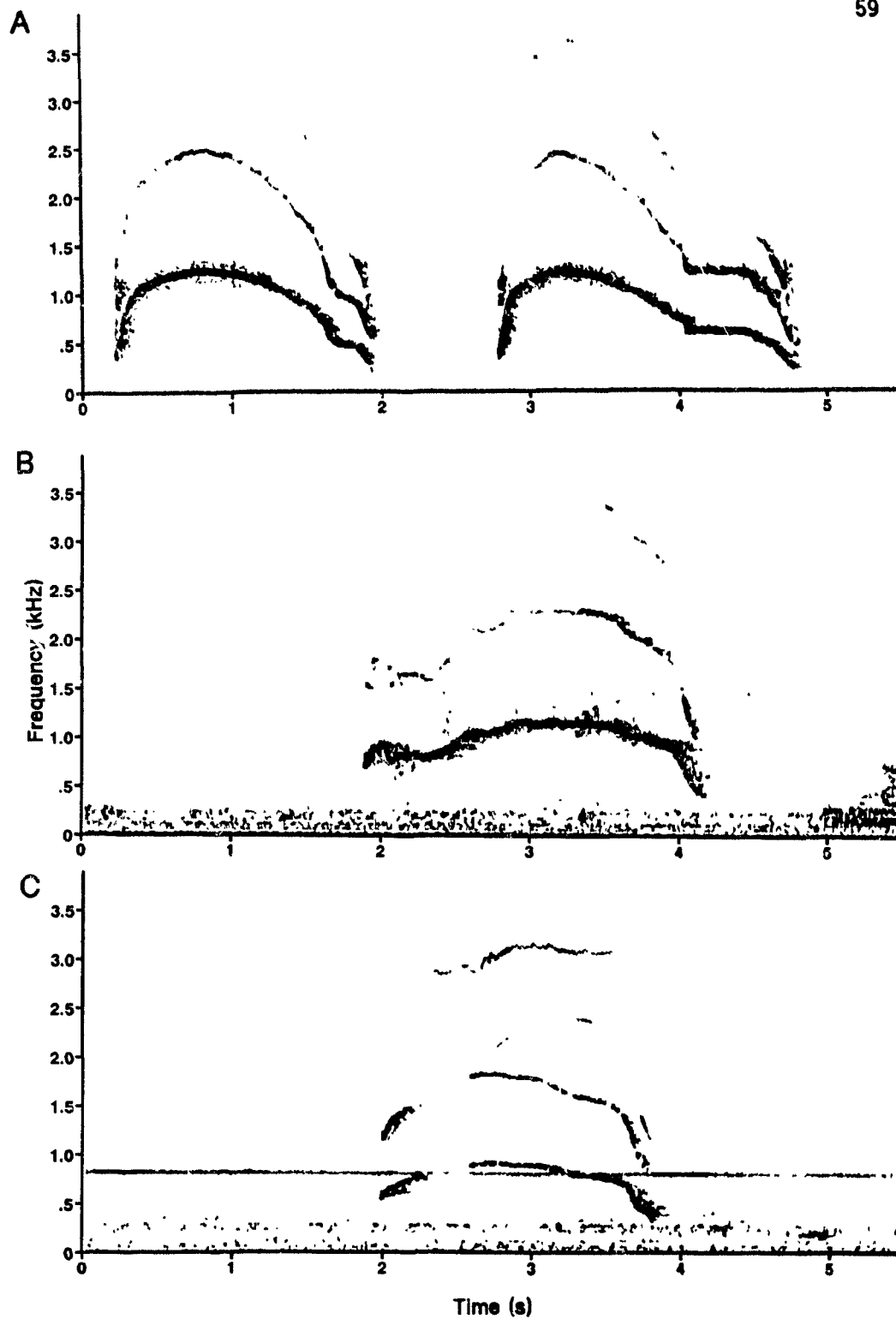


Figure 10. Howls: A. week two; B. week four; C. week six (the steady state noise below 1.0 kHz was generated by an airplane).

Table I. Acoustic properties of vocalizations averaged across litters and weeks. Below each vocal class (rows) is the total sample size (N). Standard errors (\pm) are presented with the values for mean duration (column three) and mean fundamental frequency (column five).

Vocal Class	Spectral Type	\bar{X} Duration (S)	Frequency Modulation	\bar{X} Frequency (Hz)	\bar{X} Max. & Min. Frequency (Hz)
Squeal N = 1168	harmonic or pure tonal; in series	0.27 ± 0.02	aperiodic if present	1079.2 ± 78.1	max: 2419.6 min: 222.6
Scream N = 365	harmonic, some noisy; in series	0.34 ± 0.06	slow, relatively periodic	1724.1 ± 71.7	max: 2875.4 min: 759.9
Yelp N = 19	harmonic and noisy	0.22 ± 0.02	N/A	1332.7 ± 107.6	max: 2593.8 min: 468.7
Growl N = 229	noisy, continuous spectrum	0.58 ± 0.06	N/A	N/A	max: 3930.2 min: <100.0
Bark N = 45	harmonic and noisy	0.19 ± 0.01	N/A	482.1 ± 23.5	max: 738.4 min: 270.1
Woof N = 57	noisy, continuous spectrum	0.17 ± 0.01	N/A	N/A	max: 10696.6 min: <100.0
Squeak N = 932	harmonic, in series	0.20 ± 0.03	slow, aperiodic	7552.5 ± 677.5	max: 11156.5 min: 5439.3
Howl N = 73	harmonic, some in series	1.26 ± 0.20	slow, relatively periodic	911.6 ± 79.1	max: 1327.0 min: 271.6

vocalizations presented in Coscia et al. (1991). There are several changes in the types of information that the table provides. First, the mean sound duration for all vocal classes has been quantified rather than qualitatively described. Second, measurements of sound frequency and frequency ranges are presented. Mean fundamental frequencies (\pm standard error) and frequency ranges of the fundamental (defined in terms of the mean highest and lowest fundamental frequency value obtained for each sound) were calculated for the harmonic and pure tone vocalizations (Squeals, Screams, Yelps, Barks, Squeaks and Howls). The spectral range of the harmonic overtones are not included in the table. The highest frequency component of spectral energy was measured for the noisy sounds (Growls and Woofs) to provide an estimate of the mean spectral bandwidth. Low-frequency energy in Growls and Woofs extended to <100 Hz.

In the following, each vocal class in Table I will be described separately with reference to the corresponding spectrograms.

Squeals: Squeals (Figure 3) were predominantly harmonic, although pure-tone elements were occasionally observed. Squeals typically occurred in series of two or more elements (mean = 3.17 ± 0.45), though single elements were recorded periodically. Individual Squeals were relatively short in duration (0.27 seconds on average). These sounds were highly variable in their frequency modulation (i.e., frequency contour). Most Squeals had a slow

frequency modulation with an upward and downward contour. Some Squeals only had an increasing (upwards) frequency modulation. Others, less commonly, had only a decreasing (downwards) frequency contour. Some Squeals, in contrast, were flat with no apparent modulation at all. The mean fundamental frequency of Squeals was moderately high (1079 Hz). On rare occasions, the highest frequency component of Squeals averaged over 2500 Hz. The extremely high frequency Squeals, observed with broad analysis bandwidths, were pure-tone.

Screams: Screams (Figure 4) were invariably harmonically-structured (the overtones in Figure 4(A-B) were not complete in the hard-copy reproduction of the spectrogram). Some Screams contained associated noise. Screams from pups older than two weeks of age also tended to be noisy in their spectral content. Screams were commonly emitted in series of two or more elements (mean = 3.83 ± 0.27), rarely occurring singly. When the duration data were combined for all ages, Screams were longer in duration (0.34 seconds on average) than Squeals ($F(1,1413)=11.66, p<0.001$). Screams were also longer in duration than Squeals as a function of age (weeks one to five) ($F(4,1413)=11.50, p<0.001$). In a given series, Screams often had a characteristic pattern of frequency modulation. Scream frequency slowly rose, reached a maximum frequency near the sound's mid-point and either slowly decreased or, less commonly, levelled out. Screams were higher than Squeals

in mean fundamental frequency overall ($F(1,1413)=300.79, p<0.001$), and across weeks ($F(4,1413)=22.88, p<0.001$). In addition, both the maxima and minima of the frequency excursions of Screams were higher than those of Squeals.

Although the duration and frequency measures of Screams and Squeals were significantly different, they did have overlapping distributions in both of these dimensions. Screams, however, were perceptually louder than Squeals. To examine the basis of this perceptual distinction, measurements of the relative amplitude of a representative sample of Screams ($N=84$) and Squeals ($N=84$) were taken. The mean peak amplitudes (in volts) of the time waveform was measured for all three litters during the first postnatal week, and for two litters for the second and third postnatal week. Scream and Squeal amplitude means \pm standard errors are presented in Table II. Screams were significantly higher in amplitude than Squeals overall ($F(1,132)=597.78, p<0.001$), and across weeks ($F(2,132)=46.69, p<0.001$). There were no significant litter differences ($F(1,132)=2.28, p>0.05$). There was absolutely no overlap in the Scream and Squeal amplitude ranges which indicates that these two sounds can be differentiated based on their relative amplitudes.

Yelps: Yelps (Figure 5) were extremely rare vocal outbursts. Like Screams, Yelps were harmonically structured with some noise associated with the frequency bands. Unlike Screams, Yelps typically occurred singly. Yelps

Table II. Peak amplitude range means \pm standard errors (in voltage) of Squeals and Screams for the first three weeks of pup development.

Vocal Class	Litter	Age in Weeks		
		I	II	III
Squeals (N=84)	1988	0.23 \pm 0.02	0.51 \pm 0.04	0.78 \pm 0.04
	1990	0.47 \pm 0.03	0.80 \pm 0.05	0.81 \pm 0.07
	1991	0.42 \pm 0.02	---	---
Screams (N=84)	1988	4.48 \pm 0.34	4.83 \pm 0.45	8.65 \pm 0.71
	1990	3.40 \pm 0.38	6.88 \pm 0.70	9.21 \pm 0.63
	1991	6.72 \pm 0.74	---	---

--- Not sampled.

were brief in duration (0.22 seconds on average). The frequency modulation of Yelps was highly characteristic with a sharp rise in frequency at sound onset, followed by a sharp fall. This uniform structure resembled that of Barks (below) but with a more rapid rise and fall in frequency. In addition, Yelps had a greater number of harmonic overtones and a higher fundamental frequency (nearly three times greater) than that of Barks.

Growls: Growls (Figure 6) were noisy sounds with an almost uniform spread of low-frequency spectral energy. Some Growls contained concentrations of energy, harmonic in structure, within the broad spectral band. Growl duration was moderate (0.58 seconds on average) relative to the duration of other vocal classes. Spectral energy in Growls consistently extended to < 100 Hz.

Barks: Barks (Figure 7) were infrequently emitted by neonates. Their spectral structure was distinctive, with one to three harmonic overtones and noisy components. The noise components, reflected as a continuous spread of energy, were more prominent for the older pups than the younger pups. At Bark onset, the fundamental frequency of the harmonic portion of the Bark arched upwards and either curved downwards or levelled out. These sounds were brief in duration (0.19 seconds on average) and were low in frequency (482 Hz) relative to the frequency of other harmonic vocal classes.

Woofs: Woofs (Figure 8) were rarely emitted by pups. Woofs were categorized as noisy in their gross structure. At onset, these sounds contained a brief period of low frequency spectral energy. This spectrum rapidly broadened, extending up to at least 7 kHz. The low frequency energy in Woofs extended below 100 Hz, into the low-level noise of the recording system.

Squeaks: Like Squeals, Squeaks (Figure 9) were frequently observed. Squeaks were narrow band elements, primarily harmonic in structure. Occasionally pure-tone elements were emitted from pups. Some Squeaks contained low-frequency energy, in common with Squeaks from adult wolves (Harrington and Mech, 1978). Squeaks were emitted in series of two or more elements (mean = 4.03 ± 0.41), and were rarely emitted in isolation. These short sounds (0.2 seconds on average) were variable in the form of their elements, ranging from no to moderate frequency modulation. The mean minimum fundamental frequency (5439 Hz) of Squeaks was higher than the mean maximum fundamental frequency for all other harmonic sounds. Their highest mean fundamental frequency was over 11,000 Hz.

Howls: Howls (Figure 10) were harmonically structured sounds, with a characteristic slow frequency modulation. Howl fundamental frequency slowly rose at onset and gradually fell at offset. Several of the early-appearing Howls from pups, however, reached a maximum frequency and ended without the

characteristic frequency decrease. For these Howls, referred to as Howl "attempts", the pup appeared to stop vocalizing midway through the sound's production. Howls were, in general, the longest duration sound emitted by pups, averaging 1.26 seconds, although the standard error was large both within and across age groups. Mean fundamental frequency of Howls was low compared to the other harmonically structured sounds (Screams and Yelps, with the exception of Barks) and highly variable. The maximum frequency components of Howls were significantly lower than Squeals ($F(2,434)=6.44$, $p<0.002$) and Screams ($F(2,128)=4.09$, $p<0.02$) across weeks three to five.

Classification of vocalizations and bivariate analyses

The preceding section provided general descriptions of the acoustic properties of the vocalization classes distinguished in this study. The most common vocalizations fell into two very broad categories: harmonic and noisy. Within these gross spectral categories, finer categorizations were made on the basis that vocalizations distinguished perceptually, were, upon acoustic measurement, found to have central tendencies that differed along at least two dimensions. For example, Growls and Woofs were both noisy but they were differentiated by both their mean durations and spectral bandwidths. Squeals and Squeaks were both harmonic but they were differentiated by their mean durations and mean fundamental frequencies.

This classification scheme resulted in the categorization of 3,396 sounds

into eight classes. Confidence in this strategy of classification could be bolstered if sounds differing along some dimensions had distributions of values that didn't simply differ in their central tendencies, but were non-overlapping. That such might be the case is suggested in Table 1, since the variance around measurement means was sometimes small by comparison with the differences between means. One method of examining this issue further is to employ a bivariate analysis scheme. Scatter plots are a means of comparing two independent variables from one or more sound classes. In scatter plots, discontinuities between the "families of data points" (data points belonging to one sound class) representing the proposed vocal categories constitute circumstantial evidence that the processes underlying the production of the vocalization types are also different. Confidence in such distinctions between categories is strong. In contrast, when the families of data points representing putatively different vocal categories significantly overlap, it is important to question whether the calls come from discrete/separable categories or consider other acoustic dimensions for further discrimination.

As shown in Table 1, Growls and Woofs are distinguished by differences in their mean duration and spectral bandwidth. Figure 11 shows, for every exemplar of each of these sound categories in the data set, the spectral bandwidth plotted as a function of duration. It is apparent that the families of data points representing Growls are clustered along the bottom of plot while those representing Woofs are concentrated within a tight column along the

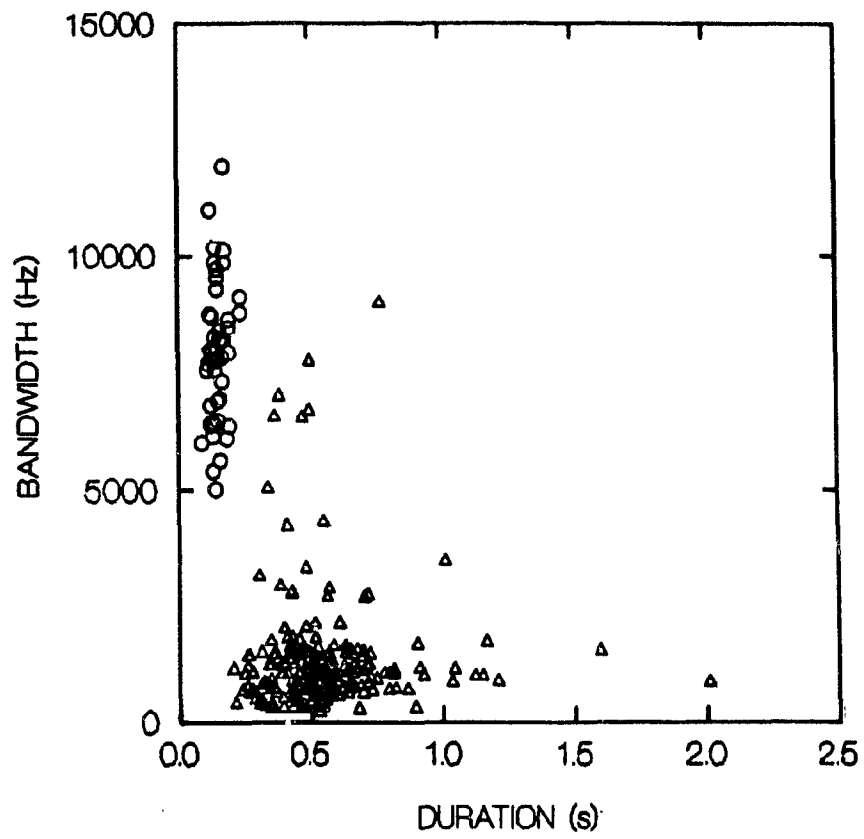


Figure 11. Scatter plot of frequency bandwidth (Hz) versus duration (s) for the noisy vocal classes, Growls (Δ) and Woofs (\circ).

upper-left side of the plot. The range in frequency bandwidth accounts for most of the acoustic variation in Woofs and the duration is the primary source of acoustic variation in Growls. There are several data points from the Growl data-set which extend into the frequency range of Woofs. The duration of these Growls, however, is over twice that of Woofs. Most significant for the present argument, however, is that the two families of data points are non-overlapping.

Figure 12 displays the mean fundamental frequency plotted as a function of mean duration for all examples of the harmonic Squeals, Screams and Squeaks. There are two distinct clusters which do not overlap in space. One cluster, that representing Squeaks, is concentrated along the upper-left side of the plot. A second cluster is concentrated along the bottom of the plot. The segregation of Squeaks argues for their being a distinct vocalization. Close inspection of the lower cluster reveals an overlap of data points representing Squeals and Screams.

The Squeal and Scream cluster is expanded in Figure 13A. Bivariate sample ellipses, centred on sample means of frequency and duration variables, were drawn at the 50 percent confidence region. The ellipses reveal two partially overlapping clusters.

Figure 13(B-D) portrays the pattern of Squeals and Screams at each of three postnatal weeks. Inspection of these figures reveals that the relative position of the two clusters in space remains constant across time. Squeals are consistently lower in average frequency and shorter in average duration than

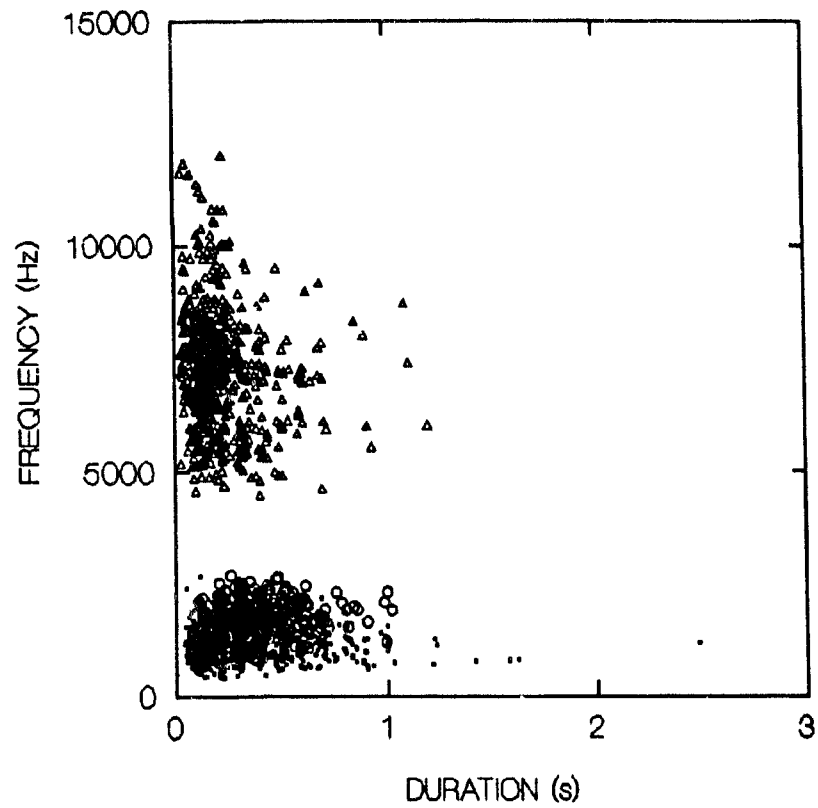


Figure 12. Scatter plot of mean fundamental frequency (Hz) versus duration (s) for the harmonic vocal classes, Squeals (◻), Screams (○) and Squeaks (△).

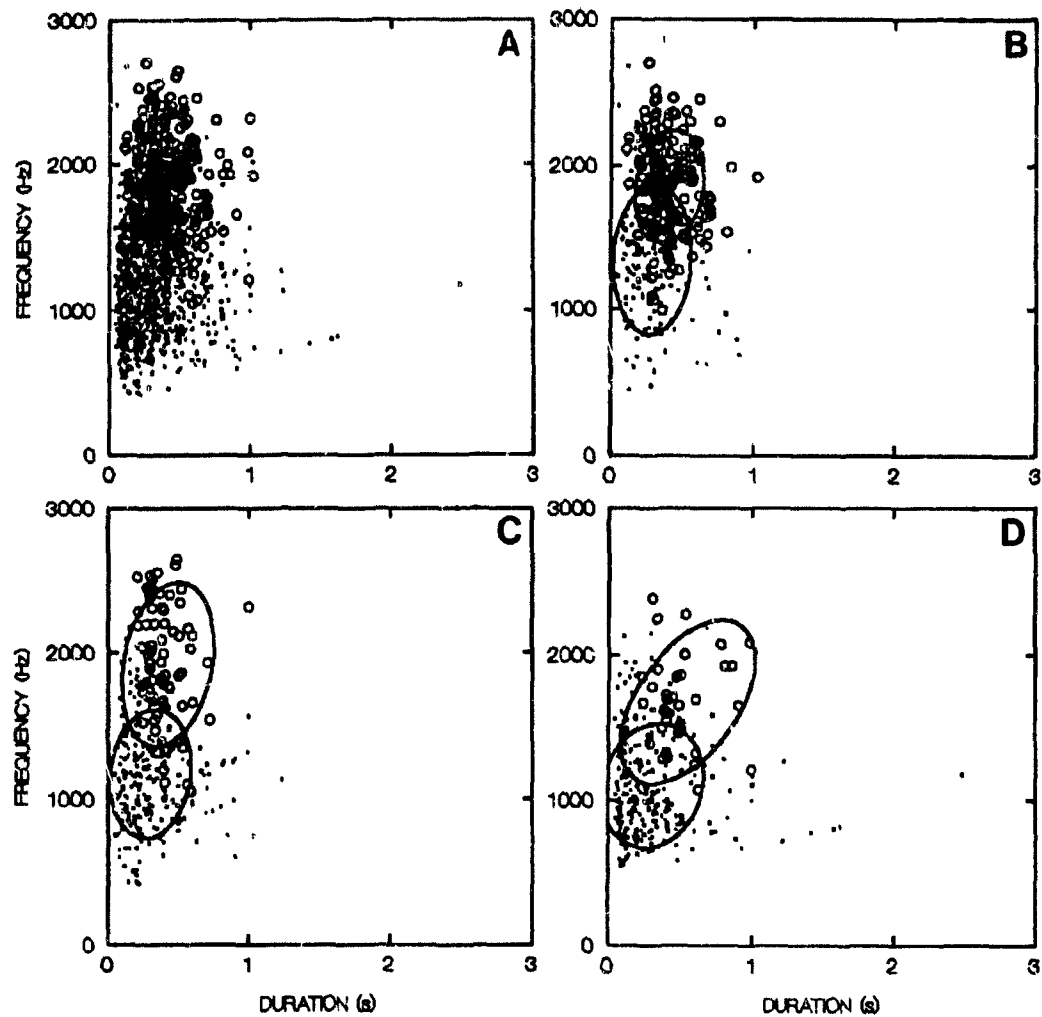


Figure 13. Scatter plots of mean fundamental frequency versus duration for the overlapping harmonic sounds, Squeals (◻) and Screams (○): A. Weeks one through five; B. Week one; C. Week two; D. Week three. Bivariate ellipses are drawn at the 50% confidence interval.

Screams. The variation within each vocal class (represented by the size and shape of the ellipse) is quite consistent across the three weeks; the smaller sample size may account for the slight variability in the Scream data points. In summary, the distinction between Squeals and Screams is not as evident as the distinction between either of these two vocal classes and Squeaks, based on a bivariate analysis of fundamental frequency and duration. In this case, however, the addition of a third acoustic dimension, relative amplitude, separates Squeals and Screams into discrete classes.

Moans, Whines and Yawns

The vocal classes described above differ from the ten vocal classes identified in Coscia et al. (1991). The earlier study did not record Yelps and included Moans, Whines and Yawns, which were not included in the present study. Representative spectrograms of Moans, Whines and Yawns at various ages are presented in Figures 14-16.

Moans and Whines are the most common vocalizations produced by neonate pups (Coscia et al., 1991). Moans and Whines, in this study, were heard on all tapes analyzed throughout pup development. Moans and Whines were invariably harmonic in structure. Figures 14 and 15 illustrate these sounds drawn from records made at different pup ages. Both Moans and Whines decreased in fundamental frequency as pups matured. This is seen in the spacing of the harmonics which decreased with maturation. Moans and Whines

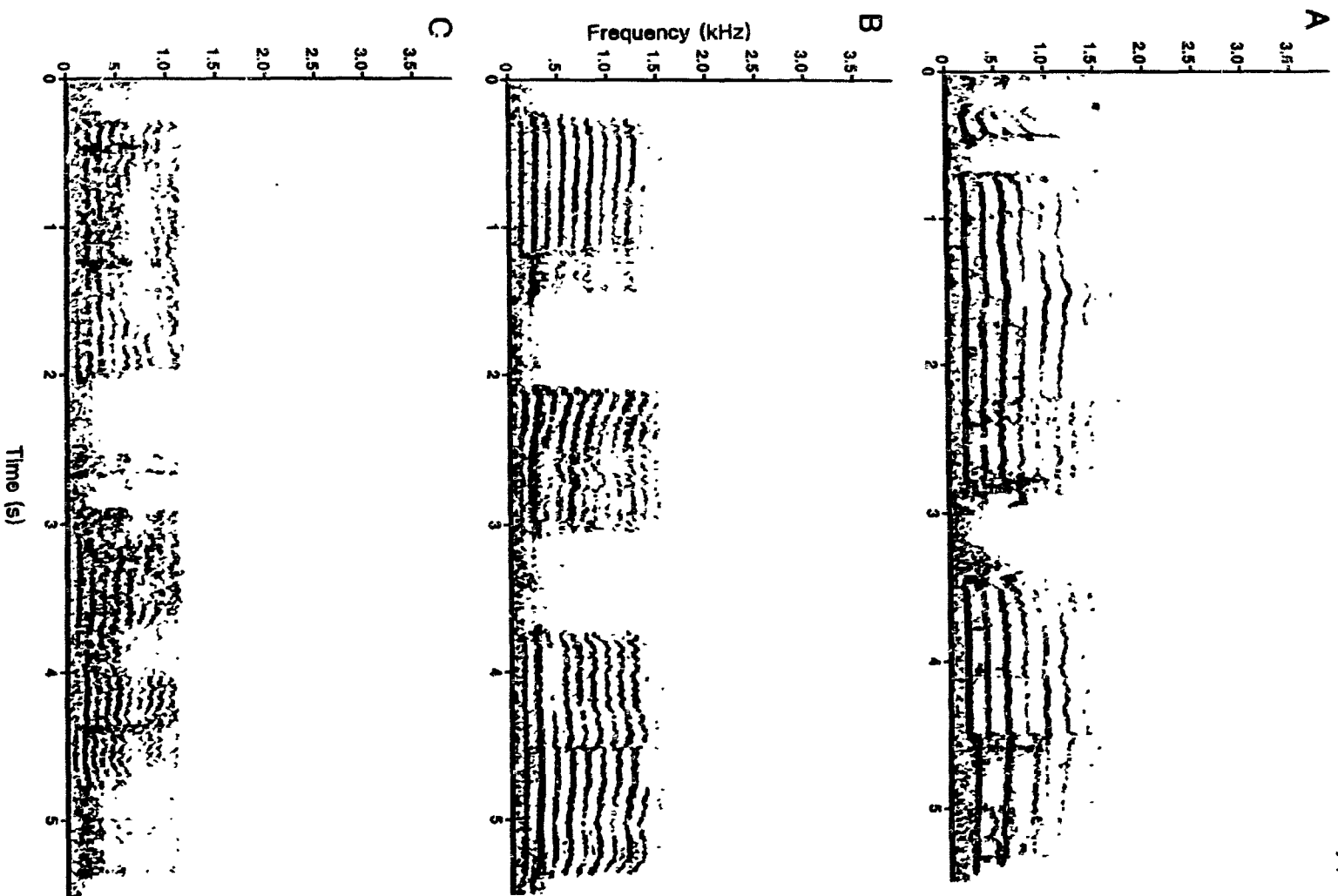


Figure 14. Moans: A. week one; B. week three; C. week six.

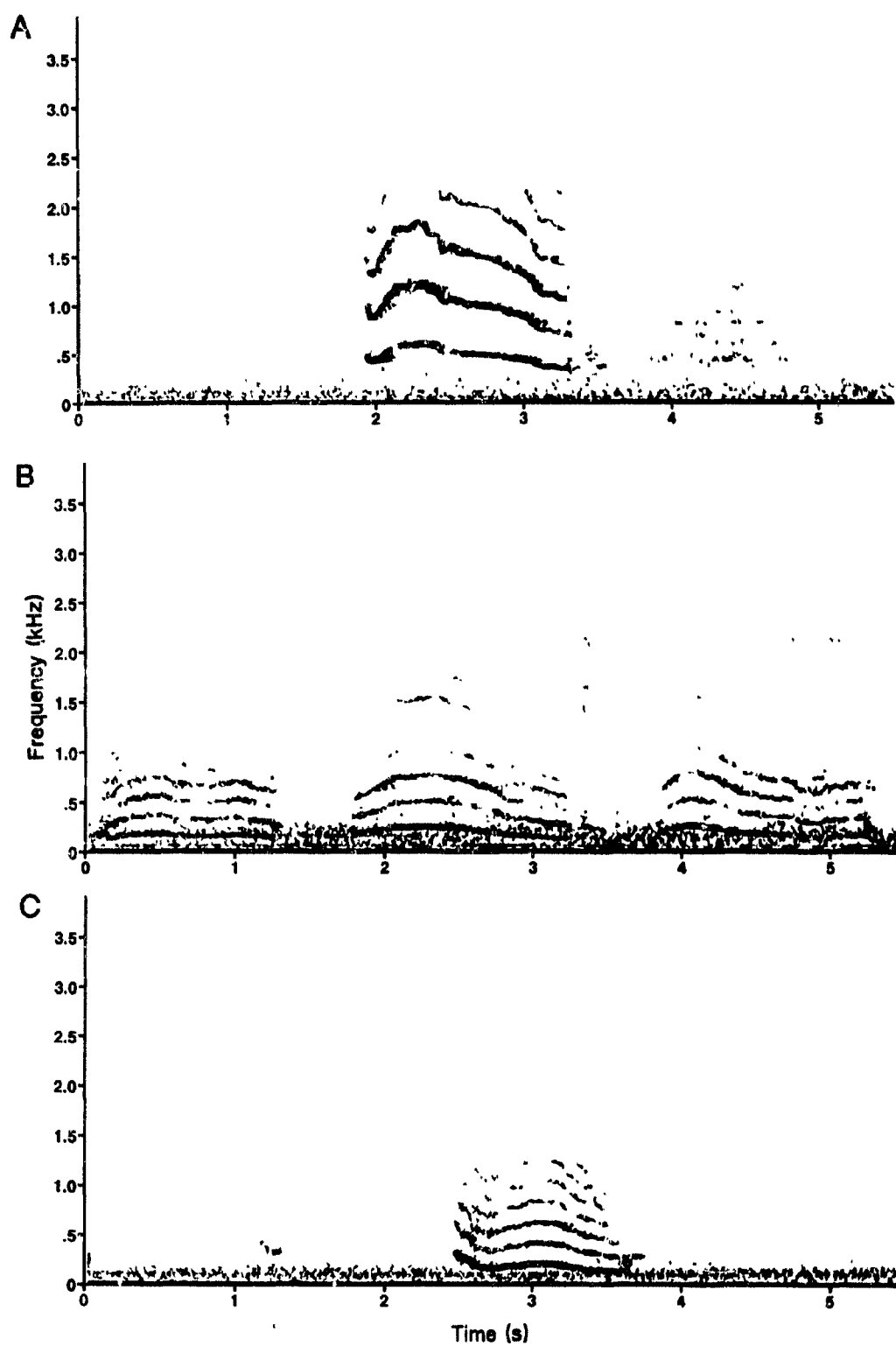


Figure 15. Whines: A. week one; B. week three; C. week six.

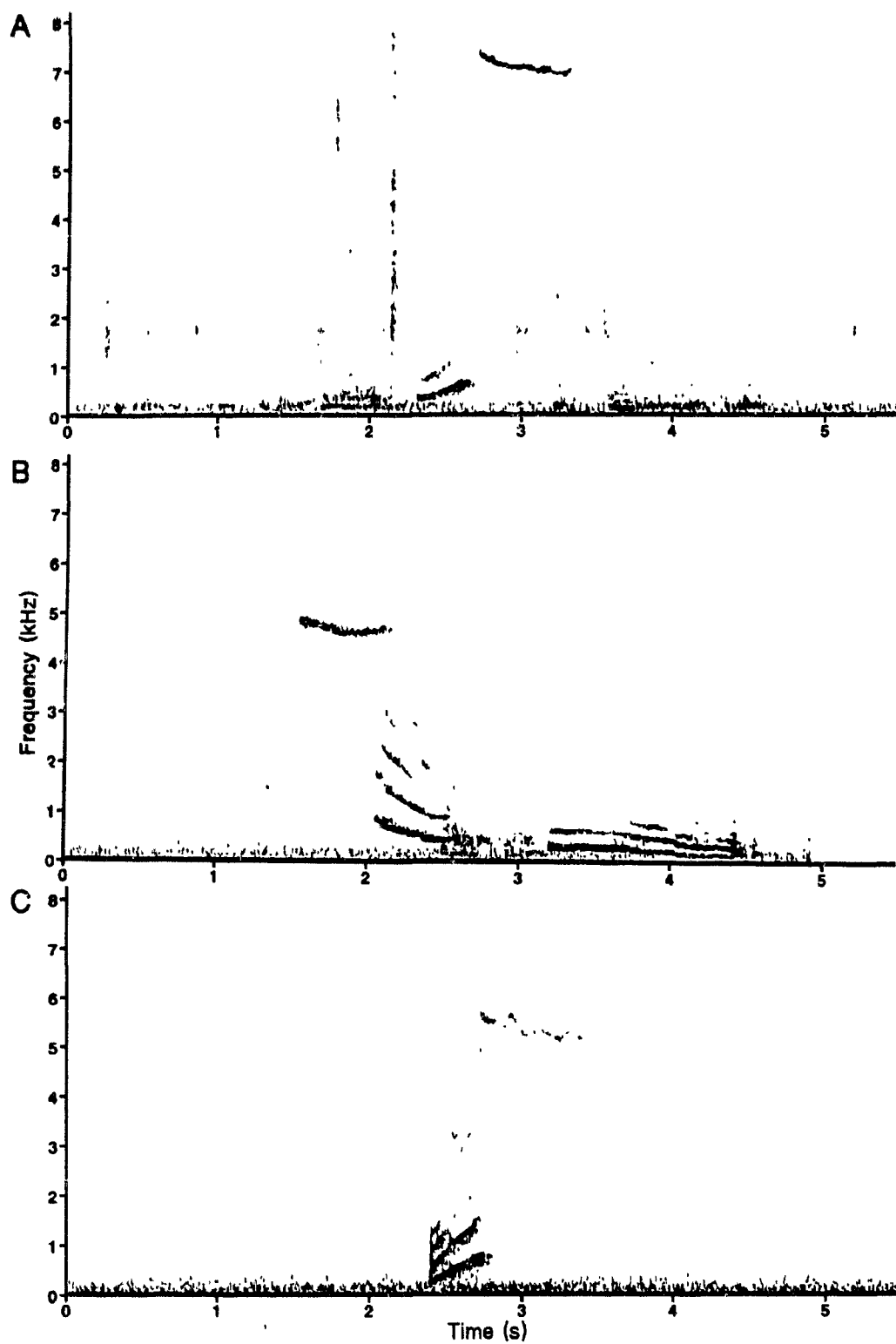


Figure 16. Yawns: A. week four; B. week five; C. week six.

were also similar in sound duration. What distinguishes these two categories from each other is the presence and rate of frequency modulation and their mean fundamental frequency. Moans either had no frequency modulation or they were rapidly modulated. Moans were low in fundamental frequency as evident in the close spacing between the harmonic bands. Whines, in contrast, always had a very slow rate of frequency modulation and were higher in fundamental frequency than Moans.

In addition to Moans and Whines, Yawns were eliminated from the present study's quantitative analysis. Yawns began to appear at three weeks of age and were observed exclusively during the physical act of yawning when pups were in a resting posture, following pup movement from a reclined position, or during repositioning within a resting posture. Over 70 Yawns were noted for all three litters combined. The vocal emission associated with Yawns was likely a result of air exhalation while yawning.

Acoustically, Yawns were variable in spectral content (Figure 16). The majority of Yawns had two distinct elements which were closely spaced in time. Typically, Yawns were initiated with a sustained and relatively flat high-frequency element. This element was variable in duration (brief to moderate in length), structure (primarily pure-tone but on occasion harmonic) and fundamental frequency (4 - 7 kHz in mean frequency). These variations did not appear to be age-related. Following the higher-frequency component of the Yawn was a harmonic howl-like component. This lower-frequency component of Yawns

gradually decreased in fundamental frequency and levelled off. This component was also variable in duration and fundamental frequency, and did not change ontogenetically. Another variant of Yawns was the reversal of the two distinct spectral components such that the higher-pitched element followed the lower-frequency harmonic structure. When this was the case, the harmonic component increased in frequency prior to the emission of the high-frequency portion of the Yawn. Yet another variable feature characteristic of Yawns was the absence of the lower frequency component.

Howls, which are distinct from Bark-Howls in the adult literature, were missing from the 1991 vocal repertoire because none were identified. In the present sample, multiple Howls were identified and measured during the analysis of the first six weeks of development for all three litters. Bark-Howls, in contrast, were observed rarely and emitted primarily outside the den.

Development of vocalization classes

In this section, the acoustic properties of wolf pup vocal classes are examined from birth to six weeks of age. Tables III-V provide detailed quantitative data on the development of vocalizations across the six weeks, averaged across all three litters. These tables have been sectioned into three divisions: 1. Table III - Early-appearing vocalizations: Neonate-specific (Squeals and Screams); 2. Table IV - Early-appearing vocalizations: Adult-structured (Growls and Barks); and 3. Table V - Late-appearing vocalizations: Adult-

Table III. Development of acoustic properties (means \pm standard errors) for the early-appearing, neonate-specific vocalizations: Squeals and Screams.

Vocal Class	Acoustic Property	Pup Age (Weeks)				
		I	II	III	IV	V
Squeal	(N)	420	265	304	64	8
	\bar{X} Duration (S)	0.32 ± 0.01	0.29 ± 0.01	0.30 ± 0.02	0.22 ± 0.02	0.20 ± 0.05
	\bar{X} Frequency (Hz)	1311.7 ± 17.1	1165.4 ± 21.4	1105.9 ± 21.1	913.4 ± 26.5	899.6 ± 97.2
	\bar{X} Variation (Hz)	611.7 ± 14.6	456.7 ± 17.0	356.0 ± 16.2	259.0 ± 24.5	175.0 ± 97.1
	\bar{X} Interval (S)	0.37 ± 0.01	0.41 ± 0.02	0.34 ± 0.01	0.43 ± 0.04	0.46 ± 0.23
Scream	(N)	213	41	26	16	18
	\bar{X} Duration (S)	0.40 ± 0.01	0.40 ± 0.01	0.51 ± 0.03	0.24 ± 0.02	0.17 ± 0.01
	\bar{X} Frequency (Hz)	1853.1 ± 20.2	1928.9 ± 46.4	1681.5 ± 52.4	1583.0 ± 92.3	1574.1 ± 42.7
	\bar{X} Variation (Hz)	787.2 ± 20.9	648.5 ± 34.8	640.8 ± 79.8	709.6 ± 83.3	415.4 ± 75.4
	\bar{X} Interval (S)	0.23 ± 0.01	0.23 ± 0.01	0.19 ± 0.18	0.16 ± 0.01	0.21 ± 0.02

Table IV. Development of acoustic properties (means \pm standard errors) for the early-appearing, adult-structured vocalizations: Growls and Barks.

Vocal Class	Acoustic Property	Pup Age (Weeks)					
		I	II	III	IV	V	VI
Growl	(N)	18	8	5	84	39	74
	\bar{X} Duration (S)	0.83 ± 0.08	0.63 ± 0.09	0.54 ± 0.05	0.56 ± 0.02	0.43 ± 0.02	0.50 ± 0.02
	\bar{X} Maximum (Hz)	965.3 ± 39.2	1181.6 ± 87.7	1278.1 ± 225.6	1601.5 ± 64.9	3537.3 ± 393.0	1967.8 ± 171.4
Bark	(N)	22	9	2	3	3	3
	\bar{X} Duration (S)	0.20 ± 0.01	0.19 ± 0.01	0.20 ± 0.0	0.17 ± 0.02	0.23 ± 0.04	0.15 ± 0.03
	\bar{X} Frequency (Hz)	521.4 ± 16.2	454.7 ± 24.6	438.4 ± 4.3	417.5 ± 62.1	572.7 ± 34.1	487.8 ± 61.6
	\bar{X} Variation (Hz)	275.2 ± 19.3	219.9 ± 31.6	268.2 ± 53.6	229.2 ± 5.2	217.8 ± 51.1	255.2 ± 70.1

Table V. Development of acoustic properties (means \pm standard errors) for the late-appearing, adult-structured vocalizations: Woofs, Squeaks and Howls.

Vocal Class	Acoustic Property	Pup Age (Weeks)				
		II	III	IV	V	VI
Woof	(N)	---	1	26	10	12
	\bar{X} Duration (S)	---	0.18 ± 0.0	0.16 ± 0.01	0.14 ± 0.01	0.15 ± 0.01
	\bar{X} Maximum (Hz)	---	10127.8 ± 0.0	8317.6 ± 252.9	7086.4 ± 539.1	7421.9 ± 378.4
Squeak	(N)	---	51	297	166	179
	\bar{X} Duration (S)	---	0.24 ± 0.02	0.21 ± 0.01	0.19 ± 0.01	0.26 ± 0.01
	\bar{X} Frequency (Hz)	---	9268.4 ± 127.2	7575.2 ± 55.8	7408.6 ± 62.6	5957.8 ± 65.8
	\bar{X} Variation (Hz)	---	1670.9 ± 137.9	962.5 ± 55.4	877.0 ± 9.5	667.4 ± 32.7
	\bar{X} Interval (S)	---	0.31 ± 0.05	0.32 ± 0.01	0.30 ± 0.21	0.38 ± 0.02
Howl	(N)	2	38	14	12	5
	\bar{X} Duration (S)	1.73 ± 0.15	0.82 ± 0.09	1.75 ± 0.27	0.92 ± 0.21	1.08 ± 0.34
	\bar{X} Frequency (Hz)	1100.8 ± 35.1	1015.0 ± 43.9	995.5 ± 112.2	742.4 ± 20.9	704.2 ± 41.9
	\bar{X} Variation (Hz)	1109.4 ± 31.2	532.0 ± 54.4	810.4 ± 72.2	457.3 ± 29.6	628.2 ± 80.9
	\bar{X} COFM	13.84 ± 3.61	9.28 ± 0.80	11.69 ± 1.72	7.84 ± 0.52	10.31 ± 1.08

structured (Woofs, Squeaks and Howls). Yelps, emitted predominantly during the first two postnatal weeks, are excluded from this tabulation because of their overall low sample size. Included in these tables are: the total numbers of each sound class to provide information on when each class first appeared; the count of each vocalization at each age category; the mean durations (\pm standard error) of each vocalization; the mean fundamental frequency (\pm standard error) is provided for the harmonic and pure-tone sounds and the mean maximum frequency (\pm standard error) is presented for the noisy sounds; the mean "variation" (\pm standard error) of the fundamental frequency was calculated for all of the harmonic and pure tone vocalizations by taking the difference between the highest and lowest fundamental frequency component for each sound; the mean duration (\pm standard error) of the inter-element-intervals for the vocalizations which occurred in series (Squeals, Screams and Squeaks) is also included; and the coefficient of frequency modulation (COFM) was calculated for all Howls longer than 0.3 seconds.

Squeals: Squeals (Table III) were one of the vocalization classes which appeared on postnatal day one (refer to "Statistical analyses of Squeals and Squeaks" below for quantification of the developmental trends of Squeals and Squeaks). There was a decrease in the total number of Squeals observed after three weeks of age. The duration of Squeals also decreased with pup maturation. The mean fundamental frequency of these sounds decreased

between weeks one through five. The mean fundamental frequency variation for Squeals was 427 Hz on average, and it gradually decreased from 612 Hz to 175 Hz between weeks one and five. The inter-element-interval of Squeals, however, revealed no consistent patterns with pup maturation.

Screams: Screams (Table III) were a second neonate-specific vocalization which occurred within the pup's first days of life. The number of recorded Screams decreased after three postnatal weeks. The duration of Screams also decreased after three weeks of age ($F(4,309)=22.22, p<0.001$). The fundamental frequency of Screams decreased after two weeks of age ($F(4,309)=9.10, p<0.001$). The mean frequency variation of Screams (640 Hz), was, in absolute terms, broader than that of Squeals. Scream inter-element-intervals (0.20 seconds in duration on average) were half the interval duration of Squeals (0.40 seconds on average). In general, Squeal and Scream acoustic characteristics followed similar developmental trends, while maintaining the quantitative differences in their acoustic structures.

Growls: Growls (Table IV), while uncommon, were also present within the vocal repertoire of neonates within their first days of life. The number of Growls increased after three weeks of age. Growl duration appeared to decrease with pup age. The maximum frequency components of Growls appeared to increase with pup maturation. Growls from pups three weeks of

age and older often had broad spreads of spectral energy at either Growl onset (Figure 6B), or within the first 0.2 seconds of the Growl. These Growls were perceptually louder than the others.

Barks: Barks (Table IV), like Growls, were observed as early as postnatal day one but were rare throughout the first six weeks of age. Barks showed no age-related trends in duration, mean fundamental frequency or mean frequency variation. In general, Bark acoustic properties were consistent across time.

Woofs: Woofs (Table V) were one of the late-appearing vocalizations, predominant in pups older than three weeks. The duration of Woofs did not change with pup maturation. The mean maximum frequency appeared to decrease slightly with age.

Squeaks: Squeaks (Table V) were another late-appearing vocalization. Squeaks were the predominant vocal class emitted by pups after three weeks of age. Squeak duration decreased between weeks three to five, but then substantially increased at week six. The mean fundamental frequency and frequency variation of Squeaks decreased across weeks. The inter-element-interval was constant from weeks three to five, but increased at week six.

Howls: Howls (Table V) were a rare and late-appearing vocal class.

There were significant differences in Howl duration between weeks, but the directions of change from week to week were inconsistent ($F(4,66)=4.79$, $p<0.002$). Howl fundamental frequency decreased developmentally ($F(4,66)=3.40$, $p<0.05$). Mean fundamental frequency variation (707 Hz) was greater than in Squeals and Screams. Mean Howl frequency variation and the COFM changed in parallel, but the direction of change was not consistent across weeks. This finding was an indication that Howl modulation did not change concurrently with changes in fundamental frequency.

In an attempt to characterize the contour of pup Howl frequency modulation, the COFM was compared to the total Howl duration for all sounds (>0.03 seconds) across development to determine the type of relationship between these two variables. Young and juvenile wolf Howls are shorter in duration and higher in frequency modulation compared to adult wolf Howls (Harrington and Mech, 1978; Schassburger, 1987, 1993). This may suggest that shorter wolf Howls are higher in COFM than longer Howls. A significant linear relationship between neonate Howl frequency modulation and sound duration may indicate that as the duration of pup Howls increases, there is less frequency modulation. In Figure 17, the COFM is plotted against duration. There was a significant negative correlation (Pearson product-moment correlation coefficients) between Howl duration and the COFM ($r=-0.343$, $df=58$, $p<0.05$) indicating that the frequency modulation within a Howl decreased with increasing sound duration.

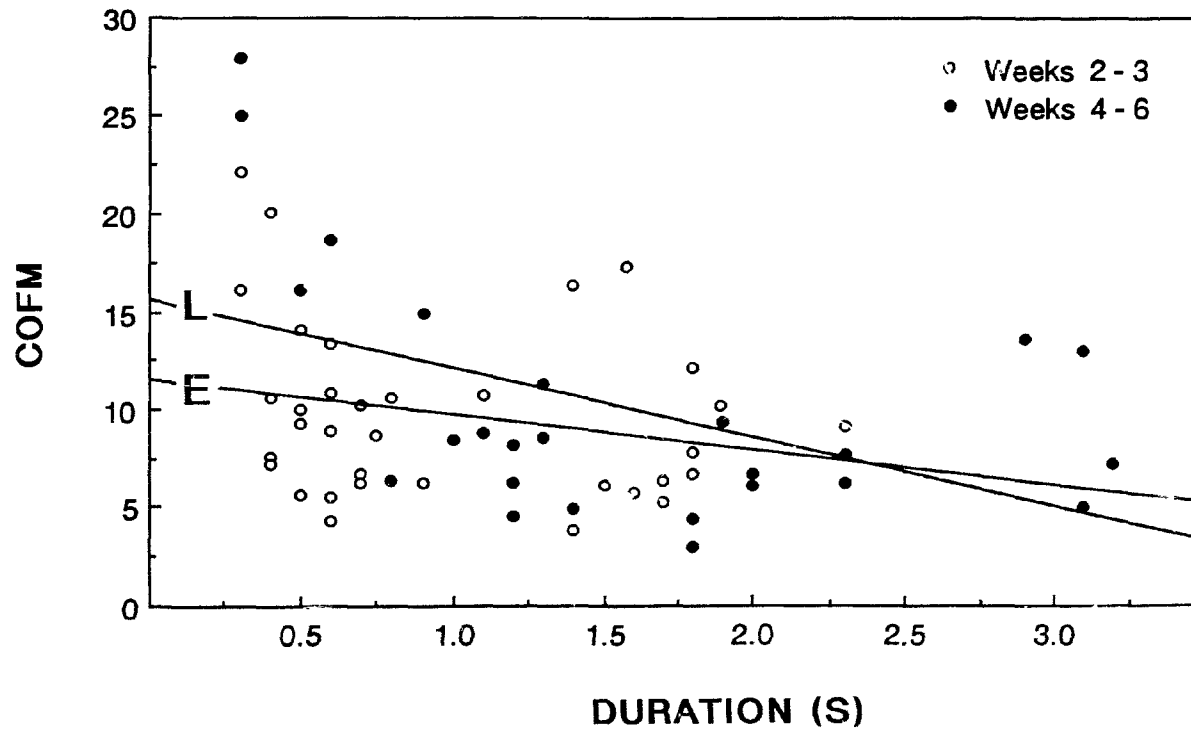


Figure 17. Bivariate plot of COFM values versus duration of Howls from weeks 2 - 3 and weeks 4 - 6. Regression lines for early Howls ("E", $r = -0.18$, $df=35$, $p>0.05$) and later Howls ("L", $r = -0.50$, $df=25$, $p<0.05$) are also drawn.

Relative proportions of vocal classes

The proportions of Squeals, Screams, Growls, Squeaks, Woofs and Howls were computed as a function of age. Proportions were computed for each litter separately to permit examination of possible litter differences. Proportions were calculated by dividing the total number of one sound category (per litter, per week) by the total number of all sounds (per litter, per week) that were measured. For example, pup Squeal proportions from the 1988 litter, week one, were obtained by dividing the total number of Squeals (for 1988, week one) by the total number of all measured sounds (for 1988, week one). These proportions are graphed separately for each litter as a function of age (Figure 18(A-F)). The total number of Yelps and Barks were included in the total number of sounds measured, but were excluded from the individual sound class proportion measurements because of their low absolute rate of occurrence. The trends for each vocal category are described collectively, and for each litter below.

Squeals: Figure 18A shows that Squeals were emitted in high proportions by all three litters for the first three postnatal weeks, after which time their relative proportions dramatically decreased. For all three litters, Squeal proportions were the most common early vocalization being highest during the second and third week of age. By postnatal week four, Squeal proportions dropped, and by week six, proportions for all three litters were close to zero.

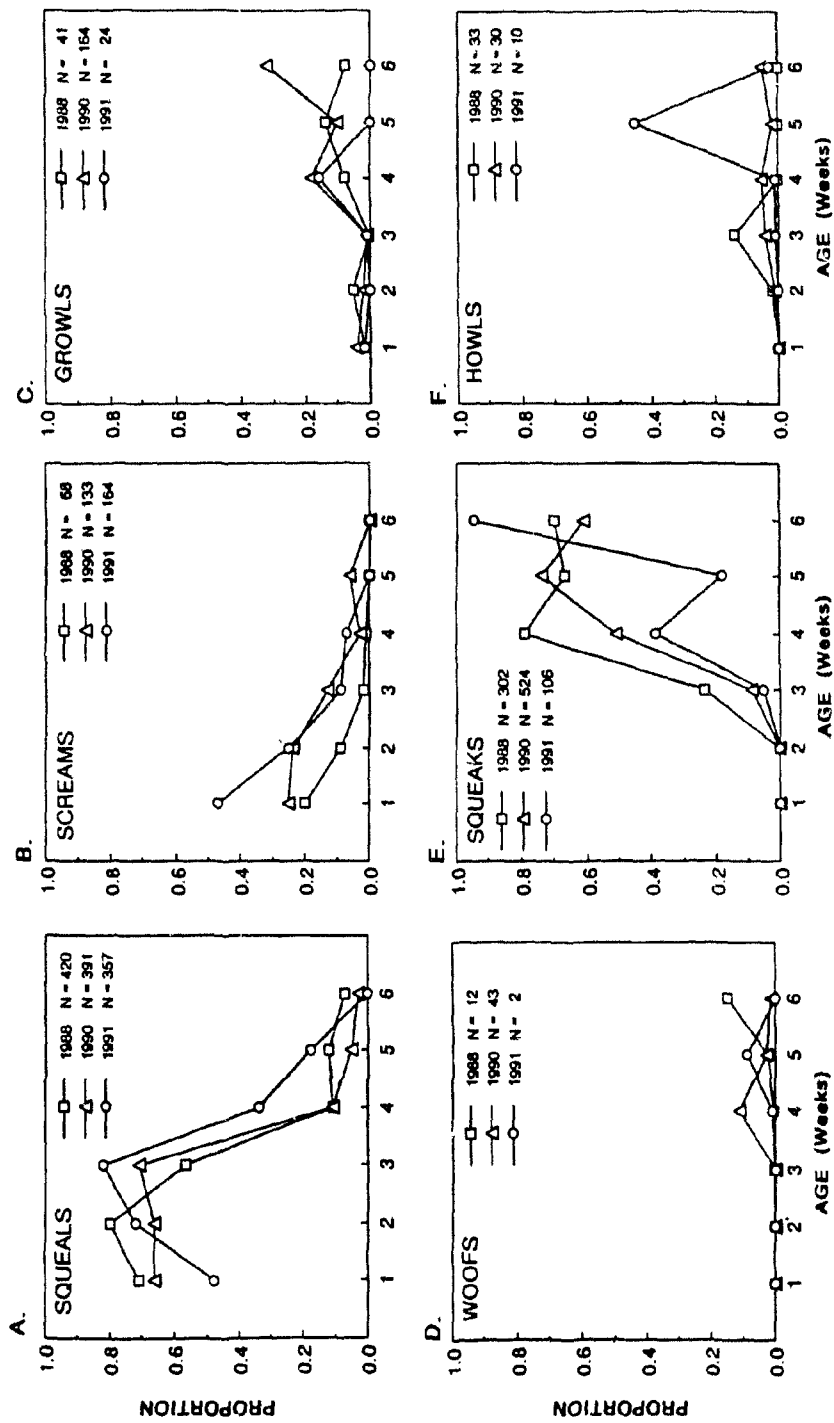


Figure 18. Relative proportions of pup vocal classes for individual litters as a function of age.

Screams: Relative proportions of Screams (Figure 18B) were highest during the first week of age for all three litters, and were greatest for the 1991 litter. Proportions gradually diminished for all three litters as a function of age although the rate of decrease was greatest for the 1991 litter. For all litters, the proportion of Screams dropped to zero by week six. The 1988 and 1991 recorded proportions of Screams diminished to zero as early as week five.

Growls: The proportions of Growls (Figure 18C) were low for all three litters during the first three weeks of age and increased at four weeks for all litters. The 1988 record for Growl proportions remained consistent across the remaining weeks of the analysis period. The 1990 litter slightly decreased in their proportions of Growls at five weeks of age and then sharply increased at six weeks. The 1991 record of Growls dropped and remained at zero by five weeks of age.

Woofs: A second late-appearing vocalization produced by wolf pups appeared between three to four weeks of age. Woofs (Figure 18D) were proportionally less common than Growls and were, in general, one of the rarer sounds which pups emitted in the den during this developmental time period.

Squeaks: Squeaks (Figure 18E) were observed at three weeks of age for all three litters. Proportions of Squeaks were low when they first appeared

but increased rapidly between three and four weeks of age. More than half of the vocalizations used by pups in the 1988 and 1990 litters were Squeaks. The 1991 litter produced fewer Squeaks than the other two litters at three to five weeks of age, but their proportions increased by six weeks of age.

Howls: Howls (Figure 18F) were uncommon vocalizations throughout the duration of the analysis for all three litters, although short-lived peaks in howling occurred at three weeks of age for the 1988 litter, and at five weeks of age for the 1991 litter.

General patterns of vocalization proportions

Comparison of the proportions of vocalizations in the six vocal classes over the first six weeks of age (Figure 18) reveals several important findings. First, the proportion data confirm the impression created by the absolute count data in Tables III-V in showing that the vocalization categories were not equally common. Second, their relative preponderance changed ontogenetically. In addition, each of the three litters showed similar ontogenetic trends. The discrepancies associated with the 1991 litter can be explained, in part, by the low vocal production recorded for that litter and by the behavioural data correlated with the vocal events (see Chapter Four).

The data from Figure 18 were averaged over the three litters at each age and the mean curves were superimposed (Figure 19). Squeals were the most

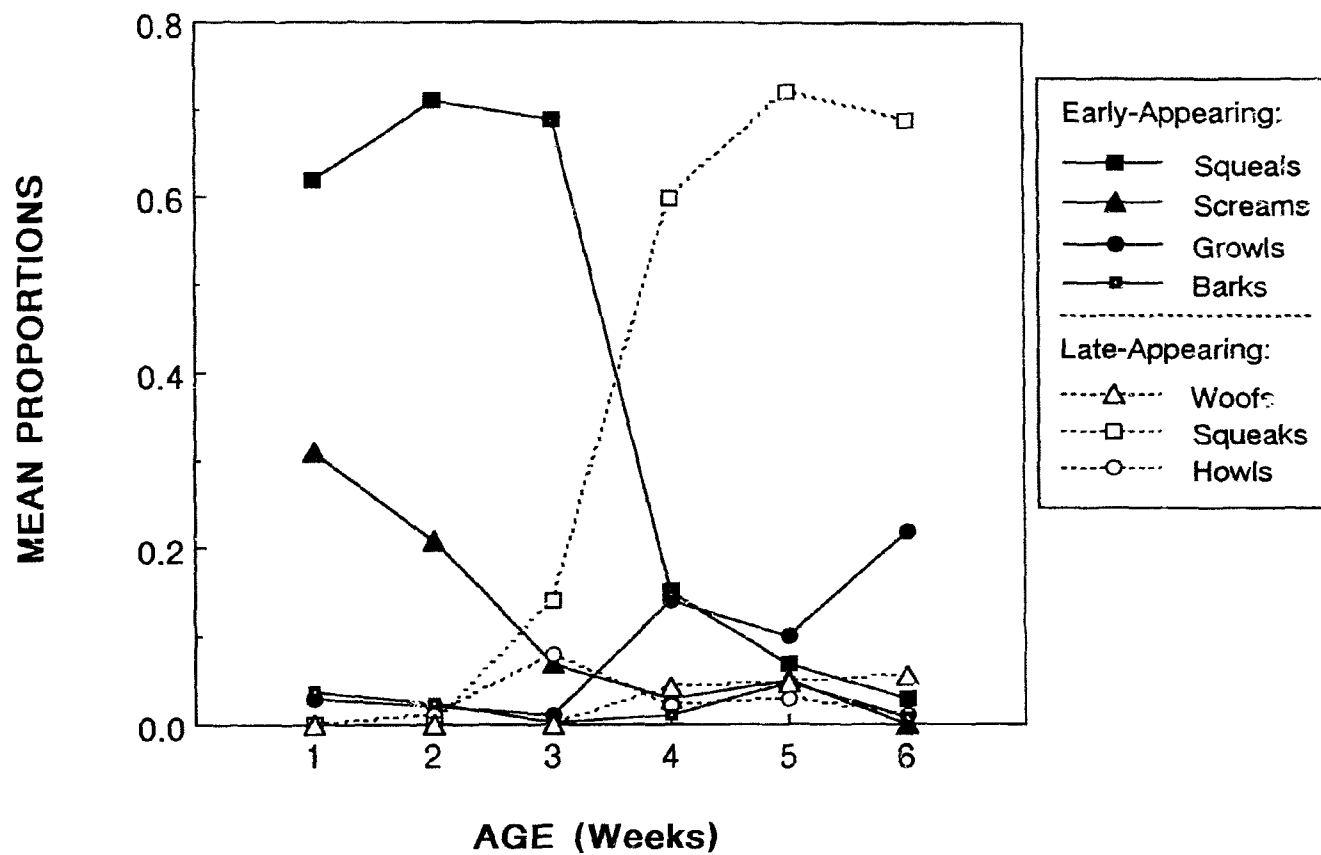


Figure 19. Mean relative proportions of pup vocal classes as a function of age.

frequent vocal class emitted during the first three postnatal weeks. After week three, the proportion of Squeals decreased sharply and the proportion of Squeaks, which did not appear until postnatal week three, sharply increased. Squeaks were the most common vocalization in pups prior to their emergence from the den. In general, the relative frequencies of all of the other sound classes were low. The proportions of Screams, like Squeals, decreased with age while the proportion of Growls, like Squeaks, tended to increase with pup maturation.

Statistical analyses of Squeals and Squeaks

Fundamental frequency

Statistical analyses of the development of every vocal class could not be performed because of the low numbers recorded at each developmental stage (See Tables III-V). Squeals and Squeaks were the two vocal classes which were produced in sufficient numbers to permit quantitative acoustic analyses of individual litter trends.

ANOVAs were performed to evaluate univariate changes in acoustic structures associated with maturation. Each litter was treated as one subject to avoid confounds related to non-independence between pups within a litter (Martin and Bateson, 1986). Data were analyzed for each litter separately. The raw data scored within the Quattro Pro Spreadsheets were transformed into Systat files for these analyses. All F tests had significance set at the $p < 0.05$

level (Sokal and Rohlf, 1981). The resulting F values are presented in Table VI.

Figure 20(A-B) depicts the mean (\pm standard errors) fundamental frequency profiles and fundamental frequency variation profiles of Squeals and Squeaks for all three litters as a function of age. There were significant decreases in the fundamental frequency of both Squeals and Squeaks with age (Table VI). Figure 20A shows the mean fundamental frequencies of Squeals and Squeaks. Note that the late emerging Squeaks have a higher fundamental frequency than Squeals. The litter trends for Squeal fundamental frequency all showed a gradual and parallel decrease in frequency. The developmental profile of Squeak frequency showed a relatively consistent decrease in frequency for all three litters.

The mean fundamental frequency variation of Squeals and Squeaks (Figure 20B) also changed significantly with pup maturation. The overall pattern is one of a significant decrease in frequency variation (Table VI). The developmental profiles of both Squeal and Squeak frequency variation of individual litter trends showed only modestly different trends.

Duration

The duration of individual Squeal and Squeak elements, and the duration of the inter-element-interval within a series, were averaged at each week of the developmental time-span. These means (\pm standard errors) are presented in Figure 21(A-D). Squeal and Squeak durations (in seconds) are graphed as a

Table VI. ANOVA *F* statistic values of Squeal (number of weeks=5) and Squeak (number of weeks=4) acoustic variables for the individual litters.

Variables	Squeal			Squeak		
	1988	1990	1991	1988	1990	1991
Litter	1988	1990	1991	1988	1990	1991
Total (N)	373	346	344	224	374	94
Frequency	25.31*	11.51*	16.74*	266.69*	54.79*	137.59*
Variation	18.00*	3.51*	32.07*	14.65*	15.65*	11.29*
Duration	0.47	3.08*	6.97*	1.52	8.68*	3.01*
Total (N)	265	245	259	162	297	64
Interval	0.99	2.54*	15.22*	5.66*	1.36	2.88

* $p < 0.05$

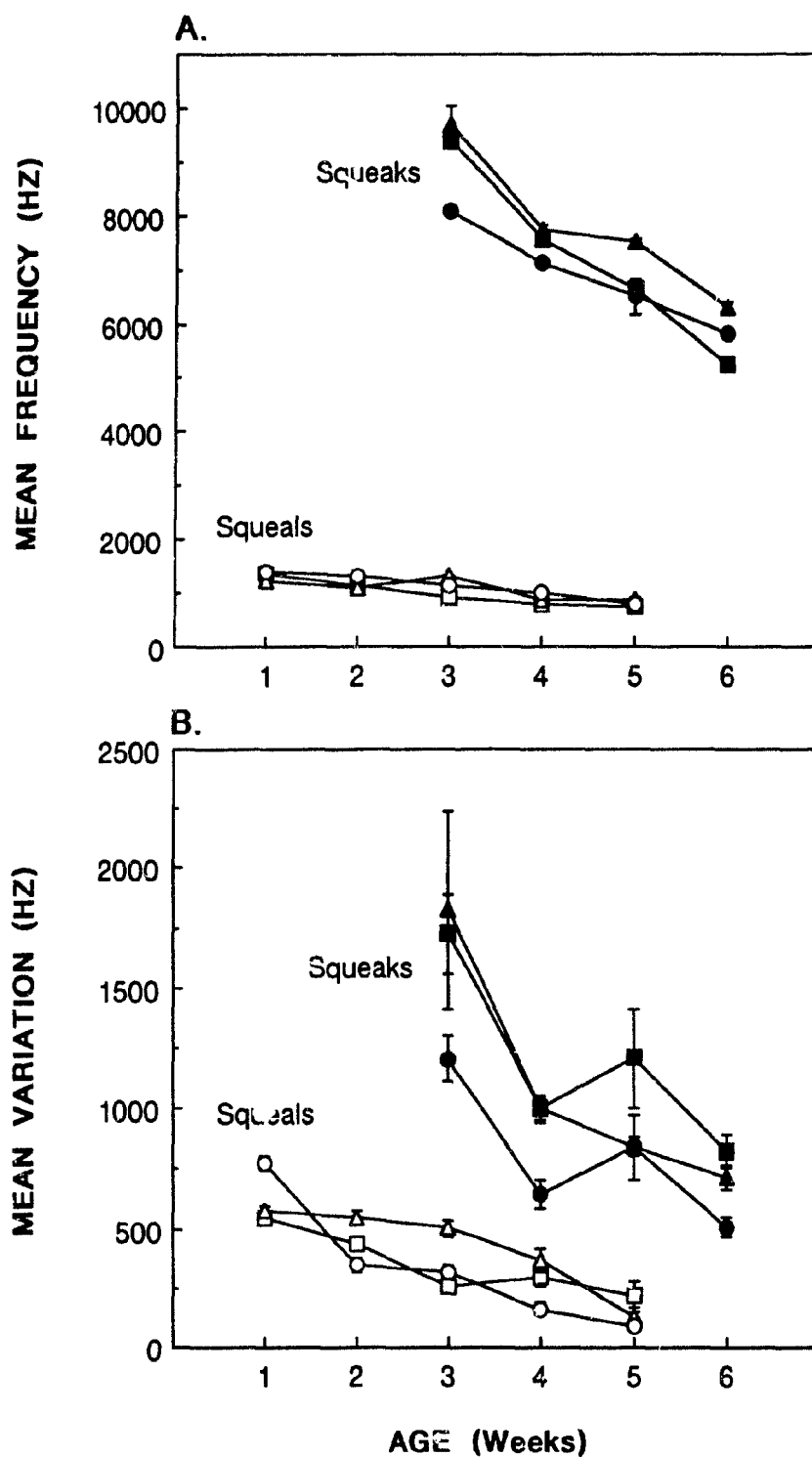


Figure 20. A. Mean fundamental frequency (\pm standard error) of Squeals and Squeaks for individual litters as a function of age. B. Mean frequency variation (\pm standard error) for individual litters as a function of age. (Note small standard error bars). Squeals: \square = 1988 (N=373); Δ = 1990 (N=346); \circ = 1991 (N=341). Squeaks: \blacksquare = 1988 (N=224); Δ = 1990 (N=374); \bullet = 1991 (N=94).

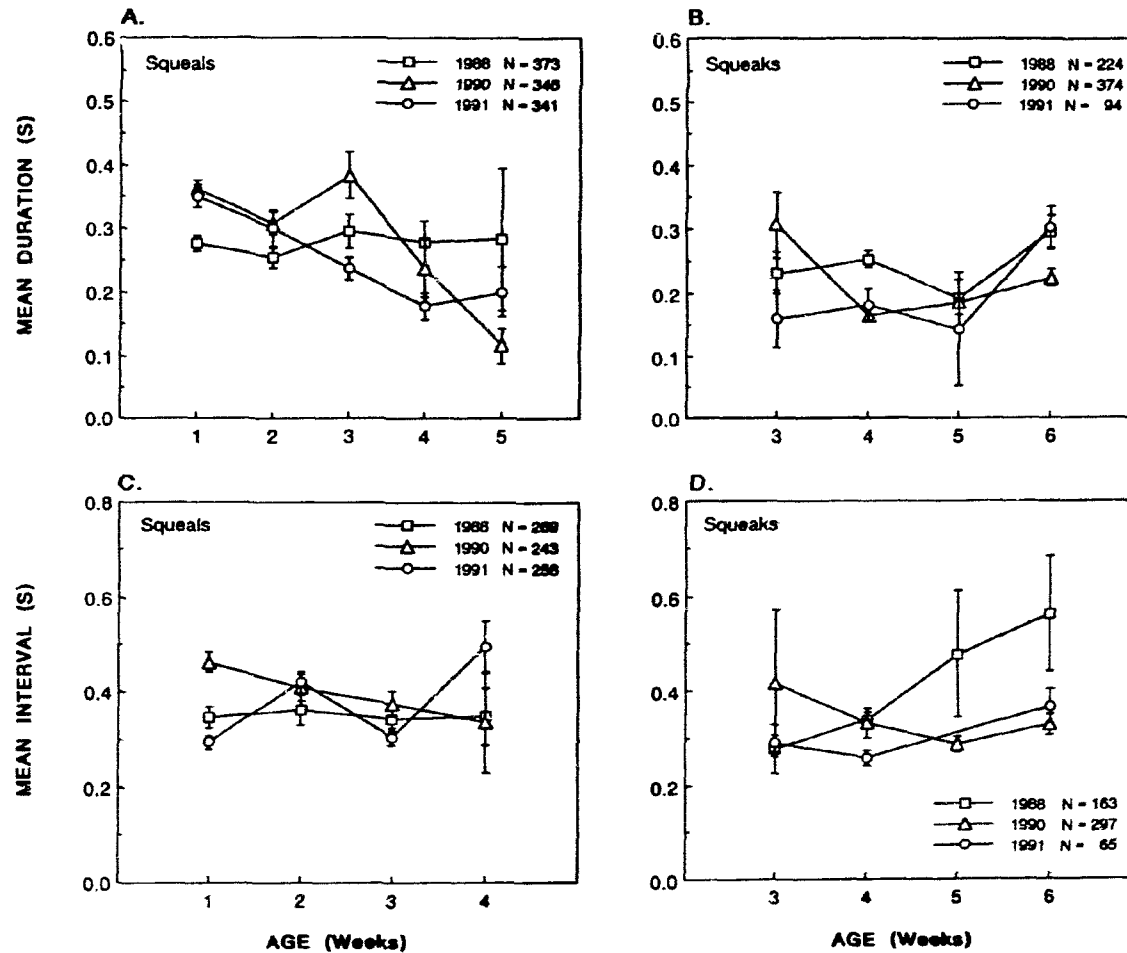


Figure 21. Mean duration (\pm standard error) of Squeals (A) and Squeaks (B) for individual litters as a function of age. Mean inter-element-interval duration (\pm standard error) of Squeals (C) and Squeaks (D) for individual litters as a function of age.

function of age in Figure 21(A-B). The developmental profile of Squeal durations revealed statistically significant decreases for two litters, 1990 and 1991 (Table VI). The duration of Squeals produced by the 1988 litter did not change significantly from one to five weeks of age. The 1990 litter profile revealed a significant increase in mean duration at week three, followed by uniform decreases between weeks three to four and weeks four to five. The Squeals emitted from the 1991 pups gradually decreased in duration until week four. Thus, not only were Squeals less common in weeks three to five (Figure 18A), but their durations were often shorter.

Squeak mean duration profiles revealed significant changes across time for the 1990 and 1991 litters (Table VI), with divergent patterns of change (Figure 21B). The 1988 and 1991 litters had similar patterns of a modest decrease in frequency between weeks three to five. This slight decrease was followed by a distinct increase in duration between weeks five and six. The 1990 litter deviated from the other two litters. The duration of Squeals initially decreased, between weeks one and two, and gradually increased through week six.

Figure 21(C-D) displays the developmental trajectories of the durations of the mean inter-element-intervals of Squeals and Squeaks. The patterns of Squeal inter-element-intervals revealed significant changes for the 1990 litter and the 1991 litter but their developmental trends were opposing (Table VI, Figure 21C). The profile of the 1990 litter revealed a modest decrease in duration

during development. In contrast, the pattern of sound duration for the 1991 litter, fluctuated with an initial increase in duration followed by a decrease, followed by a second increase. The 1988 litter trends in inter-sound duration were relatively constant between weeks one through four.

The litter profiles of Squeak inter-element-interval durations were also disparate (Figure 21D). There were no inter-element-intervals recorded for week five for the 1991 litter because the few Squeaks that were recorded for this litter were emitted singly. The inter-element-interval duration significantly increased with maturation for the 1988 litter (Table VI). The 1990 litter had no significant changes in interval duration as a function of age. The pattern of interval duration revealed from the 1991 litter data was not significant. There was no significant difference in the mean interval duration of Squeaks for the 1991 litter; few intervals were recorded during week four, none were noted for week five and only one was recorded during week six.

Pure series and elements within series

The total number of Squeal and Squeak series and the number of elements within these series was counted. In this analysis, only those Squeal and Squeak series that were composed solely of either one vocal class or the other were quantified; they are described as a function of age for each litter (Figure 22(A-D)). The litters were averaged for the ANOVA because of generally similar developmental trajectories. ANOVA's were performed for weeks one to

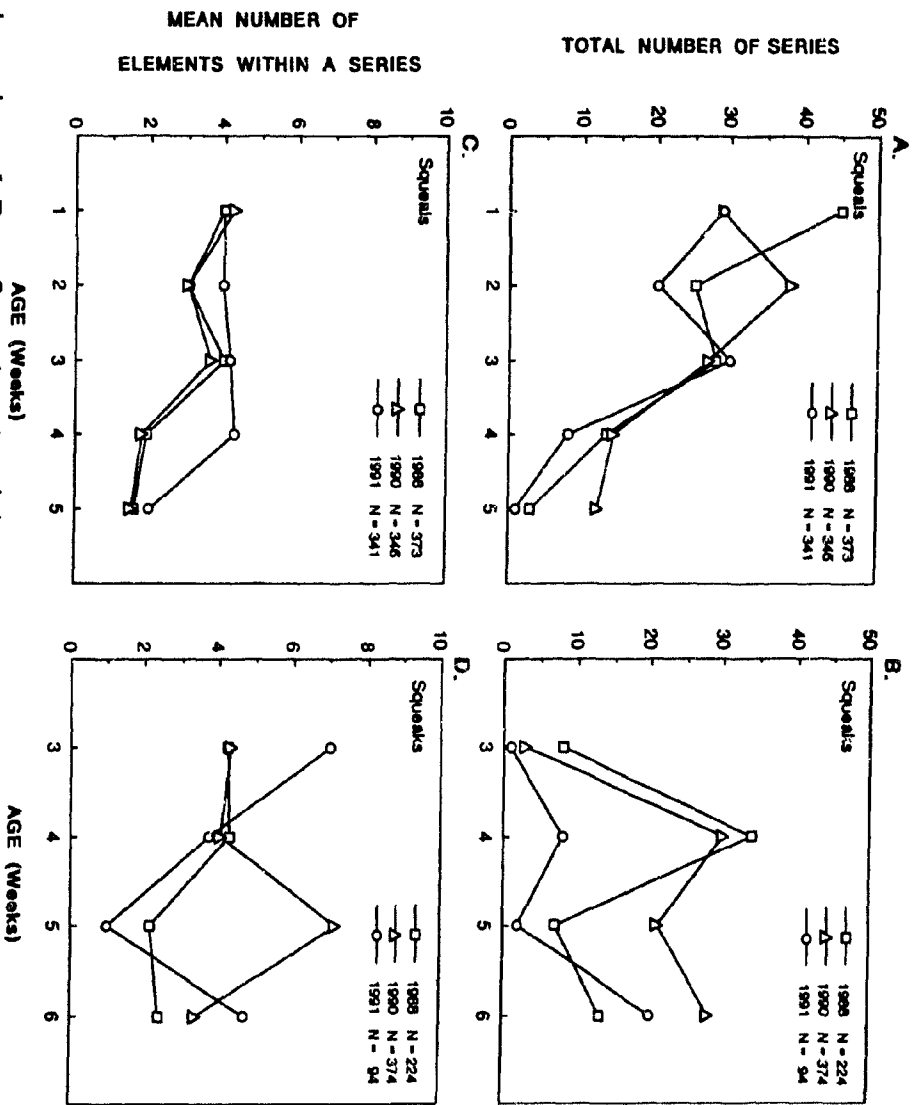


Figure 22. Total number of Pure Squeal series (A) and Pure Squeak series (B) for individual litters as a function of age. Mean number of elements within Pure Squeal series (C) and Pure Squeak series (D) for individual litters as a function of age.

five for Squeals and weeks three to six for Squeaks.

The Squeal and Squeak data revealed developmental changes associated with the total number of series (Figure 22(A-B)). The total number of elements in Squeal series (Figure 22A) decreased ontogenetically ($F(4,10)=10.42, p<0.05$). Total numbers of Squeal series were high for all three litters at week one. During week two, the 1990 litter had an increase in their total number of series in contrast to the decrease observed for the 1988 and 1991 litters. The total numbers of Squeal series dropped after week two, whereas the numbers for the 1988 and 1991 litters increased slightly and then diminished. In general, the overall trends in the number of Squeal series for all three litters reflected the same decreasing pattern of Squeal proportions across time (Figure 18A).

In contrast to Squeal series, the total number of Squeak series showed no significant age-related changes following their emergence at three weeks of age ($F(3,8)=2.81, p>0.05$) (Figure 22B). The data for the total number of Squeak series were disparate for the three litters, although litter developmental trajectories were similar. Squeak series numbers were initially low for all three litters. Total numbers substantially increased for the 1988 and 1990 litters, but only modestly increased for the 1991 litter. All three litters had a drop in total numbers by week five, followed by a second rise in numbers at week six. Patterns in the absolute number of Squeak series showed no age-related increases after Squeaks emerged at three weeks of age.

Figure 22(C-D) display the trends for the mean number of elements within a series for Squeals and Squeaks. The number of elements within the Squeal series decreased across weeks for all three litters ($F(4,10)=6.00$, $p<0.05$). In general, the mean number of Squeals within a series were relatively stable across the first three weeks of development and then declined (Figure 22C). The 1988 and 1990 Squeal trends parallel each other during development, whereas the 1991 litter, again, slightly deviates from the other two litters.

In contrast to the mean number of Squeal elements which decreased, the mean number of Squeak elements within a series revealed no consistent pattern of change as a function of age (Figure 22D). There were no significant changes in the number of elements in a Squeak series across weeks ($F(3,8)=0.55$, $p>0.05$). These data are less predictable across time in a comparison of litter profiles. The 1988 pups had similar numbers of Squeak elements between weeks three and four. These numbers fell at week five and then levelled off by week six. The 1990 litter also had similar element numbers between the third and fourth weeks of ontogeny, but their numbers increased at week five. This increase is followed by a nearly equal decrease. The trends for the 1991 litter were slightly different than the other two litters. Their element numbers dropped between weeks three to five but increased by the sixth week.

Mix series

On occasion, elements of more than one vocal class occurred within

individual series (Mix series). Of the total 3,396 sounds that were measured, 508 (15%) sounds occurred in Mix series. These Mix series included primarily one or more of Squeals, Screams or Squeaks, and rarely one or more of a number of other vocal classes (Yelps, Growls, Barks or Howls). Sixty-four measurable Mix series were recorded during the six-week observation period and are depicted in Figure 23 as series of alphabetic characters.

Several trends were revealed in these Mix series. Ninety-two percent (N=59) contained only two vocal classes within each series. The remaining series contained three (N=5). Typical Mix series combined Squeals with either Screams or Squeaks. The mean proportions of Squeal, Scream and Squeak elements (i.e., the most common elements) found in Mix Series are displayed in Figure 24. These data were pooled for all three litters because of their overall low rate of occurrence at each age category. Proportions were calculated by taking the total number of either Squeal, Scream or Squeak elements within a Mix series and dividing the total number of each sound class by the total number of elements within the series. A mean proportion (\pm standard error) was calculated for Squeals, Screams and Squeaks (in Mix series) at each week by summing the proportions obtained of each sound class at each week and dividing the sum by the total number of mixed sound series that contained either Squeals, Screams or Squeaks for each week. Note that the proportions for any given week may be greater than 1 because a Mix series can contain other elements (e.g. Yelps and Howls) in addition to Squeals, Screams and/or


```

1. LL-----LL-----LLL-LL--MMM-MMM-MMMMMM--MMMM-MMMMM-
   MMMMM--MMMMMMMMMM-----LL---MMM--MMM--MMM
1. LLL---LLL---LLLL--MMMMM--MMMMM--MMMMM--MMMMM--MMMMM--
   MMMMM--MMMMM--MMMMMM
1. yy-L--LL--LL
2. y--MMM
2. MMM--MMMM--MMMM--yyy---yy---yy---MMMM--LLL---LL---
   LLL
2. MMM---y
2. bb-gggg
2. LL---LL--LL--LLL--LL---LLLL--L---LLL-----MM--MMM-MMMM-
   MMMMM-MMMMM
2. MM--MM--MMMM-MM--MM-MMM--MMMM-MMM--MM--MM-MMM-LL
2. LLL-LLLLLL--LL--LL-LLL--LL-LLL-LL--LL-LL-LLL--LLL--LLL--
   LL-LLL-LLL--LL--MMMMMM-MMMM-LLL
2. LLL--LLL--LL--LLL--LL-LLL-LLLLL---LLL--LLLLL-MMMMMM-
   LLLL--LLL-LL--LL
3. KKKKKKK--KK--KKK--LLL
3. K--KK--KK-KK--LLLLL
3. KKKK--KK--KK--KK--LL--LL--LL-LLL--LL-----L
3. LL--LL--LL--LLL--LLL--LLL--K---KK---LL--LLL--LL-LLL-
   LLLL-LLL
3. LLL-LL--LL-LL--LL-MMM-MM-MMMM-MMMM-MMM-MMMM-MMM-LL
3. L--LLL--LL--LLL--LL--K--KK--KK--L--LLL--LLLLL
3. MMMMMM--LLLLLLLLLL--LLL--LLL--LLL--LLL--LLL--LLL
3. LLLLLL--LL--L---LLL--LLL--LLLLLLL-hhhhhhhhhhhhhhh-----
   hhhhhhhhhhhhhhhhh-----
   hhhhhhhhhhhhhhhhh-----hhhhhhhhhhhhhhhh
3. LL----LLL--LL--LLL-MMM-MMMM-MMMM--LLL

```

Figure 23(A). Mix series. Weeks 1-3 (indicated, numerically, at the beginning of each series). Each character and dash designate 0.10 second samples of the sequence. Squeal, Scream and Squeak elements are represented by the last letter (capitalized) of each sound (i.e., "L", "M" and "K" respectively). Yelps, Growls, Barks, Woofs and Howls are symbolized by the first letter (lower-case) of each sound. The inter-element-interval within a series is represented by one or more dashes ("-").

4. K-----K--K--K--KK--KK--KK-KK-KK-L--LL-LL--LL---L
 4. KK--L
 4. K-----KK--K--KK-KKKK--KK-K-KK-KK--LLL-L
 4. K--KK-----KK--KK--KKK--KK--KK-KKK--KKK--KKK--LLLL-
 KK--KK--KK
 4. MM-KK-KKK-KK--MM-KK
 4. KKKK----L---LL
 4. w-----ggggg-----w-----ggggg
 4. K--K--K-L--L-w
 4. K--KK-KK-KKK-KKK--LLL--LLL
 4. K--K--K--KK--LLL
 4. ww-----ww-----ggggggg
 4. ww-----ggggggg-----ggg
 4. L--L-K--K--KKK--KKK--hhhhhh-hhhhh-hhh--hhhhhhhhhh
 4. MMMM-MMMM--MMMM-LLL---LLLLL
 4. K---K---K--KK--KK-L
 4. L--K--KK
 4. K---K--K-----K--KK--hhhhhhhhhhhhhh
 5. KKK-----KKK-----KKK--KKK--LL
 5. KK-----KF--gggg
 5. KK---L-----L---K-----KK---KK-----
 K-----K---L---KK
 5. K--L
 5. KK--K-KKK-KK-KKK--L
 5. K---KK--KK-KK-K--L
 5. K--KK--K--KK--KK--K--L--L
 5. KKK--KK--KK--L
 5. K-KKK--bbb
 5. K---K-----KK-MM--M--KK
 5. K-KK-MM--MM--KK--KK-K--K-KK--K--M
 5. K---LLLL-----K-----K---KK--K---K
 5. K-----KK-----K---KKK-----KKK---LL
 5. K--K--KK--LL--K-KK-KK--KKK--LL--LL
 5. KK-KKK--K--L
 5. KK--KK--KKK-MM--M---MMM-MM--KK--K---K
 5. KK-MM-KK--K--KK--KK--KKK-KKK-MM--M---KKK
 5. K--K--KK--KKK--KKK-KK--KK-KK-KK--M---K---K
 5. K---KK--K--KK--K-KK-KK-K--KKK-K-KKK-KK-M-MM--MM-M
 6. K-----K--KK-----K---KK-----L--K---K
 6. KK-----K--KK-L
 6. K-----L
 6. w-----gggg-gggg--w-----w---w---ggg-----ww-----
 w----w
 6. KK-----KK--KK--LL---ggggggggggggggg
 6. K--K-----K-----KK--KK--KK--K--KK--KKK--KKK--K-KKKKK--L-
 KL-K---KKKK--KKK
 6. LKKKKKKKKK--KKKKK--LKKKKK--KKKKKKK--KKKK--KKK---
 KKK--KKKKK--KKKK--KKKK--KKK--KKK--LLLLLL---
 LLKKKKKKKKL-----LLKKK--hhhhhhhhhh
 6. LLKKKKKKKKKK--LLLKKKKKKKKKKL-KK---KKKK--KKK--KK--
 LLL---K-----KKK---K

Figure 23(B). Mix series. Weeks 4-6.

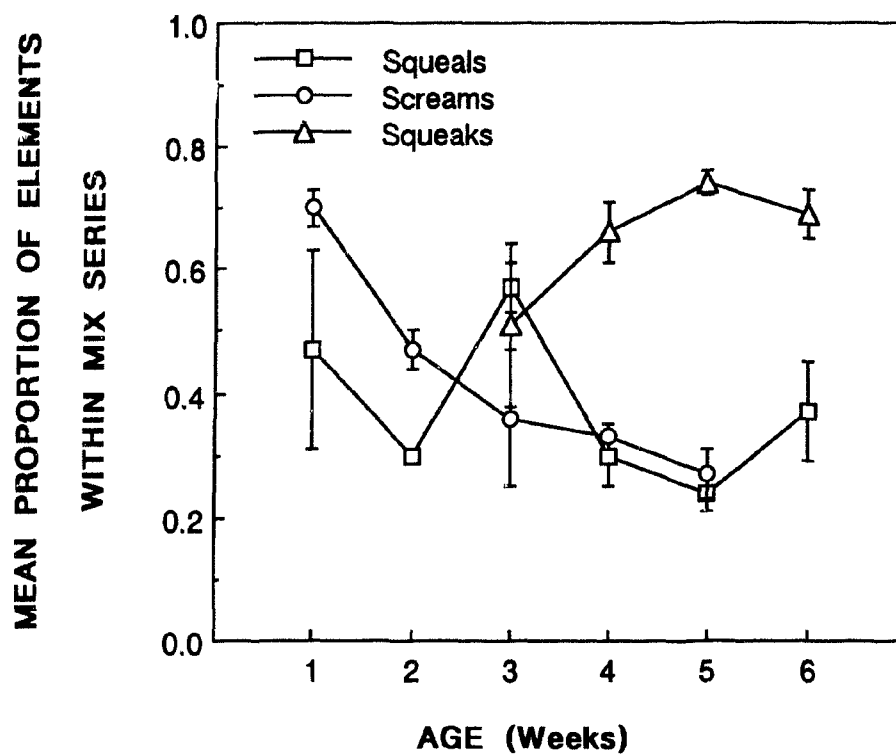


Figure 24. Means (\pm standard errors) of the proportions of Squeal, Scream and Squeak elements within Mix series as a function of age.

Squeaks (see Figure 23). Proportions were analyzed for trends across time (ANOVAs): Squeals, weeks one to six, Screams, weeks one to five and Squeaks, weeks three to six.

The proportion of Screams significantly decreased with age ($F(1,3)=20.10$, $p<0.05$) and the proportion of Squeaks appeared to increase between three to six weeks of age, although this difference was not significant ($F(1,2)=0.27$, $p>0.05$). The mean proportions of Squeals did not change significantly across time ($F(1,4)=0.81$, $p>0.05$) in contrast to their overall proportions (Figure 18A) which decreased with pup maturation.

The sequential order of the common elements (Squeals, Screams and Squeaks) in Mix series was non-random. Squeals tended to occur at the beginning and end of series, and Screams and Squeaks tended to occur in between the Squeals. In 70% of the Mix Squeal-Scream series ($N=10$), Squeals appeared both at the beginning and at the end of these series. In the Mix Squeal-Squeak series ($N=30$), the series began with Squeals 87% of the time and concluded with Squeals 77% of the time.

The duration of elements within Mix series and the interval duration between elements in these series were different for the two main combination of series (early-appearing Squeals-Screams and late-appearing Squeaks-Squeals). Paired t-tests were used to compare the mean durations of Squeals, Screams and Squeaks. The mean duration of Squeals (0.30 ± 0.03 seconds) within Squeal-Scream series was significantly shorter than the mean duration of

Screams (0.47 ± 0.04 seconds) ($t(9)=5.948, p<0.05$). These durations did not differ from the overall mean durations of Squeals and Screams measured from single sounds from the corresponding time period (Table III, weeks one to three). The mean inter-element-interval between Squeals within the Mix series (0.26 ± 0.02 seconds) was significantly longer than the mean interval between Screams (0.13 ± 0.01 seconds) ($t(6)=4.86, p<0.05$). Inter-element durations of Squeals and Screams were shorter than the overall mean values of Pure series recorded during the same time period (Table III). In both Pure and Mix series, Squeal inter-element-intervals were longer than Scream intervals. The mean duration of Squeals (0.19 ± 0.02 seconds) within the Mix Squeal-Squeak series was similar to that of the Squeaks (0.19 ± 0.01 seconds) ($t(29)=0.05, p>0.05$). Finally, the mean inter-element-interval between Squeal elements (0.26 ± 0.02) and Squeak elements (0.30 ± 0.03) were not significantly different ($t(10)=3.14, p>0.05$). Both the duration of these elements and their inter-element durations were similar to the mean values of Pure series (Tables III and V: weeks one to five for Squeals and weeks three to six for Squeaks).

Isolation Howls and Mixed sounds

Howls from an isolated pup

In addition to the 3,396 sounds described above, 201 sounds were measured but not included in the main acoustic analyses. These vocalizations were all emitted in succession, within a forty minute block of time, by a male

pup that was deserted during a den transfer by the mother when he was three weeks of age. These Howls were excluded from the overall analysis to avoid bias by sampling from one specific pup in a single and unusual behavioural context. These calls, descriptively characterized in Table VII, were perceptually louder and longer than many of the vocalizations emitted when pups were not separated. The mean fundamental frequencies, fundamental frequency variations, COFM values, durations and the inter-element-intervals of sounds within a series (\pm standard errors) were computed as a whole, and in four separate time periods to determine if there were significant changes in the acoustic structures across time. The sounds were separated into four groups by dividing the time spent vocalizing into four equal partitions (approximately 10 minutes each). Mean values were computed for each partition. In addition, the number of vocalizations and the ratio of single sounds to series of sounds is provided.

Several changes can be observed in Table VII. First, the total number of sounds decreased across time. Second, the duration of these sounds slightly increased within the first 30 minutes. Third, the ratio of singly emitted sounds, compared to sounds emitted in series, increased. The decreased rate of vocal production may, in part, have been related to fatigue. None of the frequency measurements (fundamental frequency, frequency variation and COFM) varied significantly vary across time. The inter-element-interval of these Howls was consistent during the first two ten-minute periods, tripled in duration in the third

Table VII. Means \pm standard errors of the acoustical variables used to define the Howls from the isolated pup for the 40 minute time-period and the partitioned 10 minute blocks.

Variables	Pooled	0-10 min.	10-20 min.	20-30 min.	30-40 min.
Total (N)	201	83	66	29	23
Frequency (Hz)	967 \pm 15.5	974 \pm 28.1	940 \pm 26.1	1057 \pm 22.2	904 \pm 34.4
Variation (Hz)	832 \pm 17.6	779 \pm 32.4	803 \pm 25.4	987 \pm 28.9	913 \pm 37.7
Duration (S)	1.20 \pm 0.03	1.08 \pm 0.06	1.18 \pm 0.06	1.49 \pm 0.04	1.33 \pm 0.07
Interval (S)	0.59 \pm 0.42	0.59 \pm 0.06	0.60 \pm 0.06	1.81 \pm 0.00	0.42 \pm 0.03
COFM	11.4 \pm 0.58	10.5 \pm 0.60	12.6 \pm 1.54	10.2 \pm 0.58	12.6 \pm 0.72
Sing:Sers*	25:16	1:2	2:3	26:1	9:5

* = Ratio of the number of single elements to the number of series.

period but then decreased in the fourth period. In general, the acoustic characteristics of these sounds were similar to those of Howls (Tables I and V), although their durations (mean = 1.20 ± 0.03) were notably longer relative to other Howls recorded during week three (mean = 0.82 ± 0.09).

Mixed sounds

Mixed sounds (not to be confused with Mix series) are vocalizations in which two distinct sound classes are juxtaposed in time (Coscia, 1989). Mixed sounds were observed in the present study but were not included in the main acoustic analysis because they were rare ($N < 20$) and too complex to categorize. Their mention was deemed noteworthy because their presence reflects added complexity of the wolves' vocal repertoire. Mixed sounds began to appear at three weeks of age in conjunction with the appearance of the late-appearing vocalizations. Combinations of sounds involved primarily Growls/Woofs and Squeals/Squeaks. Squeals/Squeaks predominantly occurred in Mix series, whereas Growls/Woofs appeared singly, in Growl/Woof series and in Mix series.

Summary of the Acoustic Properties of Pup Vocalizations

Classification scheme

The vocalizations described in this study represent sounds emitted by wolf pups from birth until their sixth postnatal week, prior to their integration with

the pack of adult and juvenile wolves. Neonate vocalizations were characterized based on their spectrographic structure. Variance along multiple acoustic dimensions was used to describe the sounds and to allocate them to categories. The dimensions included: the gross spectral type of the sound, the sound duration, absence or presence and rate of frequency modulation, the mean fundamental frequency (harmonic and pure-tone sounds) and the mean spectral bandwidth (noisy sounds). Additional measures of fundamental frequency variation were recorded for the harmonic or pure-tone sounds. Interval durations between sounds were quantified for sounds occurring in series. Finally, relative amplitude was measured for a representative sample from two vocal classes which had overlapping ranges in two acoustical dimensions. In total, eleven vocal classes were identified. Eight vocal classes were quantitatively defined in this study: Squeals, Screams, Yelps, Growls, Barks, Woofs, Squeaks and Howls. Three additional sounds classes were qualitatively described: Moans, Whines and Yawns.

The classification scheme utilized in this study required the use of multiple acoustic variables to assign all sounds to categories. Certain sounds within the wolf vocal repertoire can be classified on a single acoustic dimension: Squeaks were distinguished from all other sounds based on their extremely high fundamental frequency. Woofs were unique in that they had a very broad spread of spectral energy. Bivariate analyses supported the contention that some pup vocalizations had non-overlapping distributions of families of data

points (Figures 11-12). Two sound classes, Squeals and Screams, had overlapping distributions of data points (Figures 12-13). These sounds were, however, separable based on their relative amplitudes. Several additional differences in the acoustic structure of Squeals and Screams were not apparent in a simple two-dimensional analysis of frequency and duration variables. First, Squeals' gross spectral structure encompassed sounds which were pure-tone (single bands) in addition to harmonic (multiple bands). Pure-tone Squeals tended to be higher in frequency than harmonic Squeals. Squeals were never observed with more than two harmonic overtones. Screams, in contrast to Squeals, were never observed as pure-tones. Screams were always harmonic and always contained multiple harmonic bands. In addition, some Screams had noisy segments whereas Squeals were never observed with associated noise.

Acoustic properties

Tables I and III-V provide detailed information on the acoustic properties of the eight vocalization types and the sample size from which the measurements were obtained. From the tables and the proportion data for the six most common vocal classes, presented in Figure 18, come several findings regarding the acoustic properties of wolf pup sounds:

The proportion of vocal classes changed ontogenetically. It was evident that some vocal classes were more common than others at a given age. Some vocalizations appeared more frequently and others diminished as pups

matured. Squeals and Squeaks were two sounds which were produced in greatest proportions. Their proportions, however, varied across time. Squeals predominated in the early period of pup development. Squeaks, which were not observed until a pup's third week of life, predominated the later period. Other vocal classes, in contrast to Squeals and Squeaks, were quite rare but also varied with respect to their frequency distributions across time. For example, the rare-appearing Yelps were most notable during the early postnatal weeks. The sporadic Barks, however, were evenly distributed across the six postnatal weeks.

Fundamental frequency and frequency variation decreased with pup maturation. Overall, the most significant and consistent finding associated with the acoustic properties of wolf pup vocalizations was related to the fundamental frequency of the harmonic sounds. For the most common sounds, Squeals, Screams and Squeaks, and the rarer Howls, the fundamental frequency decreased as a function of age. Although the rare Barks contained a harmonic component, their fundamental frequency remained stable across time. The noisy Growls, however, were observed to increase in spectral breadth with age, whereas the spectral bandwidth of Woofs did not change ontogenetically.

Variation around the mean fundamental frequency decreased as a function of age for Squeals, Screams, Squeaks and Howls.

Sound duration did not systematically change with age. The duration of sounds varied differentially, across litters and across sounds. There were

slight decreases in the sound durations of Screams and Growls for all litters. Significant decreases in Squeal and Squeak duration with age were noted for two litters (1990 and 1991). The sound durations of the rare Barks and Woofs, however, remained constant as a function of age. Howls were more variable in duration with age. In addition to measuring sound duration, the inter-element-intervals between sounds within Pure series were recorded. Squeals, Screams and Squeaks comprised the three major classes commonly observed in series. No consistent developmental patterns in the interval durations of Pure series were observed.

Vocal classes were combined to form Mix series. Squeals, Screams and Squeaks occurred in series of mixed sounds. Mix series were observed for all six weeks of development from all litters. The acoustic characteristics of vocalizations within Mix series were similar to sounds emitted in either isolation or Pure series. Therefore, the structural integrity of individual sound classes was maintained in Mix series. Mix series were combinations primarily of two distinct sound classes, but the classes contained within a series differed as a function of age. Mix Squeals/Screams were common in the early weeks of development, and Mix Squeals/Squeaks predominated the later weeks. The sequential order of vocal classes within a series was non-random: Squeals typically preceded Screams but followed Squeaks, and Squeals were observed at the beginning and end of Mix Squeal/Scream series but usually only at the end of Mix Squeal/Squeaks series.

CHAPTER FOUR

RESULTS: BEHAVIOURAL CONTEXT OF WOLF PUP VOCALIZATIONS

Introduction

Tembrock (1976) discussed three key issues for understanding sound ontogeny in social species. In specific, the issues which need to be addressed include: 1) are there relationships between vocal classes and behavioural context; 2) who are the receivers of vocal activity and how do they respond; 3) does the informational content of vocalizations change with age. Basic descriptions of the early behavioural ontogeny of pups are a means by which to address these issues.

The ideal setting for observing the development of communication in the wolf is their natural environment, but observations in the field are difficult due to the shy nature of the wolf. Close-range observations of wild wolf pups are virtually impossible because pups are born and spend their first weeks of life within a secluded den, inaccessible to human observers. Observations of wolves in captivity are necessary for a full examination of early behavioural development. The in-den system used in this study provides a semi-natural environment for video and audio recording of behaviour of neonates with minimal disturbance to the animals. The behaviour of pups and their care-giver can be observed on a 24 hour basis. No other research facility has a recording system which examinations of the early development of wolf behaviour can be

conducted without disturbance to the study animals.

This chapter on the behavioural context of wolf pup vocalizations is divided into two sections. The first section provides a detailed descriptive background of pup behaviour and associated vocal activity. The second section is composed of statistical evaluations limited to selected behaviour associated with vocalizations as a function of age. This database represents 108 hours of video tape analyzed in real-time and over 800 scored behavioural events. Collectively, these data were examined to provide insight into the function of acoustic signalling in young wolves.

Description of Pup Behaviour and Associated Vocal Activity

The first two weeks

In contrast to the high rate of vocal production from neonatal wolf pups, neonate behavioural activities were minimal. Early pup behaviour consisted primarily of nursing, sleeping and aggregating or "huddling" with littermates and the mother, Pawnee. When Pawnee was absent, pups remained in the den. During Pawnee's absences, pups converged on debris (rocks and wood pieces) which accumulated in shallow depressions in the den floor. Pup movement within the huddle consisted of orienting the face and upper body towards the centre and top of the aggregation. On occasion, a pup rolled from the huddle when repositioning. These isolated individuals would crawl around in an apparently random manner until they contacted another pup.

The majority of pup Moans and Whines were associated with this huddling behaviour, particularly when Pawnee was absent from the den. These harmonic vocalizations were perceptually lower in amplitude compared to all other vocalizations produced during early ontogeny. Moans and Whines tended to be emitted in protracted series of elements. The duration of these sounds varied along a continuum ranging from short to long elements (Coscia, 1989). Increased vocal activity from the pups coincided with increased movement within the huddle. One pup's movements and Moan and Whine vocalizations were followed by similar movement and vocalizing by littermates. Whether pup movement evoked vocalizing or vocalizing elicited pup movement (or both) was not possible to assess.

Different vocalizations appeared in varying numbers and contexts during the first two postnatal weeks for all three litters. Squeals comprised the highest proportions of all early-appearing vocalizations occurring both in the presence and absence of the mother. Squeals were emitted by pups when the mother tended the pups by grooming them. Squeals were also heard, however, from pups which were not receiving maternal care, although the mother was present. One pup's Squealing was often followed by other pup's Squealing.

Screams and Yelps were associated predominantly with mother's movement in the den, including entering, exiting and repositioning herself or her pups. Pawnee's movement in the den elicited Screams and Yelps from the pups when they were either stepped on or carried by Pawnee. In contrast, the

rare Growls and Barks observed during the early weeks were emitted with no obvious stimulation (i.e., not associated with either movement by Pawnee or by the litter).

Pawnee was the only adult in the den during the first two postnatal weeks for all three years. She tended the pups, although her attendance was not always in response to pup vocal activity. In contrast to the highly vocal pups, Pawnee rarely vocalized in the den. The only sounds she emitted were Squeaks which often followed extended series of pup Squeals or Screams. She also Squeaked upon returning to the den. Pawnee's Squeaks, in either context, did not elicit any obvious vocal or orientation response from the pups. When Pawnee returned to the den after brief absences, pups did not move from their huddle towards her until she physically contacted them. Once contacted, the pups would quickly move to Pawnee's belly and initiate nursing. On only two occasions (during week two, 1991), were Pawnee's Squeaks followed by a single pup's movement towards her.

Pups did not attend to any external sounds or activities outside the den. Adult and juvenile wolf Squeaks and Howls from outside the den were among the sounds which could be detected by the recording equipment inside the den. In addition to pack wolves vocalizing, mechanically-generated sounds from trains, planes and trucks were audible inside the den. The calls from ravens (*Corvus corax*) and white-throated sparrows (*Zonotrichia albicollis*) could be heard. Also, precipitation, ranging from light showers to heavy rains, was

detectable. None of these sounds elicited pup vocalizations during the first two weeks of age.

Week three

Marked changes in the physical development of the pups occurred by three weeks of age. The pups' eyes opened or were in the process of opening. Their ears, which were initially pressed close to the head, were held upright. Ear opening corresponded with the time when auditory localization is reported to occur in dogs and wolves (Mech, 1970; Ashmead et al., 1986). Pups moved in the den with fragmented movements. Body-shaking was observed, similar in form to adult shaking but slower. Tail-wagging was noted prior to nursing bouts. During nursing, tails were often horizontally extended.

Pawnee exited the den frequently after the pups' first two postnatal weeks (1988 and 1990). When Pawnee exited the den, pups would cling to her teats as she entered the tunnel. Pups would not exit with Pawnee but would return to the den and actively explore. During exploration, pups moved silently with their heads to the ground, sniffing. Occasionally pups bumped into each other resulting in brief interactions in the form of mouthing of a pup's facial area. Interactions using forepaws were observed but infrequent. Vocal activity was not detected during these interactions. Following all exploration and interactions, pups returned to the huddle. Pups continued to huddle with subdued vocal activity. Pups persisted in huddling on debris during Pawnee's

absences. Pups moved about frequently in the huddle by directing their upper body towards the top and centre of the huddle.

Pup behaviour was variable when Pawnee returned to the den after periodic absences. Pups tended to orient towards Pawnee as she emerged from the tunnel and then stood motionless. Once in the den, Pawnee would simultaneously Squeak and contact pups. Pups typically oriented towards Pawnee, approached and began nursing. Several times, Pawnee entered the den, Squeaked, and reclined without contacting the pups. Pups then did not approach her until she contacted pups by grooming them. On one occasion (1990), Pawnee returned to the den and the pups approached her without any apparent vocal or physical solicitation.

There was a noticeable decline in overall vocal production at three weeks of age, but new sound classes began to emerge. Squeals and Screams declined, although the context in which they were produced did not notably change. Vocalizations were produced at a lower rate with Moans more common than Whines. Growls and Barks were still rare and not associated with a specific social context. Howls were produced by pups from all three litters. Most Howls were emitted when pups were stationary, without any apparent stimulus. One pup Howled apparently spontaneously during nursing. Another pup produced clearly-defined and sustained Howls when it was deserted in the den during a den transfer. Low-amplitude, high-frequency Squeaks emerged at three weeks of age. Early Squeaks, like Barks and Growls, were not

associated with interactive social contexts.

Weeks four through six

By four weeks of age, pup body movements were extensive and coordinated. Pups were observed to move forwards and backwards, rush into/out-of the tunnel and pounce. The majority of quick pup movements tended to be jerky. Movements of body-parts appeared more controlled with increasing age. For example, pups were capable of orienting each ear independently and without simultaneous head movement. Tail-wagging and tail-tucking were observed commonly in conjunction with social interactive behaviour. Head and body shaking was more rapid than during week three. Pups were also capable of scratching themselves with their hind-limbs.

Pups moved about in the den with greater amounts of investigative behaviour compared to that demonstrated during week three. Pups also began to explore the tunnel area and commenced excursions from the den. These excursions increased in both frequency and duration after four weeks of age. By six weeks of age, pups spent the majority of time either in the tunnel (outside of camera viewing range) or outside the den. Upon re-entering, pups typically explored the den by sniffing.

Coinciding with the pups' excursions from the den was increased vocal activity from adult and juvenile wolves outside the den. Multiple series of adult Squeaks were detected, particularly during Pawnee's absences. The majority

of these series were followed initially by Woofs from the pups, and then by pup departure from the den. The majority of Woofs emitted by pups were produced in the tunnel as pups exited. Pups did not exit to all Squeak series emitted outside the den. In addition, on some occasions, pups exited at different rates and independently with one or several pups remaining in the den, while one or several pups departed.

Pup den activities increased during both the presence and absence of Pawnee. The 1991 litter was less active compared to the other two litters. For all litters, pups were generally more active when Pawnee was absent. Pup behaviour involved reciprocated and unreciprocated interactions with littermates. Interaction types varied from mouthing areas of the face (as in week three) to mouthing and/or biting other body parts, particularly tails and limbs. Biting with simultaneous head-shaking was observed by week five. Bilateral pawing between pups was a common social activity, as well as one-up one-down interactions, ambush (one pup crouches and jumps on another pup) and wrestling. As pups matured, interactions involved a greater range of body parts. The majority of interactions appeared non-aggressive. Vocalizing during pup interactions was rare and involved primarily soft Moans and Whines and rarely Squeaks and Growls.

Pups also engaged in a variety of non-social behaviour. Such activities included digging and chewing on loose objects (e.g. woody debris, meat) or fixed objects.

During weeks four to six, pups rested for extended periods in the den between social and solitary activities. Pups continued to huddle, with individual pups moving towards the top and centre of the aggregation. Pups tended to stretch out their bodies rather than curling them, as with earlier huddling. By six weeks of age, some pups were resting apart from the huddle. Moans and Whines, though fewer in number, continued to be associated with the huddling behaviour. In addition, Yawns, primarily associated with movement to, from or within reclined positions, were noted.

Pawnee's length of stay in the den decreased with pup maturation. In the den, Pawnee would nurse and tend to pups. Pawnee frequently dug depressions in the den. Occasionally another adult female, "Ursula", was observed alone in the den with the pups during Pawnee's absences. Ursula was noted in the den during week four, for the 1988 litter, and during weeks five and six for the 1990 litter. Ursula was not observed with the 1991 litter, even though she was still a pack member.

Pup behaviour with Ursula was different from that with Pawnee in three ways. First, pups tended not to huddle with Ursula. Second, pups engaged in unreciprocated interactions with Ursula in the form of pawing, mouthing and chewing her neck and ears. Pups were not observed interacting with Pawnee in such a manner. Finally, pups responded differently to Ursula's Squeaks. Ursula's Squeaks were high in frequency, variable in frequency modulation, and contained noisy elements. Pawnee's Squeaks were lower in frequency,

relatively flat in spectral structure and purer in tonal quality. Pups sometimes avoided Ursula when she Squeaked by backing away from her and, sometimes, Growling. When Pawnee Squeaked, pups would quickly move towards her. Pups only Growled at Pawnee when she attempted to move them during a den transfer. In this situation, pups withdrew from Pawnee by dodging her and/or rolling on their backs. Pups responded to Ursula's retrieval attempts in the same manner as they did to Pawnee's. In response to these pups' Growls, Pawnee appeared more persistent in her attempts to move pups in comparison to Ursula who was more hesitant.

Several observations were made of Pawnee and Ursula simultaneously in the den with the pups (1988). On one occasion, Ursula entered the den and Pawnee Growled. Ursula remained in the den, regurgitated to the pups, groomed them, dug and then departed. On another occasion, Pawnee did not Growl as Ursula entered but, instead, Pawnee exited the den with pups attempting to follow.

Pup vocalizations in weeks four and five were, in general, few in number. There were, however, more adult-structured sounds (Squeaks, Woofs and Howls) and fewer neonate-specific sounds (Squeals, Screams and Yelps). The early-appearing Growls were more frequent relative to the first three weeks. Barks were still rare.

In summary, among all of these sounds, Squeaks were the most common and were associated with either pup interactions or adult-related

contexts. Growls from older pups were associated with pup interactions. Woofs were primarily adult-related and were only emitted when adults were in the tunnel entering the den, or outside of the den. Initially, when an adult entered the tunnel, pups Woofed and withdrew from the entrance. Once Squeaks were emitted by the in-coming adult, pups responded in two different manners depending on who produced the Squeaks; Squeaks from Pawnee elicited approach, those from Ursula elicited retreat, and, intermittently, Growls. Adult Squeaking outside of the den was followed by pups entering the tunnel and Woofing. Howls were emitted in a greater variety of contexts when compared to earlier weeks. Pup Howls were produced either spontaneously (week three and six), with no apparent stimuli internal or external to the den, or following specific external events. Pups Howled following adult vocalizations [Squeaks (week three and six); Howls (week four)] and mechanically-generated noises [train whistle (weeks three and four); plane (week five)].

Quantitative Analysis of Pup Vocal Context

Description of the quantitative analyses

In the following, pup vocalizations and their behavioural context will be described in a quantitative manner. Pup vocal context was recorded for all sounds which were characterized acoustically (Chapter Three). The context was also noted for some vocalizations which could not be measured reliably due to multiple pups vocalizing or background noise. These vocalizations

comprised primarily distress-related Screams, Squeals and Mix Series (mixed sound series). Pup behaviour, mother/adult behaviour and obvious external events were recorded only at the onset of a sound or sound series. This procedure avoided problems associated with possible changes in either pup or adult behaviour during production of a series of sounds. For example, a variety of changes of internal state or external influences may alter pup or adult behaviour during the production of a sound series.

Descriptive statistics and non-parametric analyses of independence were employed for the examination of acoustic behaviour. Descriptive statistics were used to characterize the behaviour of the three litters, across the six weeks, for purposes of exploratory data analysis (Martin and Bateson, 1986). For vocal classes with sufficient representation, the percentages of each associated behaviour were calculated for each of the three litters. Insufficient representation of all vocal classes from the three litters precluded separate litter analysis across the six week developmental period. The percentages of each behaviour for the three litters were averaged and the means (\pm standard errors) displayed in the form of bar graphs.

The three litters were pooled for contingency table analyses. Pooling of litters was based on obvious *a-posteriori* similarities evident in the mean percent data. Age classes were also pooled based on *a-posteriori* similarities: the six week developmental period was divided into two blocks of time: the "early" neonatal period (weeks one to three) and the "late" neonatal period (weeks four

to six).

"One of the first steps in a quantitative study of animal behaviour is the observation of the frequencies with which various acts occur in a group of individuals, and the study of these data for patterns, regularities, and relationships." (p.146, Colgan and Smith, 1978). In this study a procedure was needed to test frequency observations for associations among vocalizations and behaviour across time. Log-linear hierarchical modelling of contingency table data permits observations of multivariate frequency data (Colgan and Smith, 1978; Knoke and Burke, 1990). This method is a non-parametric test of independence for the analysis of multivariate frequency data (Sokal and Rohlf, 1981). The log-linear model determines whether behaviour across dimensions results from random or non-random associations by comparing observed and expected cell frequencies. However, log-linear modelling for describing the context of wolf pup vocal behaviour across time has several drawbacks. In the present study, there were multiple behaviours and events which changed (i.e. appeared and diminished) as pups matured. First, the total number of pup vocalizations changed (decreased) as a function of age. Second, the relative proportions of vocalization classes varied as pups matured. Third, the types of pup behaviour changed as a function of age. These three changes pose a problem for the log-linear analyses because they create large, sparse transition matrices which leads to spurious results (Fagen and Young, 1978). During early development, ontogenetic processes are difficult to describe statistically

because of the appearance and disappearance of behavioural events (Martin and Bateson, 1986). A related restriction to log-linear analyses is the need for relatively large samples of vocalization/context events. The sample size for each analysis was below the acceptable sample size ($2R^2$ where R =repertoire size, i.e., the number of cells in the matrix) suggested by Fagen and Young (1978) for raw frequency data. The repertoire size was either 30 or 40 but the sample sizes ranged from only 542 to 712, much smaller than the recommended 1800 to 3200.

A more suitable non-parametric procedure for analysis would be to employ two separate chi square tests of independence (two-dimensional analyses) for the "early" and the "late" periods of development. The chi square statistic is used to evaluate the size of the discrepancies between observed and expected cell frequencies in a two-dimensional contingency table (Colgan and Smith, 1978).

For the behavioural context analyses, observed cell frequencies were scored in two-dimensional tables in which rows and columns catalogued the vocal events and the associated or succeeding behavioural events. Two tables were used to index pup behavioural context. One table represented the early period in development (weeks one to three) and the second table represented the later period (weeks four to six). Expected cell frequencies were calculated using the Behaviour Events Analysis System (BEAST), Winword Technology, 1991). Calculation of the X^2 statistic and the standardized residuals (observed-

expected $\div \sqrt{\text{expected}}$) was performed using BEAST. The standardized residuals, regarded as approximate standard normal variates (Colgan and Smith, 1978), were calculated for each cell in the matrix to analyze the relationships between variables. If the absolute value of the standardized residuals of a cell is large, then the relationship between the two variables is non-random; if the value is positive, then the association is more common than expected, if negative, then the association is less common than expected. The BEAST software program automatically displays the rejection criteria ($p < 0.05$) for the standardized residuals as suggested by Fagen and Young (1978) [$\sqrt{(X^2_{0.05, df} \div R^2)}$, where R =repertoire size (number of cells), $df = (I-1) \times (J-1)$, where I =rows and J =columns] and Lefebvre and Joly (1982) [$\sqrt{(X^2_{0.05, df}) \times (1 - (1 \div R))}$]. The standardized residuals for each cell in the two tables are reported in Tables VIII-X. The Fagen and Young (1978) and Lefebvre and Joly (1982) criterion values are indicated in the tabled data of the residuals. For the following description of the analyses, however, the more conservative criterion for rejection, employed by Lefebvre and Joly (1982), will be presented. A more conservative rejection is preferred (to avoid Type I error) when there are overall low sample sizes (Milligan, 1980).

Pup vocalizations and pup behaviour

Wolf pup behaviour in the den was categorized into one of four classes:

- 1) "contact stationary" - contact with littermates or care-giver and minimal

Table VIII. Standardized residuals for the chi square analyses fitted to the data of pup vocalization and pup behaviour.

Age In Weeks	Vocal class	Pup Behaviour			
		contact stationary	contact moving	no contact	interactive
1 - 3 (447)	Squeal	0.47	-0.34	-0.98	---
	Scream	-2.12**	2.64**	-0.37	---
	GrowlBark	3.81**	-4.34**	-1.11*	---
	Squeak	-1.55**	0.84	4.54**	---
	Mix series	-2.16**	2.26**	1.50**	---
4 - 6 (262)	Squeal	1.41*	2.28**	-1.28*	-2.48**
	Scream	---	---	---	---
	GrowlBark	-2.23**	-0.73	-0.04	3.05**
	Squeak	2.03**	-0.32	-1.52**	-0.50
	Mix series	-1.76**	-0.47	3.11**	-0.44

** Suggested significance Early: >1.45 , $p<0.05$; Late: >1.47 , $p<0.05$ (Lefebvre and Joly, 1982)

* Suggested significance Early: >1.03 , $p<0.05$; Late: >1.02 , $p<0.05$ (Fagen and Young, 1978)

--- No entries

Table IX. Standardized residuals for the chi square analyses fitted to the data of pup vocalization and adult behaviour.

Age in Weeks	Vocal class	Adult Behaviour		
		stationary	groom	movement
1 - 3 (407)	Squeal	1.67**	-0.19	-2.79**
	Scream	-4.93**	2.12**	6.23**
	GrowlBark	3.79**	-3.23**	-2.71**
	Squeak	-0.63	0.89	0.00
	Mix series	-1.51**	0.66	1.89**
4 - 6 (152)	Squeal	0.49	0.06	-0.53
	Scream	---	---	---
	GrowlBark	0.23	0.28	-0.39
	Squeak	0.93	-0.04	-0.90
	Mix series	-1.80**	-0.21	1.92**

** Suggested significance Early: >1.45 , $p<0.05$; Late: >1.39 , $p<0.05$ (Lefebvre and Joly, 1982)

* Suggested significance Early: >1.02 , $p<0.05$; Late: >1.02 , $p<0.05$ (Fagen and Young, 1978)

--- No entries

Table X. Standardized residuals for the chi square analyses fitted to the data of pup vocalization and adult response.

Age in Weeks	Vocal class	Adult Response			
		no response	ears	other	other vocal
1 - 3 (416)	Squeal	1.48*	1.42*	-1.27*	-1.79**
	Scream	-4.86**	-1.25*	5.11**	0.04
	GrowlBark	5.84**	-1.57**	-4.59**	-1.73**
	Squeak	-0.83	-0.71	0.85	0.50
	Mix series	-3.86**	0.36	1.34*	6.65**
4 - 6 (124)	Squeal	2.57**	1.50**	-1.09*	-1.58**
	Scream	---	---	---	---
	GrowlBark	0.77	-0.94	-0.14	0.21
	Squeak	-0.87	0.01	0.95	-0.62
	Mix series	-1.39*	-0.32	-0.31	1.77**

** Suggested significance Early: >1.52 , $p<0.05$; Late: >1.47 , $p<0.05$ (Lefebvre and Joly, 1982)

* Suggested significance Early: >1.02 , $p<0.05$; Late: >1.03 , $p<0.05$ (Fagen and Young, 1978)

--- No entries

movements (e.g. huddling, resting, nursing); 2) "contact and moving" - contact with littermates or care-giver and substantial body movement (e.g. rolling, crawling, locomoting); 3) "no contact" - no contact with either siblings and/or care-giver and pups either stationary or moving; and 4) "interactive" - interactions with littermates or care-giver, includes reciprocated or non-reciprocated actions (e.g. pawing, chewing, wrestling, biting). Initially, the "no contact" class was divided into "stationary" and "moving" but these two categories were grouped due to their overall low sample size and their similarities with reference to their vocal context.

Figure 25(A-E) depicts the mean (\pm standard error) percent of each behaviour associated with pup Squeals, Screams, Growls, Squeaks and Mix series as a function of age. Squeals and Screams were associated predominantly with "contact" behaviour (Figure 25(A-B)). In the first postnatal week, Squeals were more associated with "contact stationary" behaviour than were Screams. From weeks two to four, Squeals were equally coupled with "contact stationary" and "contact moving". Screams were generally correlated with "moving" behaviour after the first postnatal week.

In contrast to Squeals and Screams, the context of Growls changed dramatically as a function of age (Figure 25C). For the first three postnatal weeks, Growls were mainly identified with "contact stationary" behaviour. After three weeks of age, Growl context shifted predominantly to "interactive" behaviour. Barks and Growls were emitted in the same behavioural context.

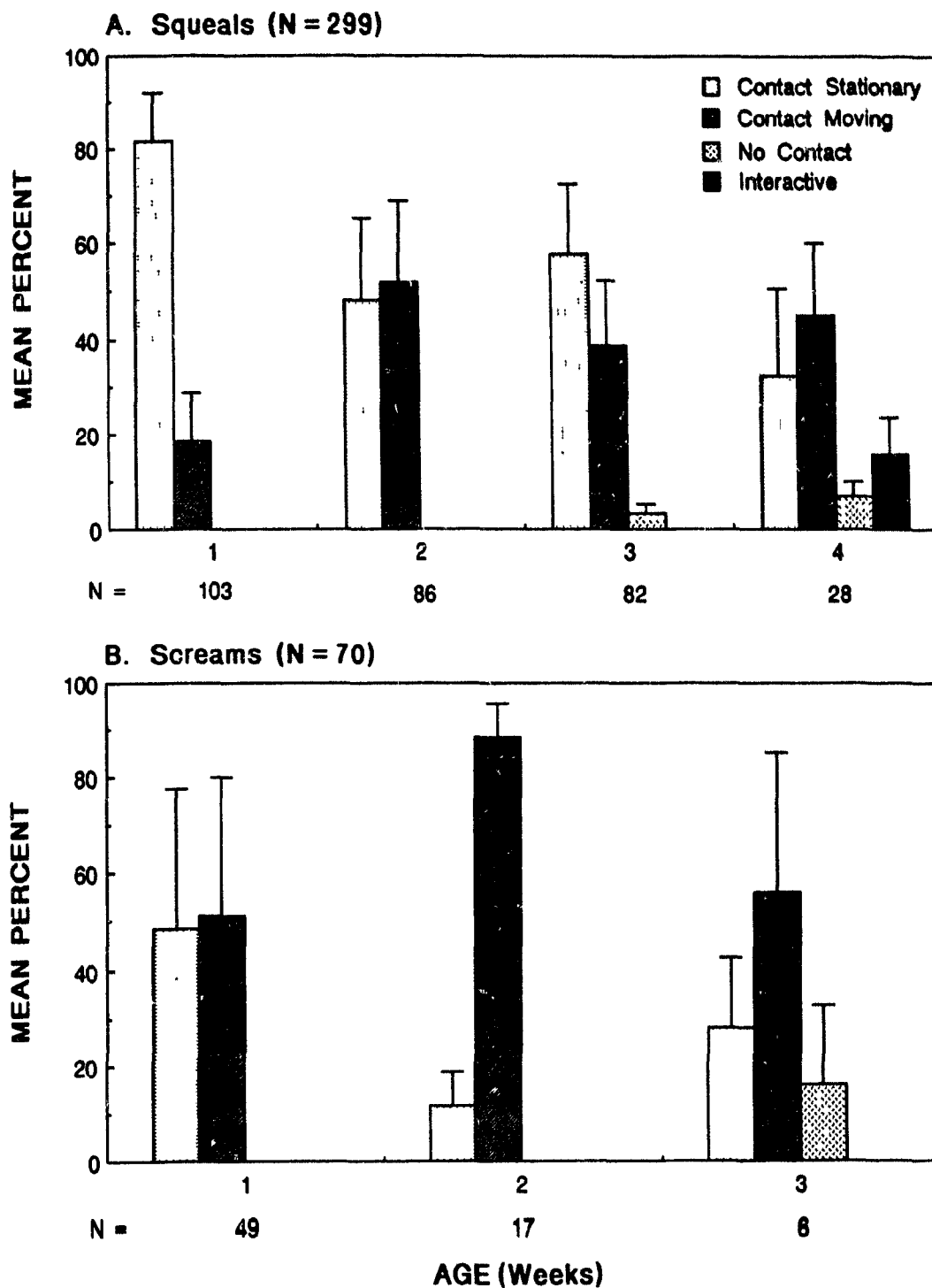


Figure 25(A-B). Total mean percentages (\pm standard errors) of the pup behaviour at the onset of pup vocalizations for specific pup vocal classes as a function of age: A. Squeals, weeks one to four; and B. Screams, weeks one to three.

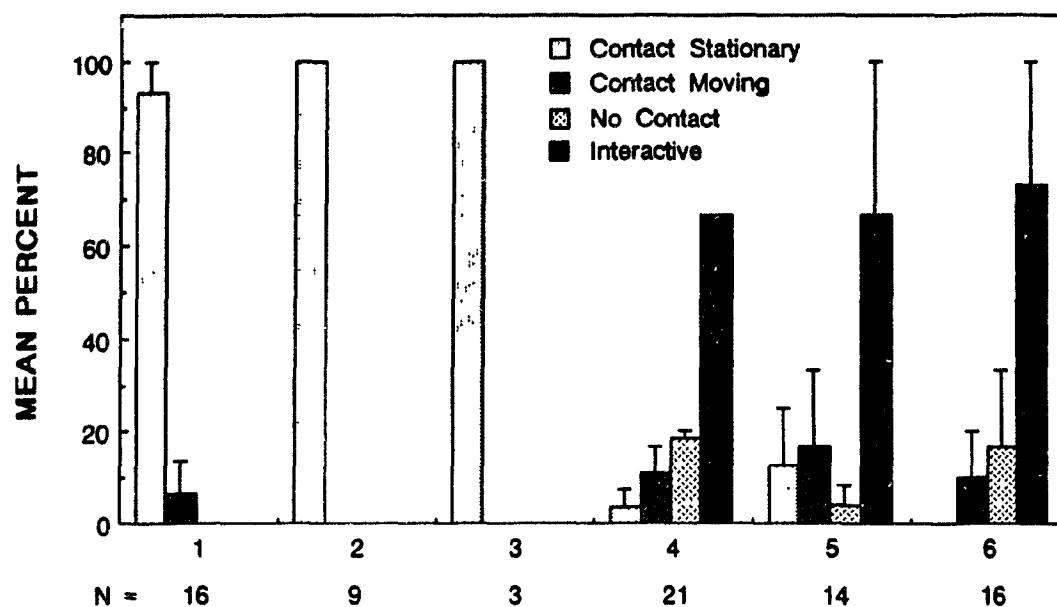
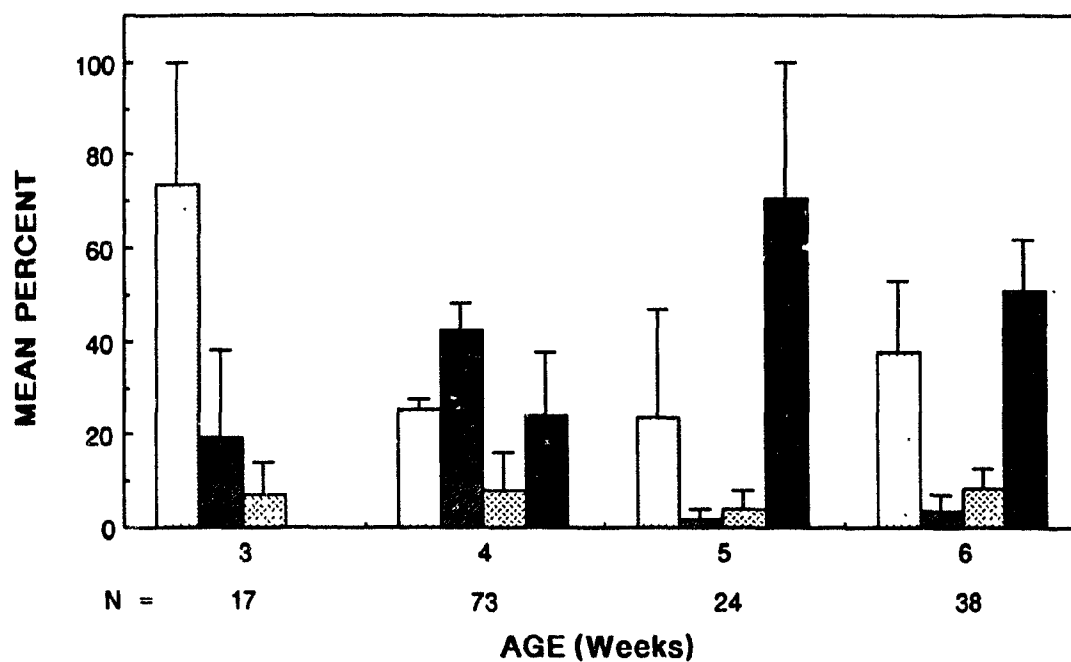
C. Growls (N = 79)**D. Squeaks (N = 152)**

Figure 25(C-D). Pup behavior: C. Growls, weeks one to six; D. Squeaks, weeks three to six.

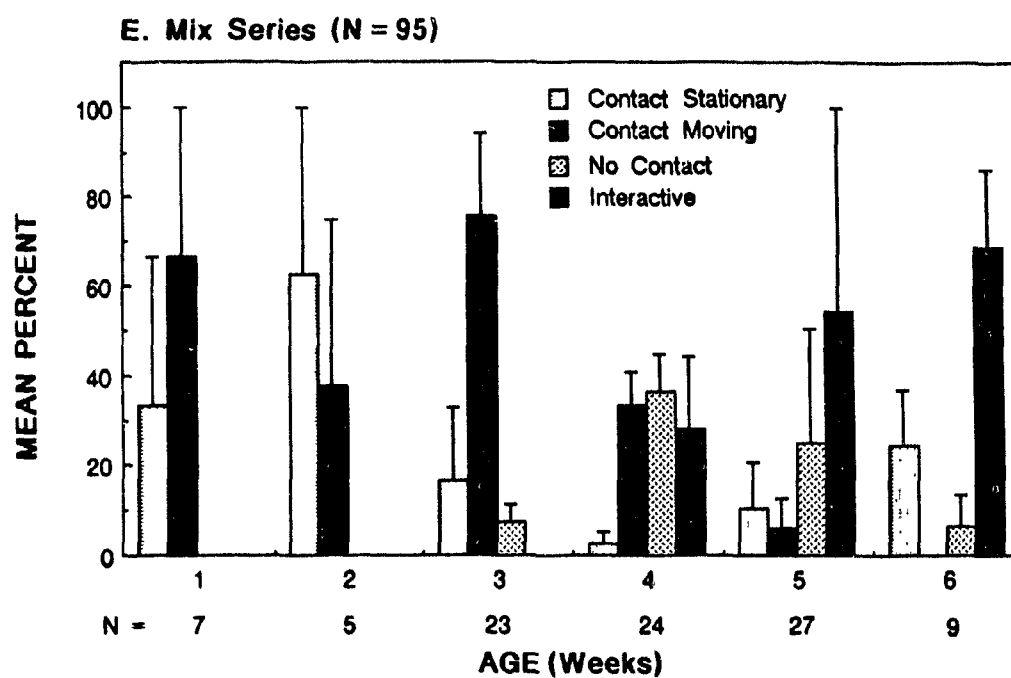


Figure 25(E). Pup behaviour: E. Mix series, weeks one to six.

Early Barks were associated with "contact stationary" behaviour (95%). After four weeks of age, Bark context, similar to Growl context, changed to either "no contact" (50%) or "interactive" behaviour (50%).

Squeak context (Figure 25D) changed from three to six weeks of age. When Squeaks were first emitted (three weeks of age), they were associated primarily with "contact stationary" and "contact moving" behaviour, but by five weeks of age they were associated predominantly with "interactive" behaviour. Like Growls, Squeaks and Mix series (Figure 25E) were associated with "contact stationary" and "contact moving" behaviour early in development and with "interactive" behaviour later in development.

The proportion of vocalizations in each class varied as a function of age (Figure 18). The proportions of the various categories of pup behaviour also varied as a function of age. To determine trends for the proportion of behaviour associated with each vocal class across time, data from the three litters were pooled and the total percent of each pup behavioural context for all five vocal classes were calculated. Figure 26(A-F) presents a week-by-week portrayal of the sound classes and their total percent in relation to pup behavioural context. This figure shows the contextual ontogenetic trends for the five vocal classes represented in Figure 25. As the neonate-specific classes (Squeals and Screams) decreased in their proportions, the adult-structured classes (Growls and Squeaks) increased (Chapter Four). In parallel with the change in vocal proportions was a change in pup behaviour. The majority of early pup

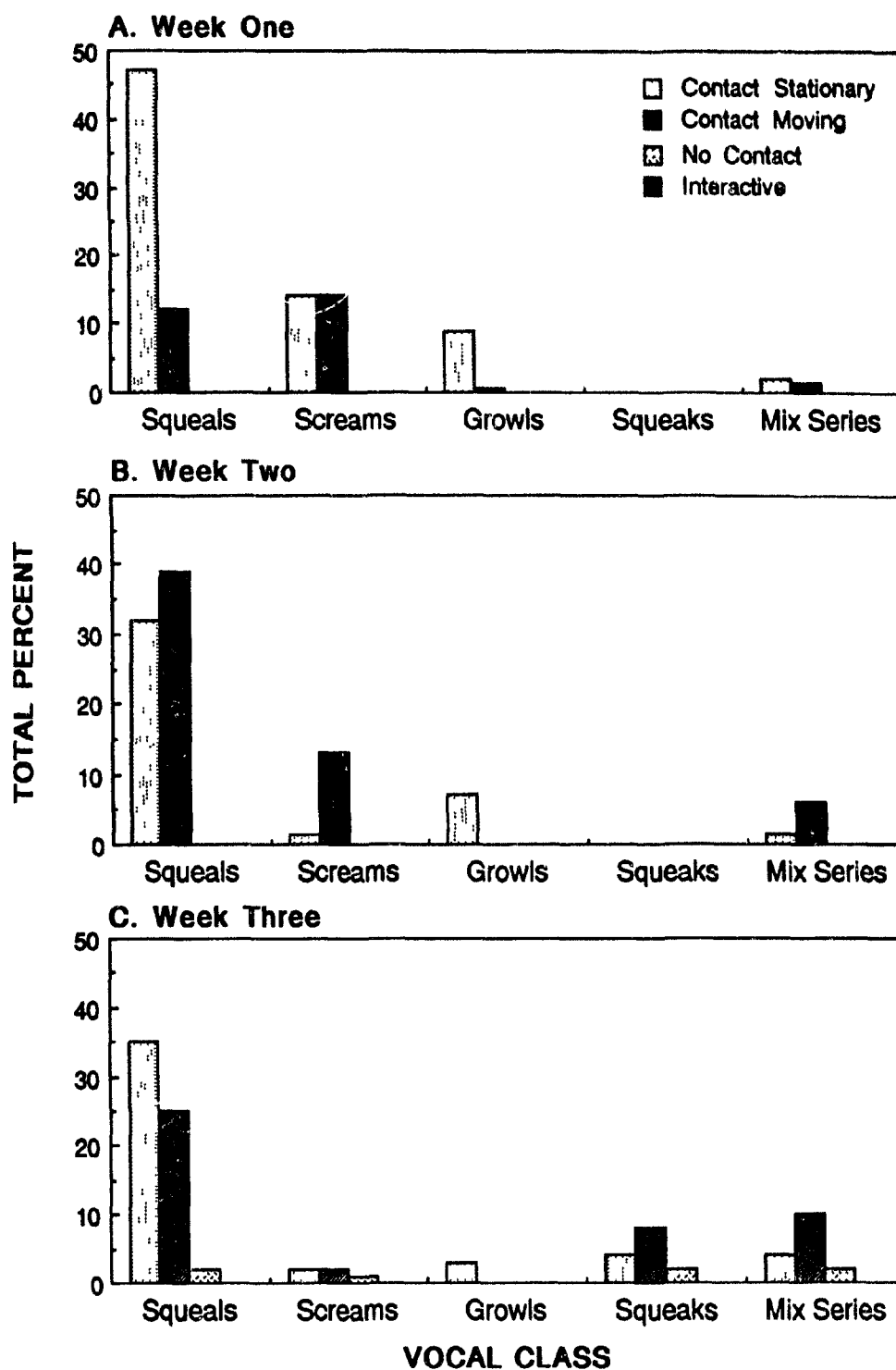


Figure 26(A-C). Total percent of each form of pup behaviour at the onset of specific pup vocal classes. D. Week one; E. Week two; F. Week three.

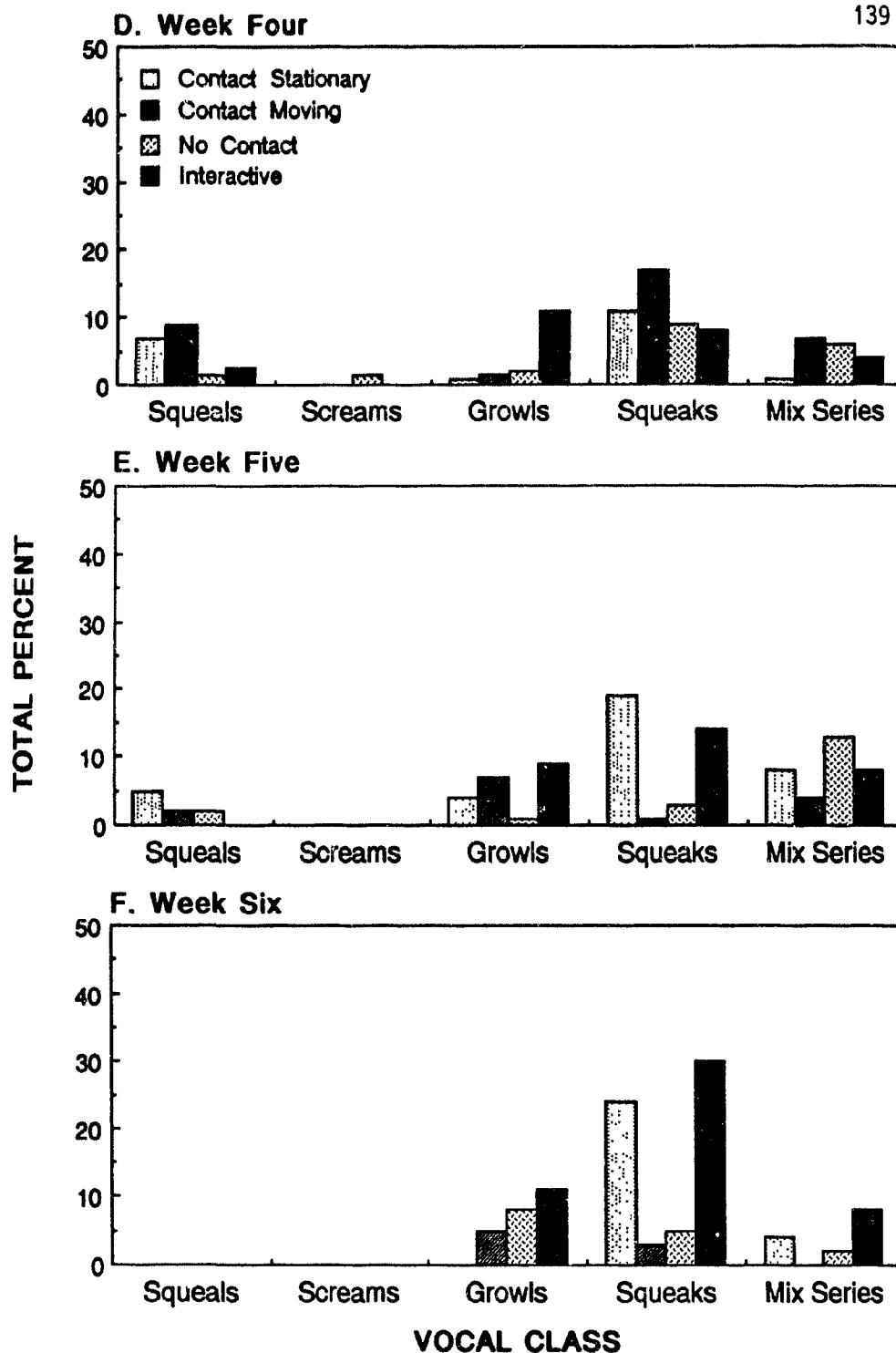


Figure 26(D-F). Total percent of each form of pup behaviour at the onset of specific pup vocal classes. D. Week four; E. Week five; F. Week six.

vocalizations were associated either with "contact stationary" or "contact moving" behaviours (Figure 26(A-C)). After three weeks of age, pup vocalizations were associated with "interactive" behaviour, as well as the other pup behaviours (Figure 26(D-F)).

To examine the relationships between pup vocal classes and behaviour in a quantitative manner, a 5 x 3 (for the early period - excludes "interactive" category, N=0) and a 4 x 4 (for the later period - excludes Screams, N=3) contingency table was created for chi square analysis. These tables represented five vocal classes (Squeals, Screams, Growls/Barks, Squeaks and Mix series), four behaviour classes ("contact stationary", "contact moving", "no contact" and "interactive") for the two age classes ("early", one to three weeks of age, and "late", four to six weeks of age). Growls and Barks were pooled because of the low sample size of Barks and the similarities in the behavioural context of Growls and Barks. The various Mix series were grouped due to their similarities of context and low rate of occurrence. Although Mix series do not represent a single vocal class, their context was of interest. Between one to three weeks of age, Mix series were comprised of Squeals and Screams, after which time they comprised mainly adult-structured vocalizations, primarily Squeaks. The behavioural context of Mix series may be similar to the context of Squeals and Screams during the first three weeks and, possibly be similar to the context of Squeaks, during the remaining weeks. Howls and Woofs were omitted because of their rarity. A total of 709 vocalization/context events were

analyzed.

There were significant non-random relations between pup vocalizations and pup behavioural contexts in which they were emitted during both age classes (early: $X^2=83.21$, $df=8$ $p<0.001$; late: $X^2=49.69$, $df=9$ $p<0.001$). Table VIII provides the standardized residuals for each cell in the two tables. These residuals allow analysis of the vocalization/context relationships to determine which combinations were more or less common than expected.

The significant associations (positive and negative) based on the analysis of the residuals are described in the following. There were no systematic relations between Squeals and pup behaviour early in development. The early Screams were more commonly associated with "contact moving" behaviour and significantly less associated with "contact stationary". Later in development Squeals were associated with "contact moving" behaviour and less commonly associated with "interactive" behaviour. During early development, Growls/Barks were found to be significantly more associated than expected with "contact stationary" behaviour, and less with "contact moving". These sounds were more associated with "interactive" behaviour, and less associated with "contact stationary" later in development. Squeaks were highly associated with "no contact" behaviour early in development and "contact stationary" behaviour later. Squeaks were less associated than expected with "contact stationary" early in development and "no contact" behaviour later in development. Both Growls/Barks and Squeaks reveal a complete reversal of association across

time. Early Mix series were significantly more common with "contact moving" or "no contact" behaviour and later Mix series with "no contact". Mix series were less likely associated with "contact stationary" both early and late in development.

Pup vocalizations and adult presence in the den

Adult presence in the den varied across the six week den period. Figure 27 depicts the percent of time an adult (either Pawnee or Ursula) was observed in the den for each litter separately. These data came from only the segments of tape that were analyzed for the vocalizations. The percent of time an adult attended the den decreased as a function of age for all litters. There were, however, notable litter differences in 1991; adults were absent from the den after four weeks of age.

Figure 28 depicts the percent of time Pawnee and Ursula were present or absent from the den in relation to pup vocalizations for each litter. The percentage of all measured pup vocalizations were identified with either adult presence or absence. Ursula's presence in the den began only after three weeks of age. In comparison to Pawnee's tenure in the den, Ursula's tenure was transitory (week four for the 1988 litter and weeks five to six for the 1990 litter). Ursula was not observed in attendance with the 1991 litter.

To evaluate whether specific pup vocal classes were different with adult presence compared to adult absence, an analysis of the total percent of each

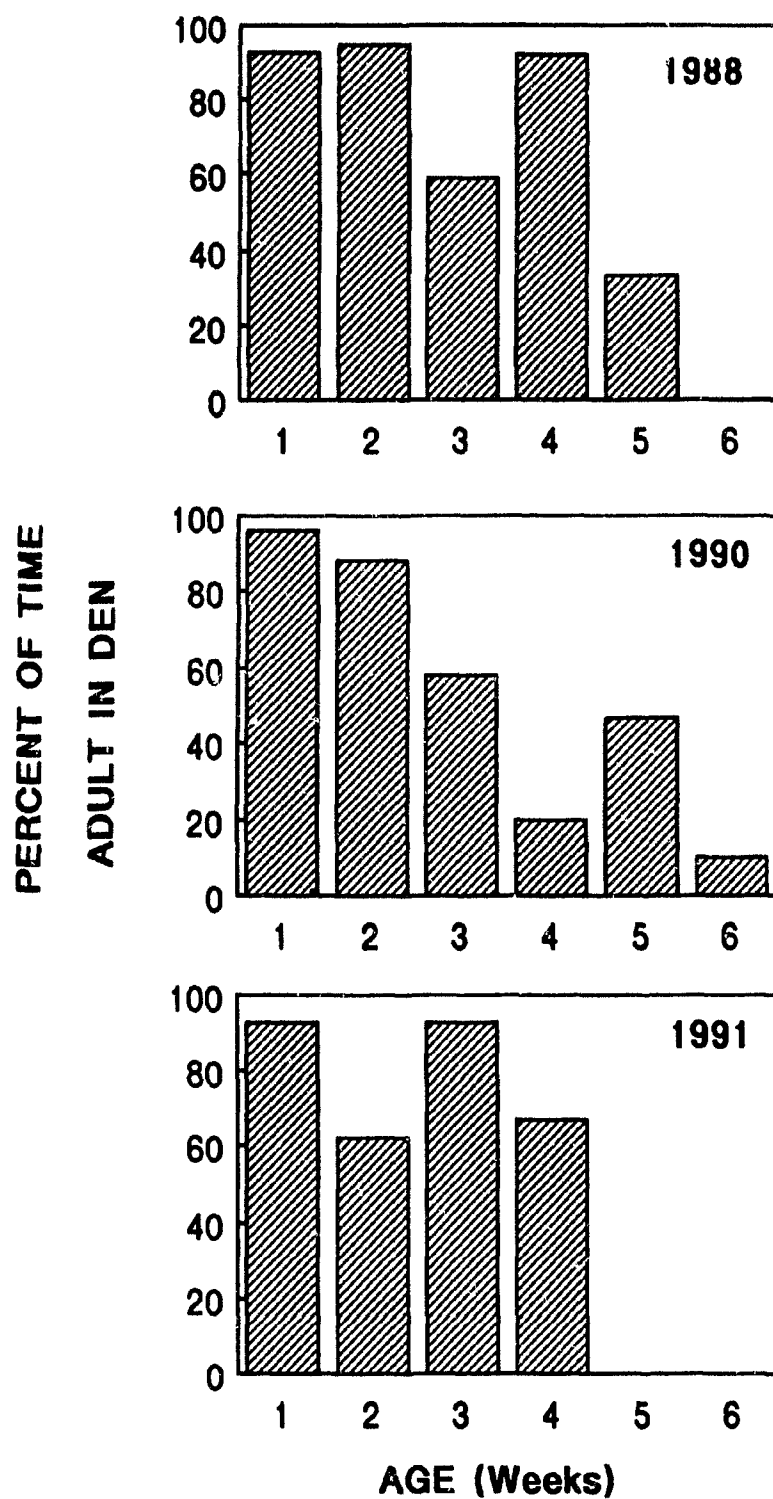


Figure 27. Total percent of time an adult was present in the den for individual litters as a function of age.

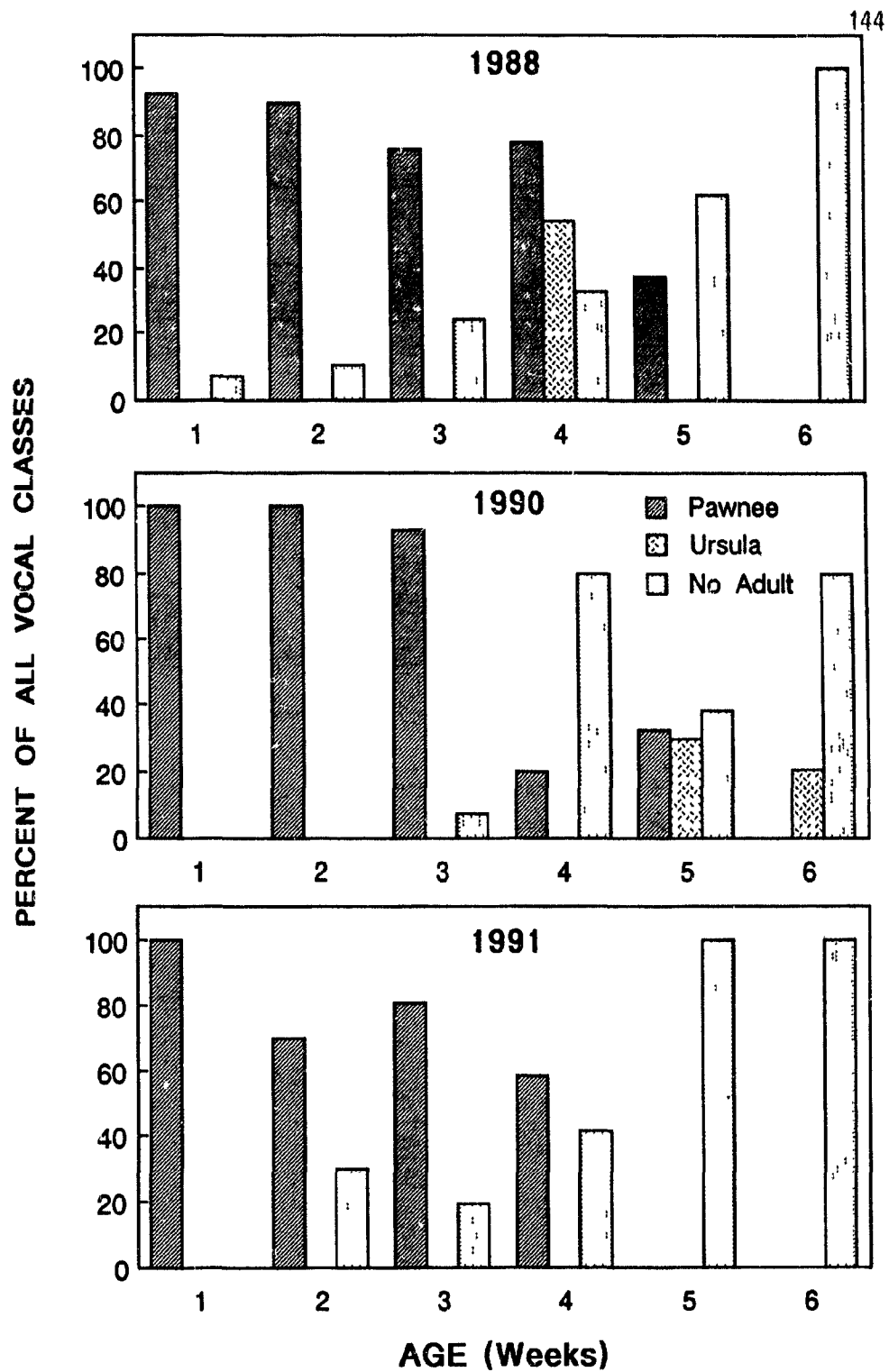


Figure 28. Total percent of pup vocal classes in which Pawnee and Ursula were present in the den for individual litters as a function of age.

vocalization was conducted for adult presence and adult absence in the den. Weeks chosen for this analysis were based on a time period when an adult was present roughly 50% of the time (weeks four and five). Figure 29 displays these percents for the vocalizations in which there was representation from all three litters. Squeals, Growls and Mix series were associated with both adult presence and adult absence in the den. In contrast, Woofs were produced in the absence of an adult, whereas Squeaks were more common when an adult was present. There was only one instance of a pup emitting Woofs during adult presence, and the adult in the den was Ursula.

Pup vocalizations and adult behaviour

Adult behaviour in the den when a pup vocalized was classified into three distinct categories: 1) "stationary", no overt movements; 2) "groom", moderate movements (e.g. grooming and/or licking pups); and 3) "movement", significant movements (e.g. repositioning, pup carry). These behaviours varied along a continuum of the degree of physical contact with the pups. For the descriptive statistical analysis, the data were pooled for all weeks. Figure 30 presents the mean (\pm standard errors) percents of each adult behaviour in relation to specific vocal classes. Squeals were associated mostly with no overt movements from the adult, whereas Screams were more closely associated with adult groom and movement. Growls and Barks were highly associated with adult "stationary" behaviour. Squeaks and Mix series, however, revealed no

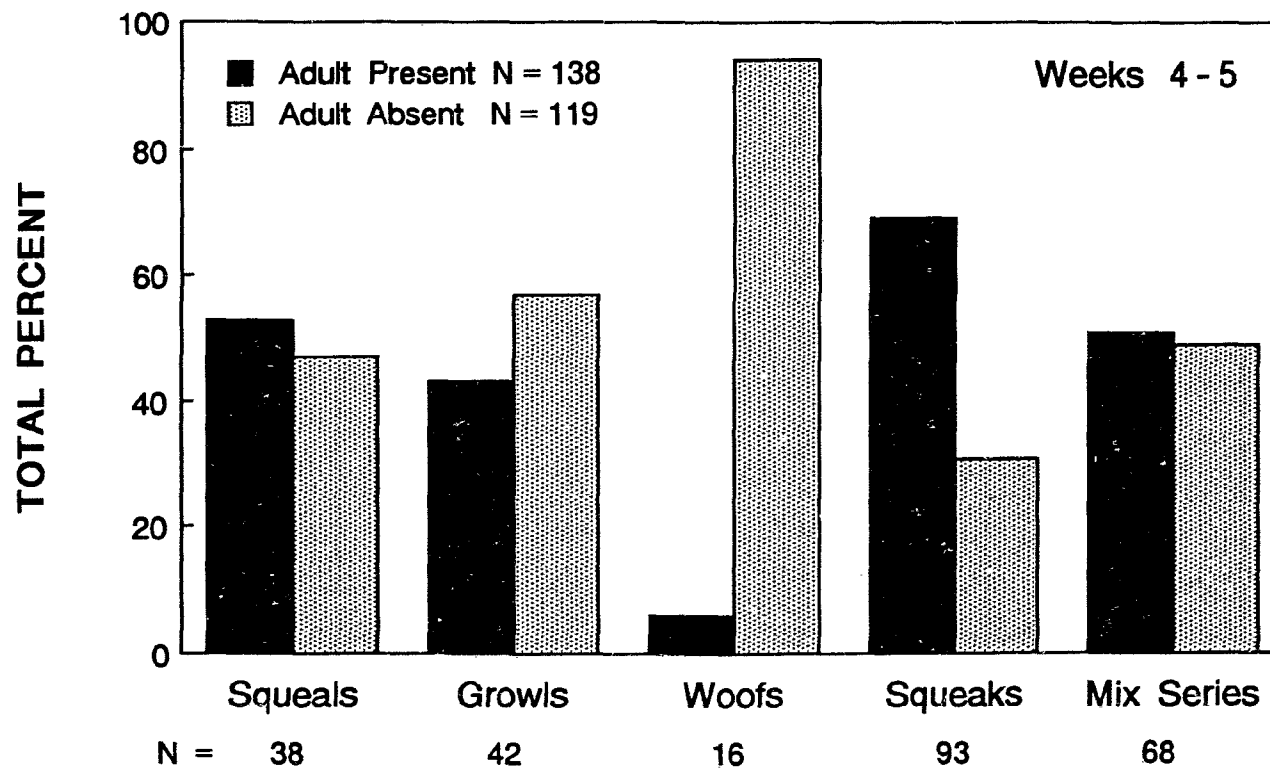


Figure 29. Total percent of specific pup vocal classes in which an adult was present or absent in the den during weeks 4 and 5.

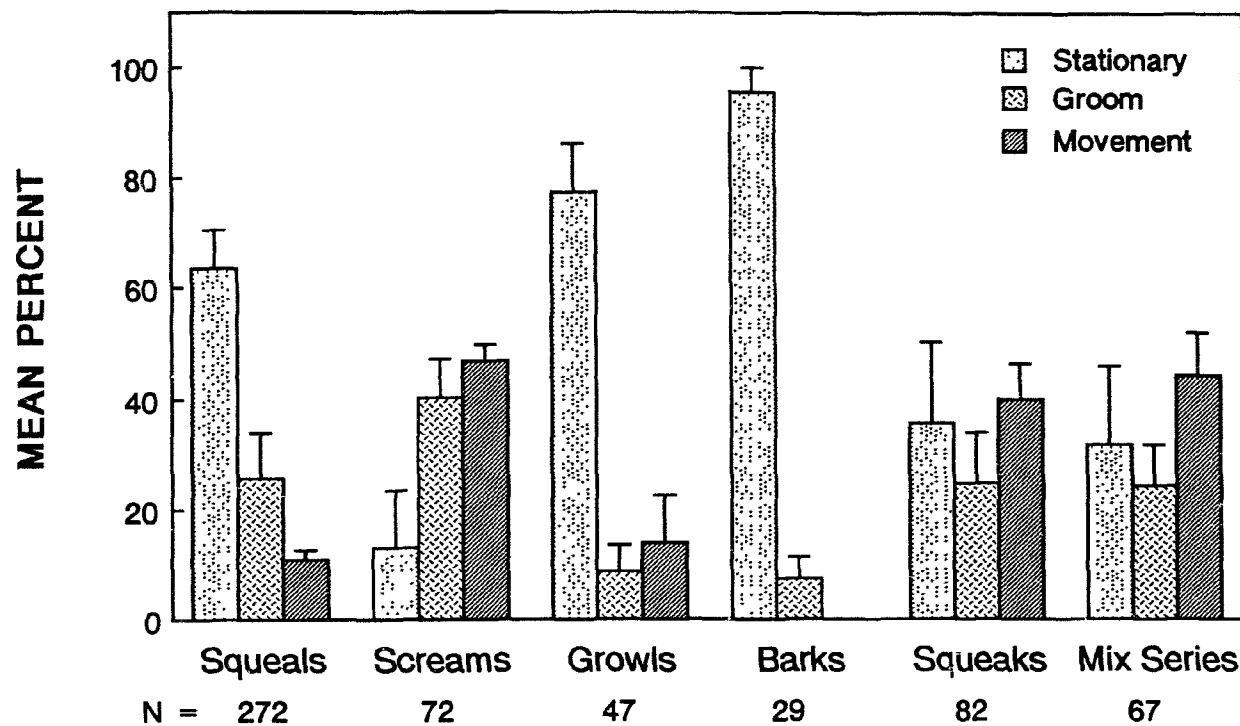


Figure 30. Adult behaviour at the onset of specific pup vocal classes: mean percentages (\pm standard errors).

obvious associations with adult behaviour at onset of pup vocal production of these sounds.

To test the interactive relationships between pup vocal behaviour and the corresponding adult behaviour, chi square analyses were conducted. A 5 x 3 (for the early period) and a 4 x 3 (for the later period -- excludes Screams, N=2) contingency table was created for the vocal classes and adult behaviour. The raw frequencies of behaviour were pooled for all three litters and for the adults. A total of 559 vocalization/context events were used for these analyses.

The chi square analysis showed that the associations between specific pup vocalizations and adult behaviour were not random early in development ($\chi^2=117.83$, $df=8$ $p<0.001$) but they were random later ($\chi^2=9.47$, $df=6$ $p>0.05$). Table IX provides the standardized residuals for each cell. Early Squeals were more commonly associated with "stationary" behaviour and significantly less commonly associated with "moving". In contrast, early Screams were strongly associated with adult movement and less likely associated with "stationary" behaviour. Growls and Barks were more likely associated with stationary behaviour and less likely associated with adult movement. Finally, Mix series were more commonly observed than expected with adult "moving", and less commonly linked to adult "stationary" behaviour. This association was maintained later in development.

Pup vocalizations and adult response

Adult responses to pup vocal activity in the den were categorized into four forms: 1) "no response", no change in adult behaviour; 2) "ear", ear orientation towards pups; 3) "other", all forms of adult contact with pups (e.g. grooming, repositioning, pup carry); and 4) "other/vocal", "other" accompanied with adult vocal behaviour. These behaviours varied along a continuum of adult attention directed towards pups. The data were pooled across time for each litter. The mean percents (\pm standard error) for each adult response to the individual vocal classes are displayed in Figure 31. Adult's response to different vocal classes was varied. In general, "ear" movement alone was an uncommon response. Adult vocalizing in response to pups was also rare but highly associated with the Mix series. Squeals were associated primarily with either no response by the adult or "other" behaviour. Screams and Squeaks were highly associated with adult "other" response, whereas Growls and Barks were not responded to overtly by the adult.

To determine if the observed relationships between pup vocal behaviour and adult response were random across weeks, chi square analyses were performed. A 5 x 4 (for the early period) and a 4 x 4 (for the late period - excludes Screams, N=2) contingency matrix was created for the pooled litters. The raw frequencies were pooled for all litters and both adults. A total of 540 vocalization/context events were available for the analyses.

The chi square analyses showed significant relationships between specific

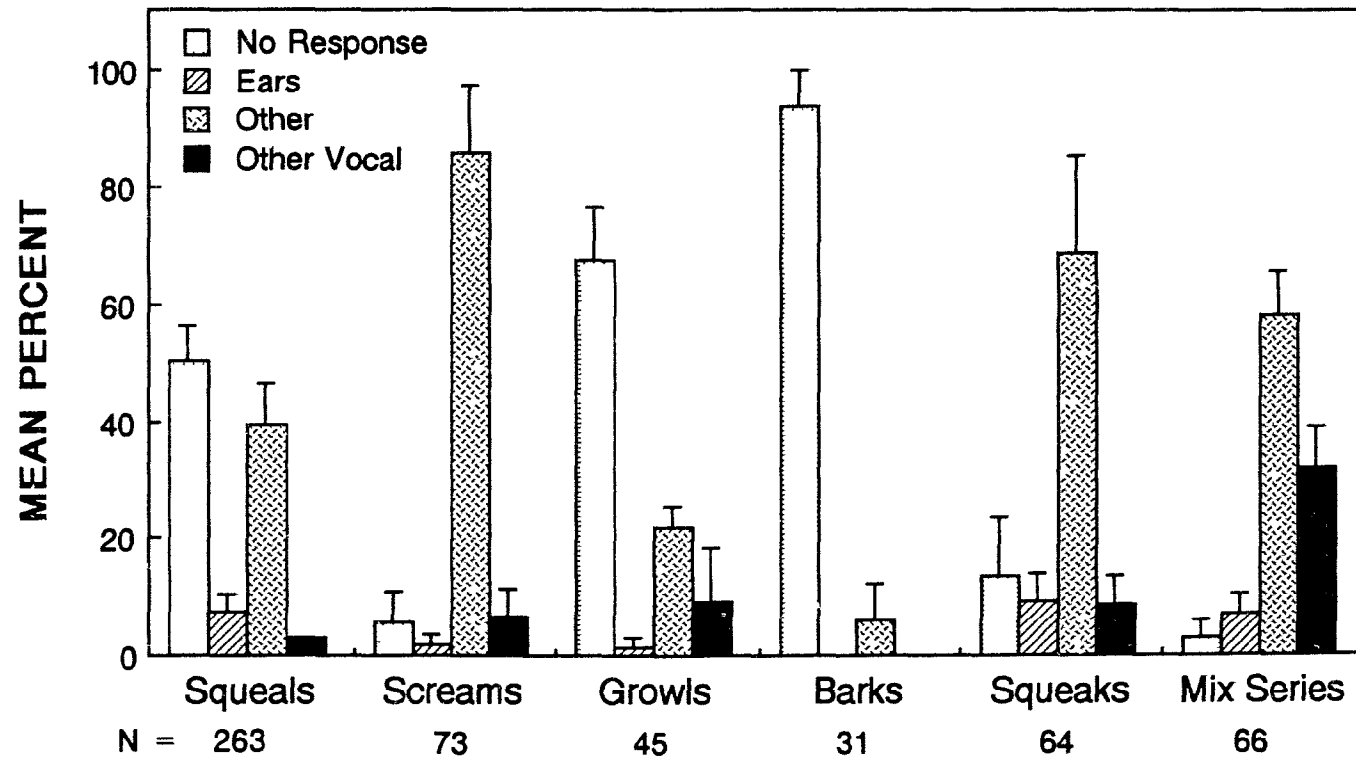


Figure 31. Total mean percentages (\pm standard errors) of adult responses to pup vocal classes.

pup vocalizations and adult response behaviour for both age classes (early: $\chi^2=184.07$, $df=12$ $p<0.001$; late: $\chi^2=21.39$, $df=9$ $p<0.025$). An analysis of the residuals in Table X reveal the significant associations between adult response behaviour and specific vocal classes. Squeals were less likely associated with "other vocal" both early and late in development. Early Squeals were more commonly associated with either "no response" or "ears". Early Screams were less commonly associated with "no response" and were responded to with "other" behaviour. In contrast Growls and Barks were highly associated with "no response" and not associated with "other" behaviour. This relationship was not maintained later in development. Finally, Mix series were observed more common than by chance with "other vocal" behaviour both early and late in development. Early Mix series were less likely associated with "no response".

Pup vocal behaviour and adult vocal behaviour

Adults rarely vocalized in the den in the presence of pups. Among all of the vocalizations within the vocal repertoire of the wolf, Squeaks were the primary sound emitted by the adults in the den. Only on one occasion was another vocal class emitted by an adult; Growls were observed when two adults were in the den simultaneously. In this situation, Pawnee Growled as Ursula entered the den. It is believed that this sound was directed at Ursula and not at the pups.

It was evident that the primary vocal interactive form of mothers with pups is Squeaking. In total, 22 events of Pawnee Squeaking in the den were noted. Forty-five percent of Pawnee's Squeaks were associated with her entering the den. All of Pawnee's Squeaks were produced when pups were moving in the den (82% associated with pup "contact moving" behaviour and 18% associated with pup "no contact" moving). Pup vocalizations associated with adult Squeaks were predominantly Squeaks (32%), Squeals (23%) and Mix Squeal/Scream series (13%).

Pup vocal behaviour and factors external to the den

A total of 34 events were recorded in which external factors immediately preceded, and thus may have triggered, pup vocal activity. All of these external factors were present on a daily basis, except for precipitation. These 34 events were observed for the 1990 and 1991 litters only, but not until pups were four weeks old. External events which elicited pup vocal response were primarily adult vocal behaviour (91%). Squeaks outside the den comprised 81% of adult vocal behaviour which stimulated pups to vocalize. Pup vocal response to Squeaks outside the den included Woofs and Woof-Growl Mix series (68%), Growls (36%), Squeaks (8%) and other sounds (8%). Rarely, train whistles, and on one occasion an airplane, elicited pup Howls. The fundamental frequency of the train whistle overlapped with the fundamental frequency of adult Howls and the frequency of sound produced by the airplane's engine overlapped with

the frequency of the pup Howl (see Figure 10C for the spectrogram with the uniform frequency band produced from the airplane). All other external sounds, including other mechanically-generated sounds (e.g. automobiles, trucks), avian calls and precipitation, were not associated with pup vocal activity.

Pup Howls from the 1990 litter

In addition to the 108 hours of video tape described above, 35 separate episodes of pup Howling, from the 1990 litter of marked pups, were examined. Twenty-nine of the Howl-attempts, full Howls and Bark-Howls emitted from the 1990 litter of four marked pups, were attributable to identified pups. One male pup produced 52% of these sounds and one female produced 28%. Differential rates of response and varying forms of response by the pups have been reported in examinations (experimental and informal) of hand-reared wolf pups exposed to a variety of stimulus sounds (Shalter et al., 1977; Ryon, unpublished data; personal observations). There were no consistent findings related to sex differences in pups' responses (i.e. sometimes males Howled more frequently and sometimes females Howled more). The 1990 litter appeared to Howl more than the other two litters. This may be attributed to the multiple den transfers (N=3) that pups were subjected to. The last pup left in the den during these transfers always Howled. Twenty-five percent of the Howls from the 1990 litter were emitted by pups isolated during den transfers.

Pup head and body postures during Howling were also examined. Head

posture during Howls was consistent. Pups would slowly raise their heads at the onset of the Howl. Heads were lowered at Howl offset. Pup's jaws were steady, their mouths were only slightly open and their lips were pursed. Body posture during Howls varied. Pups that were huddled Howled from the reclined position, whereas pups that were isolated during den transfers Howled while upright. Isolated pups Howled when stationary or while locomoting.

Summary of the Behavioural Context of Pup Vocalizations

The behavioural contexts of pup vocalizations were examined by: (1) analyzing the behaviour of pups at the onset of a vocalization or series of vocalizations; (2) analyzing the behaviour of the care-giver at the onset of a vocalization or series of vocalizations; and (3) analyzing the response of the care-giver to a vocalization or series of vocalizations. This database provided information about the behavioural context of pups at the onset of vocal activity, and how pup vocalizations were responded to by their care-giver.

The behavioural contexts of the wolf pup vocalizations were assessed with two different statistical procedures. The descriptive statistics provided information about the individual vocal classes. The chi-square analyses assessed all of the vocalizations in relation to each during early and late development. Collectively, these results revealed developmental changes in the behavioural context of pup vocal behaviour.

The behavioural contexts of neonate-specific Squeals and Screams

did not vary across time. Squeals were predominantly associated with pup and adult stationary behaviour and occasionally with movement behaviour. Squeals were rarely responded to with overt behaviour by the care-giver. Screams were consistently associated with movement by pups and the care-giver and they were consistently responded to with overt behaviour.

In contrast to the neonate-specific vocalizations, the behavioural contexts of the adult-structured sounds showed marked ontogenetic changes. Early Growls and Barks were associated with pup and adult stationary behaviour and they were rarely responded to by the adult. Later Growls and Barks were invariably associated with social interactions, and adults consistently responded to these sounds with overt actions. Ontogenetic changes associated with Squeaks were evident in the descriptive statistical data. Early Squeaks were associated with pup and adult stationary behaviour, and later Squeaks were associated with pup interactive behaviour and stationary behaviour. The descriptive statistical analysis revealed that the majority of Squeaks were overtly responded to by the adult in the den. Chi-square analysis, however, revealed no systematic relations between Squeaks and adult response. Mix series, present both early and late in development, followed patterns similar to Squeals early in development and Squeaks later in development. Mix Series were the only vocal class that was significantly responded to with vocal behaviour from the adult.

Pup vocal activity was influenced by adult presence in the den.

Pups produced more Squeaks in the presence of the care-giver than in their absence. Woofs were emitted during adult absence from the den. Pups never Woofed in the presence of the mother and Woofed only once in the presence of the second care-giver. In addition, pups rarely Howled in the presence of adults.

Pup vocal activity was occasionally influenced by external factors to the den (for two litters). Pups Woofed, Growled and Squeaked in response to pack Squeaking. Pups Squeaked and Howled in response to pack Howling, and occasionally, train whistles. Pups Woofed and Barked in response to wolf movement at/in the den entrance.

CHAPTER FIVE

DISCUSSION: VOCAL DEVELOPMENT AND ACOUSTIC COMMUNICATION

Introduction

The objective of this study was to examine the early ontogeny of vocal communication in timber wolves. To achieve this objective, observations were collected from three litters of pups within their natal den from birth until six weeks of age. Specific aims were to: a) collect larger samples of vocal behaviour from pack-reared neonatal wolves than previously available, b) provide objective criteria for classifying sounds into basic vocal classes, c) evaluate developmental changes in individual acoustic dimensions from which these classes are constituted, and d) relate developmental changes in vocal production with the behavioural contexts within which these vocalizations are produced.

In this chapter, the results from the acoustic analyses (Chapter Three) and the behavioural analyses (Chapter Four) will be discussed. These results will be assimilated to present a comprehensive examination on the ontogeny of wolf vocal communication. The findings from this study will be related to previous ontogenetic studies of social mammals.

The Vocal Repertoire and Its Development

Neonatal wolf pups emit a rich variety of vocalizations. These

vocalizations vary along a range of acoustic dimensions including gross spectral structure, duration, fundamental frequency, absence or presence/rate of frequency modulation and mean maximum/minimum frequency ranges. In this study, vocalizations were characterized on the basis of combined differences in at least two of these acoustic dimensions. This classification scheme resulted in the categorization of eleven structurally distinct vocal classes. The vocal classes appeared at different ages during the first six weeks of postnatal development. The early-appearing vocalizations, observed during the first postnatal week, included sounds which were neonate-specific and adult-structured. Neonate-specific sounds (Squeals, Screams and Yelps) are those which are produced typically by young wolves within the first two to three weeks of age, but are not usual for older animals. Early-appearing adult-structured sounds (Growls and Barks) do have similar acoustic properties to those previously characterized for mature wolves (Harrington and Mech, 1978; Schassburger, 1993). The late-appearing vocalizations (Squeaks, Woofs and Howls), observed following pup's first postnatal week, were all adult-like in their acoustic form although the harmonic sounds were higher in fundamental frequency than adult vocalizations. In general, there was an increased variety of vocal forms produced as pups matured. In addition to the number and classes of sounds which varied as a function of age, the relative proportions in which these sounds were produced varied with maturation. For example, the proportion of Squeals and Screams decreased by three weeks of age, at which

time the proportion of Growls and Squeaks increased. All vocal classes present within the repertoire of adult wolves, were identified within the repertoire of the neonates during the first six postnatal weeks.

There are at least three possible explanations which may account for the finding that the number of different classes of vocalizations emitted by neonate pups increased with maturation. First, late-appearing vocal classes (e.g. Squeaks and Woofs) are dependent on the progressive differentiation of vocal-motor/neuromuscular control before they can be produced. Second, pups may require the development of hearing for auditory feedback, prior to articulation of certain sounds. A third explanation is that pups may have the vocal-motor capacity to produce sounds, but their experience influences when particular sound patterns are expressed. Clearly, the development of vocal behaviour involves many processes which cannot be fully separated in this observational study.

All of the late-appearing sounds were adult-like in structure and were vocalizations present within the repertoire of adults. As the late-appearing vocalizations emerged within the pups' vocal repertoire, the production of several of the early-appearing vocalizations decreased. The loss of early structures and functions is well known in the developmental biology literature (e.g. Hall and Oppenheim, 1987), but has not previously been documented in an explicit manner for vocal development. The observed decreases in some vocal expressions does not imply, however, that these sounds disappear and

can no longer be generated by wolves. Wolves could be capable of producing these sounds while the conditions for their expression (whether internally or externally activated) are absent. If the appropriate internal or external stimuli were presented, adult wolves by this hypothesis should be able to produce such sounds (Fentress and McLeod, 1986).

Some of the acoustic properties of individual sound classes were modified with age, while others remained constant across time. The most significant change was a decrease in fundamental frequency as pups matured. Ontogenetic changes in the fundamental frequency of the harmonic and pure-tone vocalizations probably follows from physical maturation in pup morphology of the vocal tract (Bosma, 1975; Ehret, 1980). As the length of the vocal tract increases, lower frequency sounds can be generated. If pup sounds are produced through the route of vibration of vocal folds being filtered through the vocal tract, then a pup's vocal tract can be compared to a cylindrical tube which is closed at one end and open at the other. The length of a tube (in cm) is equal to the velocity of sound in air divided by four times the fundamental frequency (in Hz) (Greenewalt, 1968). For the fundamental frequency of Squeals to decrease from 1312 Hz (week one) to 900 Hz (week five) the vocal tract must grow by roughly 3 cm. Therefore, it is possible that the decrease in frequency is related to growth (lengthening) of the vocal tract. However, if pups produce Squeals by placing different amounts of tension on the vocal folds, then it would be the growth of the vocal folds, and not the vocal tract, that

caused the fundamental frequency of Squeals to decrease (Fry, 1979).

The observed decrease in the fundamental frequency of Squeals, Screams, Squeaks and Howls was consistent with patterns of decrease reported for neonate Moans and Whines in Coscia et al. (1991). The absolute decrease in frequency change did, however, vary for different sounds independently. For example, the pattern of decrease in Squeal frequency did not parallel the decrease in Squeak frequency. Although one might use the difference in absolute pitch change to argue that different mechanisms of production are used, the more appropriate analysis is based on relative change. The relative frequency change (i.e., the percentage of decrease in frequency for each week between weeks three and five) for these two sounds is almost identical: Squeals - $206 \text{ Hz}(\text{difference between weeks three and five})/1106 \text{ Hz}(\text{mean for week three}) \div 2 \text{ weeks} = 0.08$ or 8% per week; Squeaks - $1860 \text{ Hz}(\text{difference between weeks})/9268 \text{ Hz}(\text{mean}) \div 2 \text{ weeks} = 0.10$ or 10% per week. This comparison suggests that these sounds may indeed be generated by the same (or related) vocal-motor processes.

The observed relationships between Squeals and Squeaks raises general issues about the mechanism of vocal production of these two sounds. The mirror symmetry of the proportional data for Squeals and Squeaks (Figure 19) further supports the possibility that these sound classes are related to each other. Recall, however, that Squeals and Squeaks are acoustically very different from each other (Figure 12): Squeals recorded in this study were considerably

lower in fundamental frequency and variable in gross spectral type than were Squeaks. Squeaks which were higher in frequency (with a mean difference greater than 6 kHz), were predominantly harmonic in structure. It thus appears unlikely that Squeaks were *developmental modifications* of Squeals.

If wolves can generate sounds from two acoustical sources, then it is possible that pups may be able to generate Squeals simultaneously with Squeaks (i.e., the production of two sounds overlapping in time), once the components of the vocal apparatus that are required to produce Squeaks are developed. This possibility suggests that Squeals and Squeaks are developmentally related. Similar patterns of unrelated frequencies, observed in the songs of oscine birds, are attributable to the simultaneous activation of two acoustical sources (Greenewalt, 1968). Squeals could be generated through the vocal tract, whereas Squeaks could either be generated through tension on the vocal folds or, possibly, by air passing through the nasal cavity. This possibility is suggested by the presence of harmonically-unrelated frequencies, found below 1000 Hz in Squeaks, which overlapped in time with the high-frequency components of Squeaks (Harrington and Mech, 1978). The presence of harmonically-unrelated frequencies below 1000 Hz is observed in the spectrogram of Squeaks from a six week old pup (Figure 9C). This finding of harmonically-unrelated frequency components, therefore, suggests that Squeals and Squeaks may be produced by two different acoustical mechanisms. Why this low-frequency energy does not appear in all spectrograms may be that

these different mechanisms of sound production can be activated independently from each other. This relationship between Squeal and Squeak acoustic properties and the pup vocal/motor processes involved in sound production deserves further examination.

The majority of the acoustic properties which differentiated sound classes did not change as a function of age, although some properties varied both within and between litters. The variability observed within and between litters for some acoustic properties may, in part, be influenced by their social environment (see below). Evidence that some acoustic properties did not undergo developmental modifications during this six-week period of development when pups experienced pronounced physical and social changes (Chapter Four) reflects stability in the expression of vocal/motor processes.

Ontogenetic changes in vocalizations occur after the six week den period as pups grow and socially integrate with pack members. Harrington (1989), Harrington and Mech (1978) and Schassburger (1987, 1993) reported that pup Howls decreased in fundamental frequency as animals matured. These investigators also found that the duration of Howls increased with maturation. Finally, they reported that pup Howl modulation decreased as a function of age. Howl maturational changes in the present study were suggested by the decrease in fundamental frequency and decrease in fundamental frequency variation (Table V). The duration of pup Howls did not reveal an increase with maturation (Table V). The duration data presented in Table V, however,

included Howls which were less than 0.3 seconds in duration. Many of these short Howls were referred to as Howl-attempts because the pup appeared to stop vocalizing before completion of the stereotypic adult-like Howl. Howl-attempts were not sustained sounds, nor did they decrease in frequency (a characteristic of complete Howls). When these "incomplete" Howls were excluded from the week-by-week analysis (Table V), the duration of Howls exhibited a slight increase as a function of age.

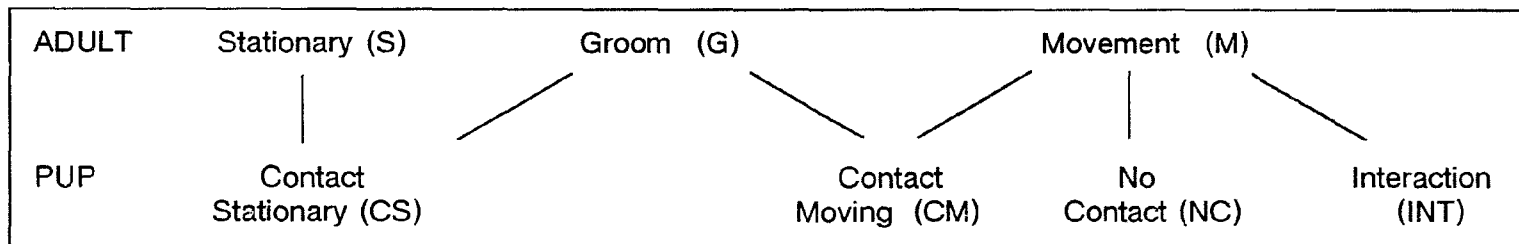
Context and Interpretation of Vocal Classes

In the following, the potential functional significance of the various vocal classes will be interpreted based on their contextual occurrence observed in this study. The potential causes of pup vocal behaviour will be related to the activity of the pups and the adult at the onset of pup vocal production. The functional role of the vocal classes will then be evaluated based on the reaction of a receiver (i.e., the adult). In other studies of development, analogous approaches to examining integrated systems have proven most valuable (Smith and Thelen, 1993; Adams-Curtis and Frigaszy, 1994). This form of systematic evaluation has not been done previously for wolf vocal behaviour.

Figure 32 provides an overview of the behavioural context of pup vocal classes summarized from the results presented in Chapter Four. This figure is divided into three parts: 1) behavioural context; 2) behavioural context and pup vocal class; and 3) adult response.

Figure 32. Summary diagram of the behavioural context of specific pup vocal classes and the adult response to these vocalizations. The box at the top of the diagram (part one) links the adult and pup behavioural categories into six combinations of behavioural context. The middle of the diagram (part two) presents the vocal classes which were *significantly associated* and *cross-represented* based on the standardized residuals from the chi square analyses of pup behaviour and adult behaviour at the onset of specific pup vocal classes. The significant "+" and "-" standardized residuals were those with the double asterisks in Tables VIII-IX. Each combination of adult and pup behaviour is divided into two periods in development, early (weeks one to three) and late (weeks four to six). The "--" indicates that no vocal classes met the criteria stated above. The box at the bottom of the diagram (part three) presents the vocal classes that were significantly ("+" and "-") associated with the specific forms of adult response, both early and late in development. Associations were based on the standardized residuals from the chi square analysis of adult response (Table X).

BEHAVIOURAL CONTEXT



BEHAVIOURAL CONTEXT AND PUP VOCAL CLASS

<div style="border: 1px solid black; padding: 2px; display: inline-block;">S/CS</div> <div style="display: inline-block; width: 40%;"> <p>Early: (-) Growl/Bark</p> <p>Early: (-) Scream</p> <p>Early: (-) Mix</p> </div> <div style="display: inline-block; width: 40%;"> <p>Late: (-) Mix</p> </div>	<div style="border: 1px solid black; padding: 2px; display: inline-block;">G/CS</div> <div style="display: inline-block; width: 40%;"> <p>Early: --</p> </div> <div style="display: inline-block; width: 40%;"> <p>Late: --</p> </div>	<div style="border: 1px solid black; padding: 2px; display: inline-block;">M/CM</div> <div style="display: inline-block; width: 40%;"> <p>Early: (+) Scream</p> <p>Early: (+) Mix</p> <p>Early: (-) Growl/Bark</p> </div> <div style="display: inline-block; width: 40%;"> <p>Late: --</p> <p>Late: --</p> <p>Late: --</p> </div>	<div style="border: 1px solid black; padding: 2px; display: inline-block;">G/CM</div> <div style="display: inline-block; width: 40%;"> <p>Early: (+) Scream</p> <p>Early: (-) Growl/Bark</p> </div> <div style="display: inline-block; width: 40%;"> <p>Late: --</p> <p>Late: --</p> </div>	<div style="border: 1px solid black; padding: 2px; display: inline-block;">M/NC</div> <div style="display: inline-block; width: 40%;"> <p>Early: (+) Mix</p> </div> <div style="display: inline-block; width: 40%;"> <p>Late: (+) Mix</p> </div>	<div style="border: 1px solid black; padding: 2px; display: inline-block;">M/INT</div> <div style="display: inline-block; width: 40%;"> <p>Early: N/A</p> </div> <div style="display: inline-block; width: 40%;"> <p>Late: --</p> </div>
--	--	---	---	--	--

ADULT RESPONSE

No Response		Ears		Other		Other/Vocal	
Early:	Late:	Early:	Late:	Early:	Late:	Early:	Late:
(+) Growl/Bark	(+) Squeal	(-) Growl/Bark	(+) Squeal	(+) Scream	--	(+) Mix	(+) Mix
(-) Scream	--	--	--	(-) Growl/Bark	--	(-) Squeal	(-) Squeal
(-) Mix	--	--	--			(-) Growl/Bark	--

Figure 32.

Behavioural Context

The first part in Figure 32 presents the objective criteria used to define the behaviour of both the adult and the pups. For the purposes of interpretation, the dimensions listed can be used to describe adult behaviour along a continuum of the degree of physical contact with the pups. While this is clearly a simplification, it allows a unifying framework to examine wolf vocal communication. When adults are stationary, the pups are not disturbed; adult grooming of pups often leads to moderate pup disturbance; and adult movement is likely to result in the greatest amount of pup disturbance (such as inadvertently stepping upon pups). For objective evaluation, the descriptive pup behavioural categories are linked to descriptive adult categories. This shows both converging and diverging relationships between the selected categories. Six combinations of adult and pup behaviour can in this way be associated in an unambiguous manner: 1) adult stationary and pup contact stationary; 2) adult groom and pup contact stationary; 3) adult groom and pup contact moving; 4) adult movement and pup contact moving; 5) adult movement and pup no contact; and 6) adult movement and pup interaction.

Behavioural Context and Pup Vocal Class

In the second part of Figure 32, the vocal classes associated with each combination of adult and pup behaviour are listed for the two periods of pup development, early (weeks one to three) and late (weeks four to six). The vocal

classes include Squeals, Screams, Growls/Barks, Squeaks and Mix series. In Chapter Four, the associations between these vocal classes and their behavioural contexts were evaluated statistically for both pup behaviour and adult behaviour. Analyses were conducted to assess whether the relationships between the individual components within each contextual repertoire were more (or less) commonly observed than expected with the classes of the vocal repertoire. At this point the issue of interpretation is pursued more fully. Only the significant positive and negative associations contained within both Tables VIII and X will be presented as a conservative measure. The significant associations were those identified in the tabled data of the standardized residuals with the double asterisks (Tables VIII-X). For each combination of adult and pup behaviour (outlined in the first part of Figure 32), the vocal classes which were both *significantly associated* and *cross-represented* (i.e., correlated with both components of adult and pup behaviour) are listed for the early and late period in pup development. For example, early in development Growls/Barks were positively correlated with adult stationary behaviour and pup contact stationary behaviour whereas Screams and Mix series were negatively correlated with these behaviours.

Adult Stationary and Pup Contact Stationary (S/CS): The vocal classes positively cross-identified with both adult and pup stationary behaviour early in development were Growls and Barks. No positive associations were significant late in development. Screams were not associated with these behaviours early

in development, and Mix series were not identified with the S/CS behavioural setting either early or late in development.

When both adults and pups were stationary, pups were in physical contact with their care-giver and either nursing or resting. There were no obvious forms of physical disturbance to the pups; pups appeared to be in a comfort state. The rare appearing Growls and Barks were associated with these periods of quiescence and were regarded as apparently spontaneous vocal expressions.

Adult Groom and Pup Contact Stationary (G/CS): No vocal classes were significantly cross-represented with these behaviours either early or late in development.

Adult Groom and Pup Contact Moving (G/CM): Screams were positively cross-represented with adult groom and pup contact moving early in development. Growls and Barks from pups early in development were not identified with the G/CM context. There were no significant cross-representations of these behaviours late in development.

Contexts in which adults were grooming pups involved pups being manipulated by their care-giver for cleaning and stimulation for elimination. Pups in these contexts were often rolled during grooming, with pups being pushed on top of each other. These conditions were potentially stressful for neonates and Screams were likely expressions of their disturbed state. Also of significance, Growls and Barks were negatively associated with the G/CM

context and therefore appear to have been suppressed within that context.

Adult Movement and Pup Contact Moving (M/CM): Screams and Mix series were strongly associated with both adult and pup movement early in development. Growls and Barks were negatively correlated with the M/CM context. No significant associations were identified with these behaviours later in development.

Adult movement in the den led to substantial displacement of pups. Adult movements included entering and exiting the den, carrying pups and repositioning in the den. These adult actions resulted in pups being pushed around, leaned on, sat on and stepped on. Pups, within these conditions, were likely subjected to mild or intense pain and distress. Screams and Mix series seem to have been expressions of these major disturbances.

Adult Movement and Pup No Contact (M/NC): Mix series were associated with the M/NC context both early and late in development.

Adult movements and pup no contact behaviour were situations in which pups were isolated from both the care-giver and littermates. Because neonate pups' primary activities involved maintaining physical contact for warmth, stimulation and satisfying hunger, isolation was likely stressful to pups. Pup vocal expressions of Squeaks and Mix series were possible indicators of their distress. Isolation distress, as opposed to distress identified with physical contact (above), elicited Squeaks or Mix series (some of which were composed of Squeaks).

Adult Movement and Pup Interaction (M/INT): Adult movement and pup interactions were only associated with later development because early pup interactions were non-vocal. There were, however, no significant cross-representations of any vocal classes with the M/INT context.

Adult Response

Adult's response to the various pup vocal classes is a potential indicator of the functional role of pup vocalizations. In the third part of Figure 32, the forms of adult response to the vocal classes are listed. For the present purpose, adult response to pup vocal activity can be viewed as varied along a continuum of adult attention. No response from the adult might indicate that attention was not elicited; adult ear movements oriented towards the vocalizing pup indicated that pups were being monitored; other actions indicated that the adult was responding to pups with overt behaviour (e.g. grooming, repositioning either pups or self); and other actions and vocalizing indicated that two different forms of attention were being directed at pups, tactile/physical and auditory/vocal. Obviously the arrangements of qualitatively distinct actions along a quantitative dimension must be pursued with caution. However, such efforts can assist in the interpretation of otherwise diverse data (Morton, 1977)

Below each category of adult response are the vocal classes which are positively and negatively associated based on the significant standardized residuals denoted in Table X. In the following, the functional roles of specific

pup vocal classes are interpreted based on the adult's response.

Squeals: When Squeals were the most common vocalization within the pup's vocal repertoire, they were not significantly associated with any combination of pup and/or adult behaviour. Squeals were less commonly associated with overt adult behaviour early in development. Later in development, adults did not direct attention to pups when they emitted this vocal class. Lack of attention was surmised from both the positive association of Squeals with no response, or ears only response, from the adult and the negative association of Squeals with overt behaviour from the adult. The functional significance of Squeals is not completely evident from these data.

Screams: Screams were only assessed early in development because they rarely occurred later in development. In response to Screams, the care-giver overtly responded to pups either through continued grooming and moving of pups or repositioning pups. In addition, Screams were negatively correlated with no response from the care-giver. Thus, Screams likely served as an indicator to adults that pups were in distress and needed attention.

Growls and Barks: Growls and Barks were positively associated with no response from adults early in development. Growls and Barks were not associated (i.e., observed significantly less than expected) with all other forms

of adult response (i.e., ears, other and other/vocal). Therefore, these sounds presumably did not serve to attract attention from the care-giver early in development.

Squeaks: Squeaks were associated with adult presence in the den but they were not significantly more or less responded to by adults. Squeaks were common from pups older than three weeks of age, at a time when adults were seldom in the den. Adult Squeak vocalizations are associated with approach behaviour. Likewise, Squeaks from neonate pups may serve to elicit approach from adults or littermates when pups are not in contact with another individual. During late development, however, Squeaks were no longer identified with the no contact contexts. Pups, later in development, were mobile and often moved both towards and away from other pups and the adult to explore the den. Pups may not have needed to Squeak to elicit approach within the den because pups' locomotor capabilities were developed enough for them to initiate approach. An alternative possibility is that pups have learned to communicate approach by Squeaking (i.e., as an adult would Squeak) and physical contact with the receiver was not always necessary for social communication in the den.

Mix series: Both early and later in development, the adult overtly responded to and also vocalized (Squeaked) to Mix series. This suggests that Mix series have a different function than Screams early in development because

Screams were not associated with adult vocal responses. Mix series, emitted by pups later in development, were associated with specific contexts: adults attempting to pick-up pups for den transfers. Pups retreated from adults and emitted Mix sound series. Thus, Mix series may serve as a sign of protest. In response to pups' protests, adults responded by Squeaking, vocalizations associated with approach. In support of this finding, there was a significant positive association of adults responding to pup Mix series by vocalizing. Adults also Squeaked to pups upon entering the den, but not when adults exited the den. If adult Squeaks are associated with approach behaviour and Mix series were composed of Squeaks, then Mix series may serve to establish social contact with adults.

Additional observations on specific vocal classes

Interpretation about the cause and function of the other vocal classes, described in this study, will be presented in the following section. Due to limited sample sizes, these data are based on only descriptive measures. Additional observations on the late appearing Growls and Barks will also be included because pertinent details about these sounds provide cues about vocal development of adult-like calls.

Yelps: Yelps appeared to serve as a distress or alarm call. Yelps are a form of high intensity alarm which pups emit when subjected to pain or distress.

In contrast to Screams, Yelps were rarely produced and they occurred as single outbursts, not as a continuous series of sounds. Adults responded to Yelps, as they did to Screams, with overt care-giving patterns. Therefore, Yelps likely serve to draw attention.

Growls: Late appearing Growls, in contrast to the early appearing Growls (above), were emitted under varied and opposing social situations: for example during play, as well as in the context of submissive, defensive behaviour. Pups were never observed to aggressively attack each other or an adult. At times, however, play appeared rough and it was accompanied by Growls with broad frequency bandwidths. Whether Growls serve as a means of threat or serious aggression is unclear before six weeks of age. Early play aggression likely serves to prepare pups for adult defensive behaviour in which Growls are used to convey threats or warnings, and thus potentially avoid physical confrontation. There were few occasions in which the facial gestures of the Growling pup were visible. Specifically, these gestures were associated with adult attempts to pick-up pups for a den transfer. Pups resisted advances by vocalizing and either retreating or rolling on their back. Pups were observed to curl their lips back, expose their teeth, and Growl simultaneously. This behaviour could be classified as early forms of defensive or threat behaviour.

Barks: Late appearing Barks were extremely rare. Similar to Growls,

Barks were emitted in diverse social contexts, during play activities and in response to sounds external to the den. Barks, like Woofs, were emitted in the den tunnel as pups exited the den. These Barks were in response to sounds external to the den and may serve as an acoustic alarm signal. Many of the Barks emitted by pups were produced as pups exited the den. Only those Barks produced in the den were included in the quantitative analyses which indicates that the relative proportion of Barks presented in this study may not be fully representative of pups.

Woofs: The rare Woofs were emitted in specific contexts when they first emerged in the vocal repertoire after three weeks of age. Woofs were associated with both hesitancy and approach. The majority of Woofs observed were not accounted for in this study because they were emitted in the den tunnel as pups exited. Only those Woofs recorded when pups were in the den were quantified. When pups Woofed inside the den it was in response to either vocal Squeaks from outside the den, or in response to an adult entering the den. In both situations, pups directed themselves towards the tunnel with their bodies erect and ears up. They first hesitated and then exited the den, Woofing as they proceeded through the tunnel. Woofs may signify uncertainty about whether to stay within the den or exit.

Howls: Pup Howls were a special class of vocalizations also emitted in

a wide variety of contexts. Because of their context variability and their rarity, they were the most difficult vocalization to categorize and ascribe a function for. Most of the pup Howls were emitted when they were separated or isolated. Separation Howls were emitted in series, and in conjunction with extended bouts of Screams which typically followed the Howls. In addition, pup Howling occurred in contexts other than isolation or separation. Some pups Howled spontaneously, with no apparent visual or auditory stimulus. Pups Howled or Bark-Howled in response to mechanically generated sounds. Howls were elicited by train whistles although not all whistles were followed by pup Howls. The frequency of the train's whistle corresponded with the frequency range of wolf Howls. Captive wolves also often respond to this same stimulus (Field, 1978; Ryon, unpublished data). One pup responded to the sound of a plane which passed over. Interestingly, the sound generated from the plane's engine matched the fundamental frequency range of the pup's Howl. Pups also Howled in response to adult Squeaks emitted outside of the den, and to adult solo Howls, chorus Howls and Bark-Howls. Individual pups responded differentially. For example, one pup Howled in response to external vocalizations while its siblings appeared to ignore the external stimuli. There was only one incident when several pups Howled inside the den. Pups were, however, occasionally heard chorus Howling with adults outside the den.

Moans and Whines: Moans and Whines were the most common

vocalizations observed in neonates. The steady-state and rapidly-modulated Moans were more common than the slowly-modulated Whines. Although these harmonically structured sounds were common, their significance as a voluntary expressive vocalization class remains unclear. Moans and Whines may well be produced as a passive consequence of respiration. These quiet harmonic vocalizations are often associated with pup huddling and resting. Moans and Whines may be regarded as comfort-state sounds. These richly harmonic vocalizations may, however, serve as a passive form of communication. It could be that the absence of these recurrent sounds elicit maternal care-giving behaviours. Thus, Moans and Whines may be "tonic" communicators (Schleidt, 1973) which serve as continuous signals to a receiver of a behavioural state. If a mother does not hear this vocal activity from the pups, it may indicate the need for attendance. Moans and Whines were also common when the mother was absent from the den. Another role that these vocalizations may serve is as a form of vibratory/tactile communication between pups which would be especially important before pup's auditory functions develop. Data in the present study are insufficient to test these hypotheses. Further studies are necessary to clarify such issues.

Yawns: Yawns were emitted by pups moving from or into a resting, reclined position. Pup Yawning appeared to be involuntary expressions associated with these movements. Whether neonate pup Yawning serves a

communicative function is unknown. There are various references to the function of Yawning in the literature on social communication. Yawns or "mouth gaping" have been used as threat gestures in Old World monkeys (e.g., Hinde and Rowell, 1962; Troisi et al., 1990). Adult monkey yawns were characterized by direct orientation towards an individual and typically involved visual displays of canine teeth. In contrast, wolf pup Yawns were non-directive and did not involve obvious dental exposure. Teeth eruption in neonate wolves has been reported to begin around postnatal day 15, with adult canines only half-way developed by 168 days (Mech, 1970). An empirical investigation of human yawning provided no evidence that yawning was contagious in social situations. Yawning in humans was associated with the absence of social, mental or physical stimulation (Baenninger, 1987). Pup Yawning may be more similar to Yawning reported in captive African lions, *Panthera leo* (Baenninger, 1987). Lion yawns were non-directed and characterized as non-aggressive. Non-vocal lion yawns were observed when the animal was in a reclined position, in a warm environment, and commonly prior to feeding.

Structure of the Vocal Repertoire

Many investigations assessing the vocal repertoire of social species have documented that certain vocalizations within repertoires serve as distinct acoustic signals for communication (e.g. Dittus, 1984; Gouzoules et al., 1984; Cheney and Seyfarth, 1990). Whether structurally-distinct vocal classes were

used by neonatal wolves as representational signals, with each class representing a specific external referent, is doubtful because of the broad range of contexts in which the majority of vocal classes are emitted. That pup vocalizations do not communicate specific referents does not imply that their acoustic repertoire is structurally graded although graded repertoires are considered common among social animals with complex vocalizations (Marler, 1965; Nelson, 1985). In graded vocal repertoires, the structure of vocalizations vary along one or more continua with vocal structures overlapping in their acoustic dimensions (Rowell, 1962). If the vocal repertoire of a species is structurally graded, individuals may use their vocalizations to indicate changes in their motivational state, rather than transferring specific messages through distinct vocal classes. However, even with graded vocalizations functionally discrete subclasses may be perceived within them (Green, 1975). It appears on the basis of this study that the majority of pup vocalizations are structurally discrete classes which convey information about the motivational state of the caller.

In contrast to the findings reported in this study, a number of researchers have postulated that vocalizations within canid vocal repertoires constitute a single system, composed of a continuous series of intermediate sounds (Tembrock, 1963; Cohen and Fox, 1976). While some investigators consider the vocalizations of adult wolves to be largely discrete (e.g. Joslin, 1966; Theberge and Falls, 1967; Harrington and Mech, 1978), others describe the

repertoire as continuous gradations of several basic sounds (Schassburger, 1987, 1993). Field (1978) described neonatal wolf vocalizations as variable and irregular in their acoustic structures. She suggested that young wolves have a vocal repertoire with graded acoustic properties and graded expressions of motivation. This graded repertoire transformed with maturation into a repertoire composed of discrete signals. In contrast to Field, Schassburger (1987, 1993) proposed the reverse. According to Schassburger, the neonate vocal repertoire is composed of a few discrete sound classes. He refers to this period (1-15 days of age) in pup development as "stage one". During the next three stages of pup maturation leading to adulthood, the pup's vocal repertoire is expanded with new sounds which form graded transitions with the sounds produced during stage one. Therefore, as pups mature, their vocalizations become more graded.

In this study, it was evident that pups produced multiple structurally-distinct classes of sounds. By three weeks of age, pups from this study produced all of the adult vocal classes identified by Joslin (1966), Harrington and Mech (1978) and Schassburger (1987, 1993). Even within the first postnatal days, pups produced sounds which were similar in structure to adult Growls and Barks, sounds which Schassburger stated did not emerge until pups were one-to-two months old. The early Growls and Barks noted in this study were rare and not emitted in the same context as adults. The differences between Schassburger's study and the present study may be that Growls and

Barks were not recognized by Schassburger until they were emitted in the appropriate adult-like context. Schassburger also stated that pup Screams (which were similar in structure to the Screams described in the present study) were sounds restricted to pups which were four to eight weeks of age. In the present study, pup Screams were also considered to be unique to early development. Screams in this study, however, were identified during pups' first days of life and were rare after four weeks of life. Screams may reemerge later in pup development (i.e., after six weeks of age). These differences in the age of first emergence of specific vocal classes may, in part, be explained by the sampling technique and the sample size from which Schassburger based his claims. Schassburger did not fully describe his sampling methods or present quantitative data for each vocal class emitted during the various developmental stages which he proposed.

A few of the sound classes which pups produced did overlap in some acoustic dimensions. These classes of wolf pup sounds could subsequently be grouped because of additional similarities in behavioural context. The various distress-related vocalizations (Squeals, Screams and Yelps) represent one such group: Squeals indicated mild distress, and Screams and Yelps indicated an intense form of distress. These sounds may have been related to varying degrees of arousal or motivation. But whether the *acoustic structures* of these sounds represented *continuous gradations* is questionable. When an animal is in distress (e.g. isolated, in pain) the acoustic content of its vocalizations may

reflect this distress. Vocalizations of distressed animals tend to be high in frequency and long in duration (Moelk, 1944; Romand and Ehret, 1984). Among the vocalizations of distressed pups in this study, Screams were longer in duration and higher in frequency than Squeals although the distributions of frequency and duration were partially overlapping. Screams were, however, significantly greater in amplitude compared to Squeals. Thus, Squeals and Screams may be graded structures which communicated intensity of distress with Screams signifying greater distress than Squeals. Masataka (1982) also reported structural merging of distress-related sounds in the infant-specific calls of Goeldi's monkeys, *Callimico goeldii*.

Elowson (1989) reported that spectacled bear cubs (*Tremarctos ornatus*) juxtapose sounds to signify an increasing sense of alarm. The hypothesis that Mix series represent graded motivational intensity has also been suggested for wolves (Cohen and Fox, 1977; Schassburger, 1987, 1993). In the present study, specific combinations of sounds were mixed together in series. In particular Squeals were juxtaposed with Screams. In these Mix series, Squeals commonly preceded and followed Screams. If Squeals were produced to signify mild distress and Screams to signify urgent distress, Squeals followed by Screams may therefore signify an increasing state of arousal. Squeals occurring at the end of a series, in turn, signify a decreasing state of arousal. Perhaps, in these sounds, the structural characteristics of some of the neonate-specific sounds are not graded, but the information being transmitted is. Thus,

increased excitement or urgency is represented by a change in vocalization class (with each class representing a gradation of urgency or excitement level).

Vocal Signatures

A question addressed by previous studies into the wolf vocal repertoire is whether there are individual acoustic identifiers for members within a social group. Vocal signatures have been reported in gregarious mammals (e.g. pygmy marmosets: Snowden and Cleveland, 1980; ring-tailed lemurs: Macedonia, 1986). This thesis did not address individuality of wolf pup calls, in part due to the difficulty of recording sounds from individually identifiable pups. Even if individuals were marked, identification of the vocalizing animal would be difficult because most pup vocalizations were emitted with no obvious oral-facial gestures. The likelihood of vocal signatures present in the repertoire of neonates will be discussed in the following because of its importance as an area for future research of young and adult wolves.

Individual differences in the acoustic structures of young bat calls has been reported in colonial-breeding bats (e.g. Mexican free-tailed bats, *Tadarida brasiliensis*: Gelfand and McCracken, 1986; microchiropteran bats: Jones et al., 1991). Female bats give birth to a single young. The singletons from multiple females are grouped together to form a creche. Periodically, mothers leave the creche to forage. Vocal signatures are likely important cues to enable mothers to identify their offspring within the creche upon their return, to avoid

misdirected care. Vocal signatures in the distress calls of young have also been reported in other colonial breeders (e.g. reindeer, Espmark, 1975). Experimental evidence to show that vocal signatures are used to identify young is lacking. A few studies report mother's localizing their young's characteristic distress cry: Acoustic recognition of young has been reported in Northern elephant seals (Petrinovich, 1974), Japanese macaques (Pereira, 1986) and squirrel monkeys (Symmes and Biben, 1985).

Whether neonate wolf pup vocalizations encode vocal signatures is unknown. It is, however, doubtful that the neonate-specific sounds associated with distress have individual identifiers. Wolves are not normally communal breeders, although multiple litters may be born 20-40% of the time in packs with several mature females (Harrington et al., 1982). Pups are born typically within a protected den. At birth, they are altricial, requiring constant nurturing. Mothers periodically leave the den for excretion of metabolic waste. There is no need for the mother to leave the den for extended periods to forage for food because pack members provide the mother with food (Harrington and Mech, 1982; Fentress and Ryon, 1982). It is unlikely that *neonates* need a vocal signature in the form of a distress call since they are collectively cared for in the den.

Several studies have suggested that harmonic sounds, in particular Howls and Squeaks, are (or are potential) information-bearing acoustic signals in wolves (Mech, 1970; Fentress et al. 1978; Schassburger, 1993). Both

vocalizations are associated with social communication, Howls as a form of long-range communication and Squeaks as a form of short-range communication. Theberge and Falls (1967) and Harrington and Mech (1978) initially described the presence of vocal signatures in wolf Howls. Tooze et al. (1990) and Goldman et al. (1995) provided evidence for potential individuality of Howls and Squeaks, respectively. Goldman et al. (1995) documented the acoustic distinction of the Squeaks of two female wolves and provided circumstantial evidence for pup discrimination of these Squeaks. If pup vocalizations have vocal signatures, Howls and Squeaks may be a starting point for investigation of acoustic signatures in young wolves.

An acoustic basis for individual recognition in Howls and Squeaks is debatable and is of current interest. Tooze et al. (1990) discussed the role Howls serve to unite familiar wolves and distance unfamiliar, potentially dangerous hostile wolves. This information could be transferred based on specific structural features of the Howl, if Howls were expressions of the animal's motivational state (Morton, 1977; Harrington, 1989). Thus, wolves would approach higher-frequency (friendly) Howls and avoid lower-frequency (aggressive) Howls. Playback studies to examine the response of wolves to identifiable individuals is required to address these issues.

The functional significance of vocal signatures in Squeaks is even less well understood than Howls. Squeaks are a form of close-range communication. If vocal signatures in wolves are used to communicate

identification, and Squeaks are a vocalization restricted to close-range usage, then it's questionable why individual identifiers would be necessary. Squeaks are typically produced when animals are within visual proximity to each other (Field, 1978; Harrington and Mech, 1978). Wolves can use either visual or olfactory cues for recognition; vocal cues for identification may not be necessary.

Squeaks were the most common care-giving vocalization between adults and pups (Field, 1978; Harrington and Mech, 1978; Coscia et al., 1991). Pups were first exposed to Squeaks inside the den. Squeaks, primarily emitted by the mother, were virtually the only adult sound pups were exposed to in the den. As pups developed, they were exposed to Squeaks from pack members outside of the den. Adults appeared to entice pups to exit the den by Squeaking to them at the den entrance. Pups three weeks of age discriminated between Squeaks from the mother and a second care-giver (Goldman et al., 1995). Squeaks from the mother, the dominant female, were lower in frequency compared to Squeaks emitted from the second care-giver, a subdominant female. Whether other pack members had Squeaks within the same frequency range as the mother is a question for further investigation. During interactions between dominant and subdominant wolves, the vocalizations of the subdominant are reportedly higher in frequency than the dominant's (Fox and Cohen, 1977). Thus, if subdominant vocalizations were higher in frequency than dominant's, frequency differences reported in Goldman et al. may be attributed

to dominance ranking and not simply vocal signatures. In this example, pup discrimination on a familiar versus unfamiliar basis may be all that is required by pups. However, Holt and Harrington (in preparation) documented stability in the fundamental frequency in the Squeaks of three captive female wolves longitudinally during which time females' dominance rank or maternal status changed. Holt's and Harrington's findings support Goldman et al.'s (1995) view that Squeaks encode vocal signatures.

Why pups differentially responded to Squeaks may be explained, in part, by the fact that pups are most familiar with their own mother's Squeaks. The mother often Squeaks to her pups as she enters the den. Once in the den, the mother regurgitates food to the pups or allows pups to nurse. Therefore, when the mother Squeaks, pups may anticipate feeding. Pack members cooperatively rear pups, providing pups with food and protection (Harrington and Mech, 1982; Fentress and Ryon, 1982). The second care-giver, however, regurgitated to pups as well as providing warmth and a social stimulus for play interactions. Why pups don't exit to all adult Squeaks if pups are communally cared for may simply reflect pup's fear of a novel stimulus (i.e., acoustically different sound). Continued exposure to the stimulus may lead to a cautious approach. There is some data to suggest that pack members may endanger pups. Infanticide of a subdominant's pups by the dominant female has been documented (McLeod, 1990). Infanticide, however, occurred when pups were newborn, prior to their development of hearing and their socialization with pack members. In

the wild, intruding wolves from different packs may endanger pups. This potential threat to pup survival supports the need for pups in the den to be able discriminate their pack-mate's Squeaks.

Vocal recognition of mother's calls has been reported in young Japanese macaques (Masataka, 1985). Young squirrel monkeys responded more to the vocalizations of other adult females who acted as care-givers ("allomothers"), than to the vocalizations emitted by the mother (Biben, 1992). For this species, young are first exposed to vocalizations of allomothers because their mothers rarely vocalize to their own infants during early development. Allomothers commonly vocalize to other mother's infants when they are being carried by the mother.

Transitional Vocalizations

This thesis provides acoustic and behavioural evidence that some wolf adult vocalizations were either structurally similar to, or produced in similar contexts as, specific neonate sounds. The similarities between Squeals and Squeaks were discussed above. The relationships between Growls and Moans, Yelps and Barks and Screams and Howls will be explored in the following section.

Growls and Moans: Among the neonate-specific sounds, Moans appeared in the same context as early-appearing Growls. At the acoustic level,

the spectral structure of early Growls in part resembled harsh, modulated Moans. This conclusion follows from the presence of spectral energy concentrated at integral frequency intervals. Whether Moans are generated by the same processes as Growls is an issue for further investigation of vocal/motor processes. However, if Moans and Growls are generated by the laryngeal muscles in the vocal chords they are both likely to contain harmonic content (Fry, 1979). In turn, this finding raises issues of whether early Growls were distinct from Moans and/or whether they were developmentally related. Early Growls were short in duration compared to the majority of early Moans. As further illustration, early Growls were emitted in isolation and early Moans were typically emitted in series. The distribution of spectral energy of Growls changed ontogenetically. The later Growls had an increased spread of energy in comparison to the early Growls. This spread of energy may, in part, be related to increased vocal-motor control; as pups mature they may have increased control of their vocal-motor gestures and the physical strength to produce sounds with greater spreads of spectral energy. Circumstantial evidence of increased amplitude with maturation was observed in the analysis of Squeal and Scream waveform ranges (Table II). With maturation, the relative proportion of Growls emitted by pups increased whereas the production of Moans appeared to subside.

Yelps and Barks: The spectral structure of Yelps resembled the gross

structure of Barks, although the context of Yelps and Barks was vastly different early in development. Specifically, Yelps were associated with mother stepping on pups and Barks with huddling/stationary settings. Yelps and Barks were vocalizations composed of harmonic and noisy components. Early Yelps were high-frequency and high-amplitude sounds. Early Barks, in contrast, were lower in both frequency and amplitude. Later Barks had the same frequency range as early Barks, but they were perceptually higher in amplitude. Yelps were rare late in development but are reported to be emitted from subdominant wolves in distress or pain (Schassburger, 1987, 1993). Early Yelps were responded to by the care-taker, whereas early Barks were ignored. Later in development, Yelps were extremely rare. Barks were also rare and, in most cases, they were produced in response to an acoustic stimulus external to the den, or they were emitted during play interactions. When an adult was present, Barks were localized by the adult and overtly responded to.

Screams and Howls: The distinctive fundamental frequency contour and gross spectral structure of pup Howls resembled that of long-duration Screams. Similarities in frequency contour has led to speculation that Howls develop from neonatal Screams (also called Whines or Cries) (Schassburger, 1987, 1993; Frommolt et al., 1988). This speculation has several weaknesses related to the physical structure of these sounds, and their behavioural contexts. First, Screams and Howls occur concurrently in development. Second, the

fundamental frequency of Howls is considerably lower than that of Screams (Table 1). Third, the duration of Screams, decreased with maturation (Table III), whereas the duration of Howls increased. Fourth, pups Howled in other contexts which were not evidently stressful. In addition, early Howls emitted in behavioural contexts other than separation and/or distress typically occurred as single Howls. Screams were always emitted in obvious distressed situations.

In this study, Howls from a separated pup were long in duration and emitted in series (Table VII). The mean fundamental frequencies and durations of these Howls were similar to the Howls described in Tables I and V. In general pup Howls are long in duration and periodic in frequency modulation relative to other neonatal sounds (Table I). It is well-known that long-distance calls are typically extended in duration, presumably because long duration signals are easier to localize (Wallach, 1940). It is also known that the distress or isolation calls of infants are long in duration (e.g. Kaplan et al., 1978; Lieblieh et al., 1980). Masataka and Symmes (1986) showed that isolated infants emitted longer calls at greater distances from group members. In addition, the duration of the isolation calls of many primate species, like the duration of Howls, increases with maturation (Winter et al., 1973; Lieblieh et al., 1980). If Solo or Long Howls serve to attract members (Rutter and Pimiot, 1968), and pup distress calls serve to attract the care-giver, then it is possible that early distress signals are developmentally related to at least one group of Howls. Chorus Howls and Bark-Howls, if functionally distinct from Solo Howls, may

have different ontogenetic precursors. Preliminary analysis of Howls from captive wolves indicate that Solo Howls are longer in duration and less modulated in frequency than Chorus and Bark Howls (Coscia and Ryon, unpublished data).

Vocal Development and Concluding Remarks

In this study, wolf pups were predominantly sedentary up until two weeks of age. Associations with littermates and the care-giver were primarily related to maintaining physical contact. The primary information conveyed in pups' vocalizations were expressions of internal states (e.g. distress, comfort). At three weeks of age, pups were mobile and appeared to initiate directed social interactions with littermates. None of the interactions observed during week three were associated with distinct pup vocal activity (although occasional Moans were detected). Pups were virtually silent during these "early" interactions even though by this stage in pup development pups were capable of producing all of the adult-like social vocalizations. Why early pup interactions were non-vocal is uncertain. Early interactions were shorter in duration than interactions after three weeks of age. In addition, any given pup's actions were not necessarily reciprocated by the second pup. As pups matured, their interactions involved increased coordination of motor movements and involved reciprocated interactions (cf. Havkin and Fentress, 1985; McLeod, 1987). One reason why pups may be silent when they first begin to interact is that vocalizing

and interacting require temporal and motor control which neonates are initially incapable of exhibiting. Another explanation for silent interactions during three weeks of age is related to the development of hearing. Auditory localization to species-specific sounds in dogs is reported to begin around postnatal day 16 (Ashmead et al., 1986) which corresponds to postnatal week three in this study. Therefore, it is likely that pups' auditory systems were not functional so that vocalizations were not clearly perceived by pups. If pups use their vocalizations as cues to communicate motivation about an interaction, then hearing may be essential for learning about the relationships between vocalizing and interacting.

The vocal context of some sounds changed with maturation. Early Growls and Barks were "non-associative", emitted with no obvious overt stimulus. The evidence for this was that both pups and adults were stationary at the onset of these sounds and adults showed no response to them. It is possible that these sounds were merely examples of vocal practice. Marler and Peters (1982) initially reported vocal practice, termed "babbling", in oscine birds. Subsequently, Snowdon et al. (1986) described babbling in non-human primates. The neuroethological literature has many documented cases where animal movements can, and often do, occur prefunctionally, even without practice (e.g. Bekoff, 1988). In the same sense, it is possible that wolf pups also produce Growls and Barks prefunctionally, separating sound production from its apparent communicative function. The abrupt change in vocal context of Growls (after three weeks of age) appears at the time when pups initiate

interactions with their siblings and their care-giver. Growls and Barks from pups older than three weeks of age were clearly associated with social interactions between pups and adults. The role that learning plays in the development of the use of Growls and Barks is unclear, especially since these sounds were emitted by pups who had minimal or no exposure to adult Growls and Barks in the den. Barks from the care-givers were never heard in the den. Growls from adults in the den were heard only once, when a second care-giver entered the den when the mother was present. Pups presumably heard these sounds from juvenile and adult wolves as they emerged from the den, after three weeks of age, and socialized with pack members.

The care-giver did not overtly respond to the majority of pup vocalizations, particularly during early development. The mother did not respond to all pup Moans, Whines, Growls and Barks or to many of their Squeals. The cues that elicit a response from the mother to some pup Squeals may be non-vocal. In accordance, there were pup Squeals that were associated with pup movement. It is possible that two forms of signalling convey to mothers that attention to the pups is needed. In other words, the mother is primed to respond if pups Squeal and move simultaneously (Goldman et al., 1990).

The development of communication in wolves cannot fully be explained based on the ontogeny of one sensory or one motor channel. The importance of considering multiple sensory channels in describing the function of vocal

classes is stressed by Cohen and Fox (1976) in their description of acoustic communication. These authors suggested that Barking in the domestic dog serves to attract the attention of the receiver, and *not* to convey a *specific referent* about the class of receiver. Harrington and Mech (1978) make a similar point about the potential information contained within the Bark and suggest there may be additional information besides "look at me". The specific message, if one does exist, of the Bark may be conveyed through either visual or olfactory channels. Postural and chemical signals can provide the receiver with information about the signaller's motivation. Olfactory and postural cues are relevant to discussions of close-range communication.

Although this study was not able to examine the role of olfactory communication, varying postural and facial displays associated with vocal activity were evident. For example, pup Barks and Growls after two weeks of age were emitted during obvious play interactions. Pup play involved individuals approaching and contacting each other. During play, pups would wrestle and mouth or bite each other. Pups also emitted Barks and Growls when alarmed and during defensive behaviour. The postures of pups in these situations were quite different. When pups were alarmed, their ears were erect and their heads held upwards and oriented towards the direction of the stimulus. When pups were in a defense position, they retreated with their tails tucked, often by rolling on their back. These varied postures likely provide the receiver with additional information about the message of close-range acoustic signals. Schenkel

(1947), Havkin (1981) and McLeod (1987) described the various postures of dominant and submissive wolves and facial displays of young and adult wolves. These displays were postulated to communicate information about the social relationships of individuals. Clearly, postural communication is important in the wolf. In summary, it is likely that information from multiple channels of communication is required to assess fully the function of neonate sounds, as well as the function of adult sounds.

Social influences may, in part, explain differences in vocal production associated with the 1991 litter of pups. In particular, the pups from 1991 were less vocal, after three weeks of age, than the pups from the other two litters. Interestingly, adult presence in the den differed for the 1991 litter in two ways. First, the mother was absent from the den after four weeks of age. Second, a second care-giver did not enter and reside in the den. It is suggested that pup vocal behaviour was affected by adult presence in the den: pups Squeaked more when an adult was present, and, Squeaks were the most common vocalization emitted by pups after three weeks of age. In addition, pup behaviour with a second care-giver was, in some respects, qualitatively different with a second care-giver than with the mother. For example, pups were observed to play with the second care-giver more, and, pups would, on occasion, retreat from advances from the other female. It is believed that adult presence in the den affected pup vocal/behavioural activity; one of the consequences being that pups were more vocal in the den.

Marler and Peters (1982) suggest that bird song becomes more stereotyped (i.e. less varied) with maturation. One explanation for greater variability of sounds early in development is that young animals have less laryngeal control. In contrast, numerous reports on the development of vocalizations in primates report no or subtle changes in the amount of variation in acoustic structures as a function of age (Seyfarth and Cheney, 1986; Snowden et al., 1986; Elowson et al., 1992). These and other studies (Gouzoules and Gouzoules, 1989; Hauser, 1989) do, however, report on developmental trends in acoustic parameters (e.g. changes in fundamental frequency and duration). The present study of vocal production in neonate wolves in part parallels these studies of vocal ontogeny in primates in that developmental trends in acoustic parameters were observed. Specifically, significant decreases in fundamental frequency were observed for some vocal classes (Squeals, Screams, Squeaks and Howls), and increases in sound duration were observed in one class (Howls). However, evaluations of wolf pup vocal stereotypy would need to be addressed by examining the development of individual, identifiable pups. This is an issue for future investigations. In addition, analysis of wolf vocal production after six weeks of age, when pups leave the den, is required to assess how vocal stereotypy is affected by further physical development and social development (i.e. pup integration into the pack).

Parallels between the development wolf vocal communication and the

early development of human language exist (Coscia, 1989). Oller (1981) refers to pre-speech vocalizing in human infants as babbling. Babbling in humans, similar to that reported in non-human primates and in the present study, is composed of two groups of vocalizations, neonate-specific sounds and adult-structured sounds. Researchers investigating human infant vocal development have labelled sounds similar in structure with different names. Regardless, these researchers have divided the infant repertoire into the same two primary groups of sounds. The neonate-specific sounds have been termed "crying" or "syllabic" (Hollien, 1980 and Bloom et al., 1987 respectively). Structurally, these sounds are richly harmonic, both steady-state and rapidly modulated in frequency (Kent and Murray, 1982) similar to wolf neonate-specific vocalizations. The adult-structured sounds are called "vegetative" or "vocalic" (Hollien, 1980 and Bloom et al., 1987 respectively). It is the vegetative/vocalic sounds which persist into adulthood to comprise the adult acoustic repertoire. Presumably, these are the sounds shaped by social experience through selective reinforcement. In contrast, the crying/syllabic utterances gradually drop out of the repertoire. Similarities in mammalian vocal ontogenetic processes are intriguing, particularly because vocal tract anatomy and its development are vastly different across these species (Kent, 1981).

In conclusion, this study documented the process of early vocal development in wolves. The neonate vocal repertoire developed rapidly within a six week postnatal period from a repertoire composed primarily of neonate-

specific vocalizations, necessary to elicit care-giving behaviour, to a repertoire of adult-like vocalizations, required for pack social integration and their survival. At birth, pups produced a broad range of vocal classes. Between the second and third postnatal week in development, wolf pups produced a repertoire of sounds that has the same classes as those documented for the adult repertoire. The new vocalizations (e.g. Woofs and Squeaks) added to the pup's repertoire occurred at an age of major physical and social changes. Significant increases in the number of calls within mammalian vocal repertoires has been reported to occur with maturation (Sebeok, 1977; Ehret, 1980). Although pups produced some adult call types, the behavioural context of the calls did not completely resemble adult behavioural contexts. The majority of the adult-like acoustic units that pups emitted were produced under varied social contexts. Adult wolves also produce distinct sounds under multiple and divergent contexts as well (Harrington and Mech, 1978). When structurally similar sounds are emitted in divergent context, additional cues (i.e. non-vocal signals) likely transmit information.

The ontogeny of behaviour involves complex interactions of genetic and experiential factors (Fentress, 1983). Systematic investigations of ontogenetic events are a means by which to explore the intricacies of developmental processes. This thesis on the early ontogeny of vocal communication provides a model for future studies of vocal development and acoustic communication in wolves and other social mammals.

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