

CALL TRADITIONS AND DIALECTS OF KILLER WHALES (ORCINUS ORCA)
IN BRITISH COLUMBIA

by

JOHN KENNETH BAKER FORD

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Department of

Zoology

The University of British Columbia
1956 Main Mall
Vancouver, Canada
V6T 1Y3

Date

December 3, 1984

ABSTRACT

Underwater vocalizations were recorded from pods of wild killer whales (Orcinus orca) off Vancouver Island, British Columbia, during 1978-83. Acoustic exchanges within pods are dominated by repetitious, pulsed calls which can be organized into discrete categories. Repeated encounters with 16 photographically-identified 'resident' pods demonstrate that each pod produces a repertoire of 7 to 17 (mean = 10.7) discrete call types. Recordings of captive whales of known pod origin and historical field recordings indicate that pod repertoires remain stable for periods of at least 18 years (1965-83) and possibly 25 years (1958-83). Each individual whale appears capable of producing most or all of the calls in its pod's repertoire. Repertoires are apparently learned. All discrete call types tend to be used in all 'active' contexts, which consist mainly of foraging and travelling. Few call types are clearly correlated with specific behaviours. Activities involving tight group formation and physical interaction among pod members were accompanied by an increase in the use of whistles and variable pulsed sounds.

Significant differences exist among the call repertoires of different pods. The 16 resident pods on the B.C. coast can be arranged into 4 acoustic associations, each of which has a unique set of discrete call types. These associations are referred to as 'call traditions', and the pods belonging to a

tradition form a 'clan'. Pods within each clan share some call types, but may also produce unique calls. Shared calls often have different pod-specific renditions. These differences form a system of related dialects within each call tradition. Three of the four resident clans belong to a single community, and pods from these clans frequently associate with one another. Observed patterns of association were often unrelated to acoustic relationships. The fourth resident clan forms a community with a separate range. A community of 17 'transient' pods is sympatric with but socially isolated from the resident communities. This community has a wide range, and appears to consist of a single call tradition.

The call traditions and dialects described here are apparently unique among mammals. Various hypotheses to account for their origin and adaptive significance are discussed. Clans could represent independent lineages which arrived on the B.C. coast through a series of unrelated founding events. As the founding pod of each clan grew and divided, its group-specific call repertoire diverged, either through functionless cultural drift or by an active process promoting acoustic differentiation of related groups. Dialects may have no selective value, or they may serve as kin-recognition signals for maintaining pod cohesion and identity or avoiding excessive inbreeding.

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GENERAL INTRODUCTION

Prior to the 1970's, our knowledge of the natural history and behaviour of cetaceans was based primarily on carcass analysis from whaling operations and observations of captive specimens. Studies of the underwater acoustic communication of captive dolphins consisted predominately of attempts to catalogue their complex signals and assess their potential for information transfer (e.g., Dreher and Evans 1964; Lang and Smith 1965; Dreher 1966; Bastian 1967). Few of these studies seriously considered how the sounds might serve the animals in their natural habitat. Reports of underwater vocalizations of free-ranging cetaceans were based on sporadic, brief encounters and also dealt mainly with physical descriptions and classification of the sounds (e.g., Schevill and Lawrence 1949; Schevill 1964; Busnel and Dzeidzic 1966). Functional interpretations relied on anecdotal observations of behaviour and social organization, since little systematic field work had been carried out (e.g., Dreher and Evans 1964; Evans and Bastian 1967).

In recent years, a trend towards research into the life history and social behaviour of wild cetaceans has developed. Despite the many difficulties associated with studying these animals at sea, a great deal has been discovered. Most of these investigations have made use of new methods for identifying individual whales and dolphins from naturally-occurring markings (e.g., Bigg et al. 1976; Darling 1977; Wursig and Wursig 1977; Wursig 1978; Norris and Dohl, 1980a; Payne (ed.) 1983). These

and other new techniques have also been employed in pioneering studies of vocal communication in mysticetes, especially those concerning the song of humpback whales (Megaptera novaeangliae) (Payne (ed.) 1983; Tyack 1981) and the calls of right whales (Eubalaena australis) (Clark and Clark 1980; Clark 1982, 1983).

Several intensive, long-term studies of the behaviour and social organization of odontocetes have been conducted recently (e.g., Wursig and Wursig 1977, 1979, 1980; Saayman and Tayler 1979, Norris and Dohl 1980a; Wells et al. 1980) but few of these have dealt with underwater communication. One exception is a study of the acoustic behaviour of Hawaiian spinner dolphins (Stenella longirostris) carried out by Brownlee and Norris (1983) in conjunction with a broad investigation of the natural history and behaviour of the species (Norris and Dohl 1980a; Wells and Wursig 1983; Wursig and Wursig 1983; Wursig et al. 1983). Other important work on odontocete communication includes Watkins and Schevill's (1977) study of the 'codas' of sperm whales (Physeter catodon) using multi-hydrophone arrays.

In this thesis, I describe the results of a five-year field study of the underwater vocalizations and behaviour of killer whales (Orcinus orca) in British Columbia coastal waters. When I began this acoustic study in 1978, much of the fundamental biology of local killer whales had recently been discovered (Bigg et al. 1976). Killer whales were found to live in stable social groups, or 'pods', many of which could be encountered reliably in predictable locations on the coast at certain times of the year. This seemed to be an ideal population upon which

to base an in-depth examination of the role of vocalization in the social behaviour of a free-ranging odontocete. My initial objectives were rather broad, since no previous accounts of the sounds of wild killer whales were available. I planned to encounter and record as many pods as possible in a variety of social and behavioural contexts to examine possible correlations of vocalizations and activity. In addition, I hoped to compare the vocal patterns of different pods to test a hypothesis that acoustic communication may be important in maintaining the stable social structure in the population.

Early in the study, it became apparent that marked differences existed in the vocalizations of certain pods. Following this discovery, I decided to place an emphasis on this aspect of the whale's vocal behaviour to document in detail what appeared to be a unique phenomenon among mammals. This emphasis continued throughout the field research and is maintained in this thesis.

The thesis is divided into three independent sections. The first, Part I, examines the vocalizations of selected pods in relation to the social and behavioural contexts in which they occur. The principal aim of this section is to describe the manner in which sounds are used within a typical social group, and to discuss their probable communicative functions. Part II describes the similarities and differences in group-specific vocal repertoires within a population of 16 'resident' pods occupying the B.C. coast. The geographic distribution and social associations of these pods are compared to their vocal

traditions and dialects in an attempt to explain the origin and adaptive significance of the acoustic variations. The final section, Part III, considers the vocal dialects within a population of 'transient' killer whales which is sympatric with but socially distinct from resident pods.

PART I

BEHAVIOUR AND VOCALIZATIONS OF RESIDENT KILLER WHALES

INTRODUCTION

Our understanding of the function of acoustic communication in cetaceans is poor. This results in part from our lack of knowledge of the social organization and behaviour of whales and dolphins in their natural habitats. Until these aspects of the animals' biology are well understood, it will not be possible to arrive at any realistic interpretation of their communication systems.

Most previous studies on the vocalizations of killer whales have been conducted on captive animals, held either alone or in groups of three or less. They have dealt primarily with physical description and classification of the signals (Newman and McGeer 1966; Schevill and Watkins 1966; Spencer et al. 1967; Singleton and Poulter 1967; Poulter 1968; Dahlheim and Awbrey 1982). Reports of killer whale vocalizations in the wild have relied on recordings acquired during short encounters with unidentified groups and have also dealt mainly with descriptions of signal structure (Valdez 1961; Steiner et al. 1979; Awbrey et al. 1982).

In this chapter, I describe the underwater vocalizations of resident killer whales in the coastal waters of British Columbia. I attempt to interpret the communicative functions of these sounds from the social and behavioural contexts in which they occur. The recordings and behavioural observations reported here were collected systematically over a period of five years, from a population of approximately 230 individually-identified resident killer whales (Bigg 1982). The results show

that there are consistent correlations between the types of sounds used within social groups, or pods, of killer whales, and the activities of the group. It is also apparent that much of the communicative function of killer whale calls may be related to factors responsible for the development of group-specific repertoires, or dialects, among pods (Part II).

MATERIALS AND METHODS

1. The Study Animals

Killer whales in British Columbia coastal waters live in stable social groups, or pods (Bigg et al. 1976; Bigg 1982). The population is made up of 16 'resident' pods which can be seen reliably in certain locations during the summer months, and 17 'transient' pods which are uncommon and irregular in appearance. Resident pods are divided into two communities which occupy separate ranges (Fig. 12, Part II). Pods within each community frequently associate, but the two communities do not mix. Resident pods range in size from 4 to 50 individuals, with a mean of 13.4. Size and composition of each resident pod are listed in Table VIII (Part II). Further details of the structure and dynamics of resident and transient pods are given in Parts II and III.

2. Field Observations and Recordings

Resident killer whales were encountered on a total of 154 days during 1978-83 in various locations around Vancouver Island. Pods were located and identified from unique naturally-occurring markings in the manner described in Part II. All 16 resident pods known to occur in B.C. waters were observed and recorded. Observations of the spacing pattern, movements, and other behaviours of whales throughout each encounter were noted either by hand or on a tape recorder. In most cases, concurrent behavioural observations were also recorded on a second track of

the underwater recording. Spacing patterns and movements of whales were logged on small-scale charts in the field. Positions of whales were determined by reference to nearby landmarks and used later to calculate speed of travel.

Underwater acoustic recordings were made with several recording systems described in detail in Part II. Depending on ambient noise levels and local sound-propagation characteristics, useful recordings could be obtained at ranges up to 2 km from the animals.

3. Behaviour Classification

Most of the behaviours of resident pods can be grouped into five categories: foraging, travelling, group-resting, socializing and beach rubbing. Generally there was a degree of synchrony of activities within a pod. However, individuals or subgroups in a pod occasionally engaged in a different activity than the rest of the group. In these cases, I considered the activity state of a pod to be the behaviour displayed by most of its members. A sample of 416 h of observations collected on 93 days spent with northern community pods was used to determine the durations of activity bouts and the rate of travel during different activities for resident whales. Bout durations were measured from the start of the encounter or the onset of the activity, until a change to a different activity occurred or until the encounter ended. Occasionally, more than one activity bout was recorded simultaneously when two or more pods travelling in the same vicinity were engaged in different

activities.

4. Sound Analysis

Most killer whale social signals, or calls, can be classified by ear into discrete categories based on distinctive structural characteristics. Following preliminary aural classification, samples of call types were analyzed using a Kay 7029A spectrum analyzer. Most spectrograms were made using an 80-8000 Hz frequency range with a narrow 45 Hz filter bandwidth. For a more detailed description of call classification methodology, see Part II.

To examine the patterns of call occurrence and correlations with behaviour, continuous sections of tapes were divided into 10-min time periods, each labelled as to the pod or pods present at the time and the prevailing activity state. Proportions for each call type in each time period were calculated. These were transformed using the arc sine square root, and used as replicates in an analysis of variance (ANOVA) with Barlett's test of variance homogeneity and Scheffe's test for determining the significance of differences among means. This technique was chosen over analysis of frequencies since it more accurately reflects the variability in the data.

Associations of different call types were examined by calculating the preceding and following transition frequencies for calls within each min of the 10-min time periods. These frequencies were arranged in a matrix, and compared to a random model of expected frequencies. Each transition pair was

examined for departure from the random model by condensing the matrix into a 2x2 contingency table about the transition of interest, then testing this using the G-statistic (Sokal and Rohlf 1981).

As pointed out by Slater (1973, 1983), it is often of interest in such analyses to remove 'self transitions', or transitions between repetitions of the same call, before condensing the matrix. This eliminates the strong influence of these transitions on other interactions within the matrix, and provides a better representation of the relationship of different call types. For this analysis, expected values for each transition pair and the degrees of freedom for a goodness-of-fit test were calculated by the method described in Lemon and Chatfield (1971, pp. 14-16). Following this analysis, the preceding/following frequencies for each call combination were summed and used to calculate an index of association. This index is a modified form of Dice's coefficient of association (Morgan et al. 1976) and normalizes the data to account for differences in the abundance of call types:

Index of Association =

$$\frac{2(\text{transitions } i \rightarrow j + j \rightarrow i)}{(\text{transitions involving } i) + (\text{transitions involving } j)}$$

A cluster diagram was then created using these values to display the hierarchy of associations within the call repertoire.

RESULTS

1. Description and Definitions of Sound Types

The underwater sounds of killer whales fall into three different classes:

A) Clicks

Clicks are brief pulses of sound, typically given in series, which are generally employed as echolocation signals in odontocetes (see reviews by Norris 1969; Popper 1980, Wood and Evans 1980, Watkins 1980). Killer whale clicks have been described from field recordings by Steiner et al. (1979) and Awbrey et al. (1982), and from observations of captive animals by Schevill and Watkins (1966) and Diercks et al. (1971 and 1973). These studies demonstrate that killer whale clicks are quite variable in structure. Durations of clicks range from 0.5 to 25 ms, and click repetition rates from a few to over 300/s. Frequency content can be relatively narrow to broadband, with emphases ranging as high as 30 kHz. Some clicks are composed of pairs of pulses, or doublets, with interpulse intervals of 1.3 to 2 ms (Awbrey et al. 1982).

Clicks were not analyzed extensively in this study. They were commonly heard in most contexts, usually at repetition rates of 2 to 50/s. Fluctuations in repetition rate over the duration of click series resembled those produced by actively echolocating killer whales (Schevill and Watkins 1966) and other odontocetes (Norris 1969, Watkins 1980).

B) Whistles

Whistles are characterized by a non-pulsed or continuous waveform, which appears on a spectrograph as a single narrowband tone with little or no harmonic or sideband structure (see example in Fig. 2, Ford and Fisher 1983). Killer whale whistles have been reported by Steiner et al. (1979), Dahlheim and Awbrey (1982), Awbrey et al. (1982) and Hoelzel and Osborne (in press). In the present study, whistles occurred at frequencies of 1.5 to 18 kHz, although most were between 6 and 12 kHz. Whistle durations ranged from 50 ms to 10-12 s, and most contained a number of modulations or abrupt shifts in frequency. A great variety of whistle forms were recorded, but no attempt was made to determine structural categories.

C) Pulsed Calls

Pulsed sounds are the most abundant and characteristic vocalizations produced by killer whales. These signals have distinct tonal properties because of high pulse repetition rates. Pulsed sounds usually contain abrupt and patterned shifts in pulsing rate, resulting in a wide variety of unique-sounding calls. The pulses making up these calls can have either wide or restricted bandwidths and repetition rates extending to 4000/s or more. The fundamental frequency structure and repetition rates of pulses can be varied independently in the same call. Some signals are composed of two different pulsing frequencies, likely caused by resonance in

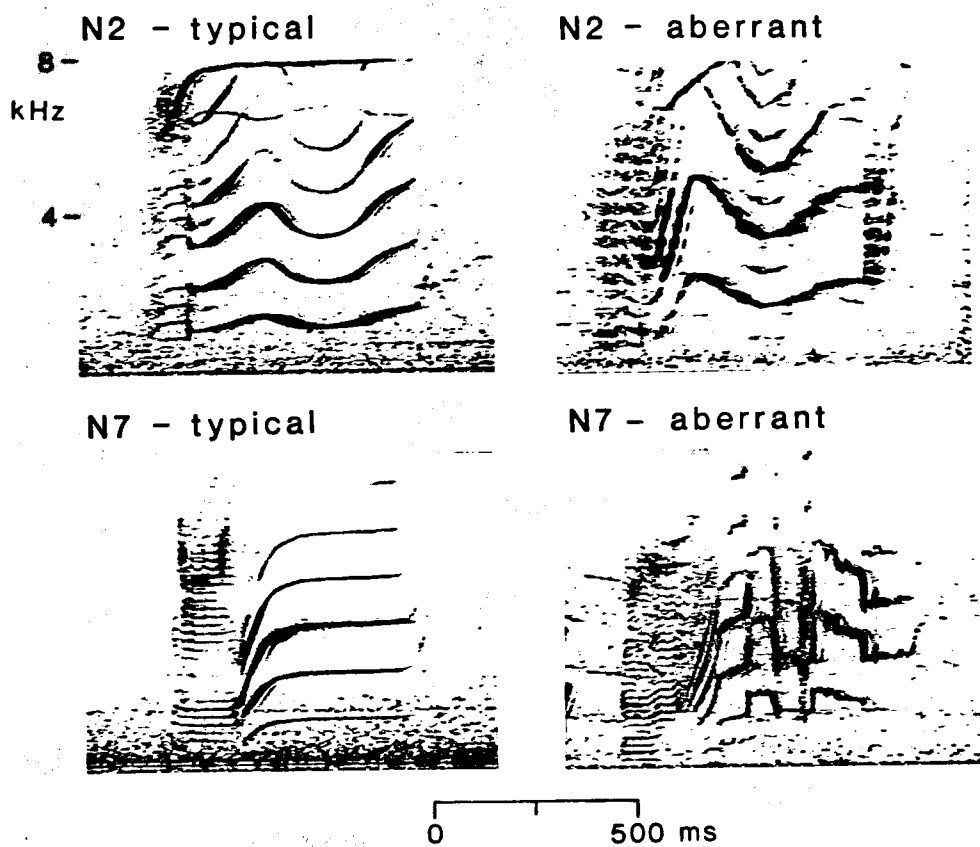
the sound generating structure. Many also contain an overlapping narrowband tonal (or whistle) component. Examples of these variations can be seen in Part II.

In spectrographic analysis, pulses generated at repetition frequencies surpassing that of the analyzer filter bandwidth are resolved as harmonics or sidebands at intervals equivalent to the repetition frequency (see Watkins 1967 for more details). Most pulsed calls recorded in this study had repetition frequencies of 250 to 2000 Hz. Primary energy was usually between 1 and 6 kHz, with high frequency components extending to > 30 kHz. Call durations ranged from less than 50 ms to > 10 s; the majority were between 0.5 and 1.5 s long.

Pulsed Call Classification:

The majority of killer whale pulsed signals fall into discrete structural categories. These call types can nearly always be distinguished by ear. Variability in structure occurs within all discrete call categories. Certain categories tend to be more variable than others. Different call types are so distinct, however, that most calls can be assigned to distinct categories without ambiguity. Occasionally, highly irregular versions of discrete call types can be heard. These "aberrant calls" are clearly based on a given discrete call format, but are greatly modified (Fig. 1). On rare occasions, pods were observed to produce imitations of call types that were not part of their repertoire. Several examples of these are shown in Figure 2. Imitations always involved calls belonging to other

Figure 1. Spectrograms of typical and aberrant versions of calls N2 and N7. See Part II for explanation of call numbering scheme.



pods in the same community.

Discrete pulsed calls predominate in acoustic exchanges within pods. Some pulsed signals, however, are highly variable and cannot be classified into clearly-defined categories. This "variable call" category includes complex, intergrading signals ranging from short squeaks and trills to long, raucous squawks. The variable call category probably contains some highly aberrant renditions of discrete call types.

A total of 78 discrete call types and 42 subtypes were identified in this study. Resident pods have repertoires of 7 to 17 different call types (mean = 10.7), while transient pods appear to have smaller repertoires of 2 to 6 calls (see Part III). A complete classification of call types and a description of pod repertoires is given in Parts II and III.

2. Description of Behavioural Activities

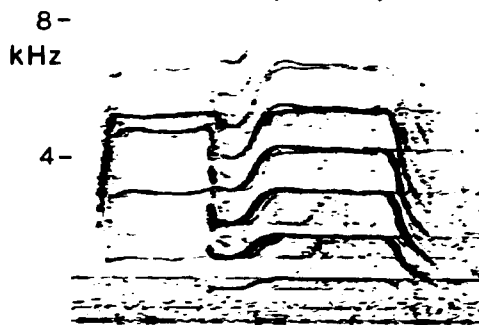
Most activities of killer whales were grouped into five major categories. Rate of travel and duration of activity bouts were determined from a 416 h subsample of observation of resident pods in the northern community. With the exception of beach rubbing, described below, southern resident whales behave similarly.

A) Foraging

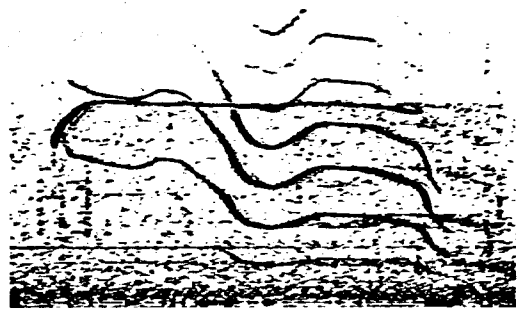
Foraging is the most common group activity of resident pods. This behaviour accounted for 66.51% of the total observation period (Fig. 3). The category includes all

Figure 2. Spectrograms of northern resident call types N23, N25, and N32, and imitations of these calls by the A-pods.

N23i - I11, I31 pods



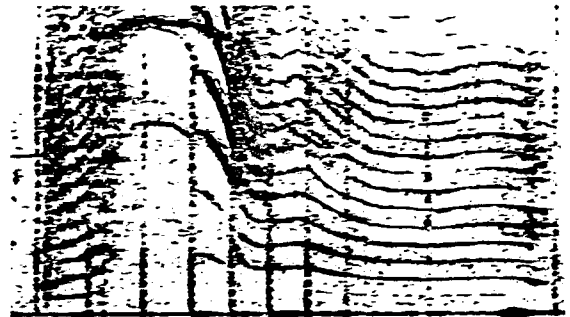
N23i - A-pod imitation



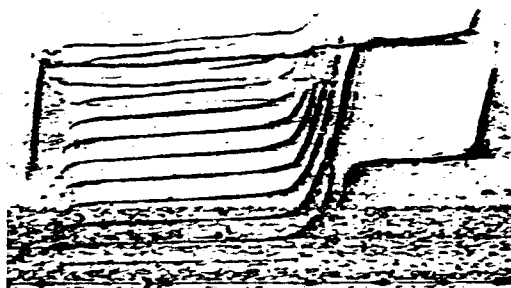
N25 - I11 pod



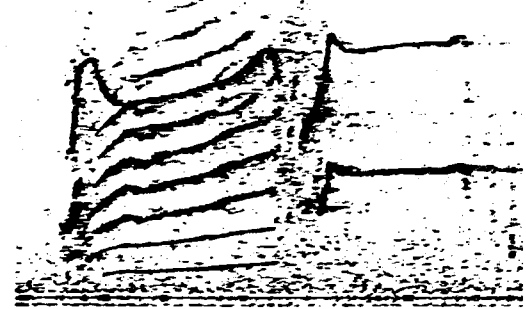
N25 - A-pod imitation



N32ii - R pod

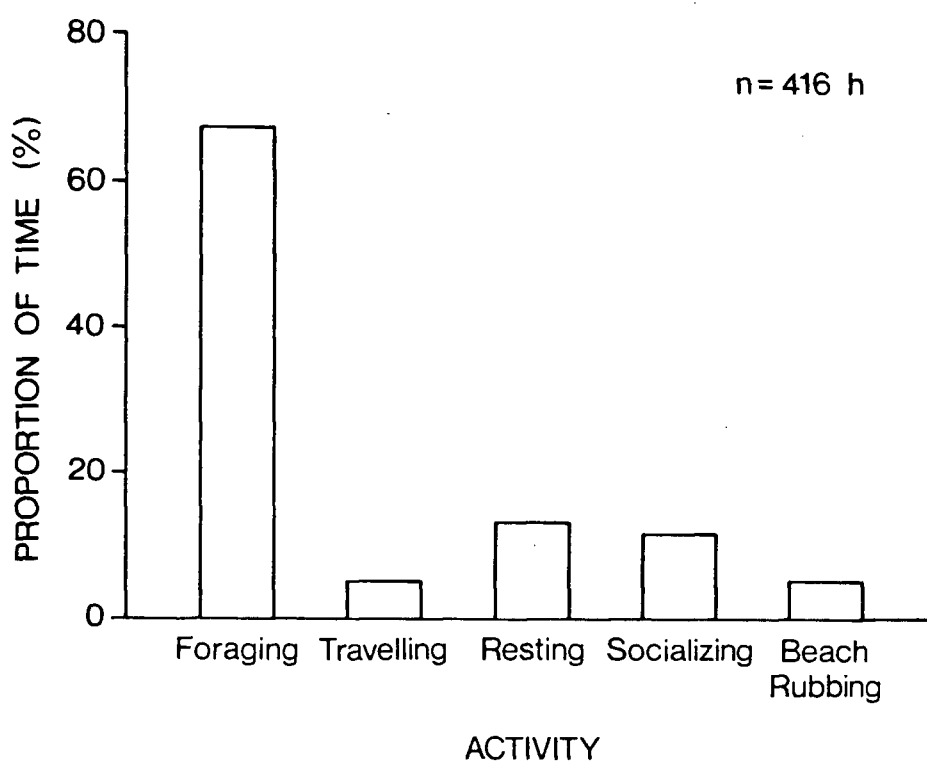


N32ii - A-pod imitation



0 500 ms

Figure 3. The distribution of activities of northern-community resident killer whales. Values based on 416 h of observation collected on 93 days.



occasions where the whales were known or suspected to be feeding actively or searching for prey. Whales were sometimes seen carrying fish, either whole or in parts, in their mouths following a kill. Sites of presumed kills were inspected whenever possible, and often scales and other scraps could be collected. Prey species taken were primarily Pacific salmon (Oncorhynchus spp.), but rockfish (Sebastes spp.) and herring (Clupea harengus) were also noted. Other indications of feeding included sudden lunges and changes in direction by individuals, high-speed swimming just under the surface, and milling in tide rips and other good feeding areas. Kills were most often made by single animals, but occasionally subgroups of 2-4 whales were seen to corral and catch fish close to shore. Apparently organized encirclement and capture of prey in open water as described for killer whales feeding on herring (Steiner et al. 1979; Christensen 1978, 1982), pinnipeds and cetaceans (Zenkovich 1938; Brown and Norris 1956; Norris and Prescott 1961; Norris and Dohl 1980b) was not observed during this study.

Although the details of group spacing and movements during foraging varied, a general pattern was evident. Pod's typically separate into smaller subgroups that disperse widely over areas of several square km. Subgroups are usually composed of cows and their offspring. Although all members of the pod travel on a similar course, subgroups dive at different times, and may independently change direction and mill for short periods.

Two or more pods commonly forage in association. Of the 130 days that northern resident whales were observed, pods were

alone on only 39 occasions (30%). The average number of pods present in the northern community per encounter was 2.81 (range = 1-10, sd = 1.79). When foraging in the same vicinity, members of different pods may either mix or remain separate. Movements of the pods are usually closely coordinated.

Foraging bouts averaged 2.59 h in duration (range = 0.45-7.4, sd = 1.50) (Fig. 4). Rates of group progression varied from 3.1 to 10.2 km/h, with a mean of 6.0 km/h (sd = 1.48, n = 107 bouts; Fig. 5). Dive times during foraging tend to be short, averaging 0.34 min (sd = 0.20, n = 89; Fig. 6). While swimming, individuals will sometimes make 2 or 3 short, shallow dives followed by a longer, 1-2 min dive. Other behaviours noted during foraging include occasional breaches, tail and flipper slapping, spyhops (vertical raising of the head above the surface), and play or 'socializing' activities in subgroups.

B) Travelling

A pod was considered to be travelling when all its members were moving on the same course and at the same speed, and there was no evidence of feeding.

Travelling whales tend to be less dispersed than while foraging. Often pod members line up abreast in a single cohesive group and dive synchronously for short periods (mean = 0.49 min, sd = 0.38, n = 19; Fig. 6). At other times, tightly-knit subgroups dive and surface independently while travelling in a line, often parallel to the shore. Aerial behaviour is generally restricted to porpoising during bursts of high-speed

Figure 4. Durations of activity bouts in northern-community resident killer whales. Bars represent means, lines above and below bars enclose 95% confidence intervals. Total sample = 208 activity bouts.

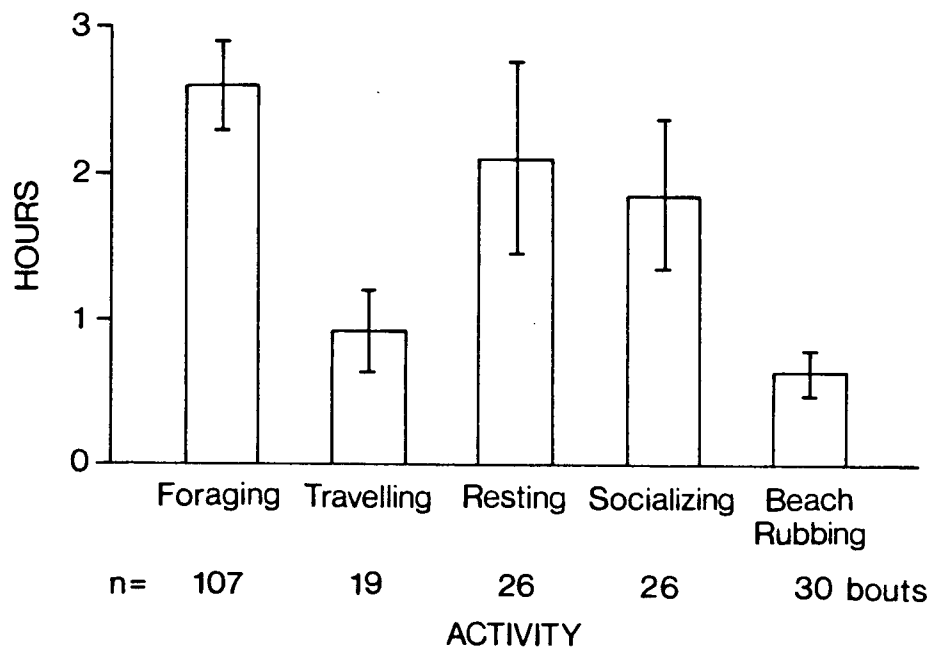


Figure 5. Speed of progression of northern-community resident whales during different activity states. Bars represent means, lines above and below bars enclose 95% confidence intervals. Sample sizes as in Figure 4.

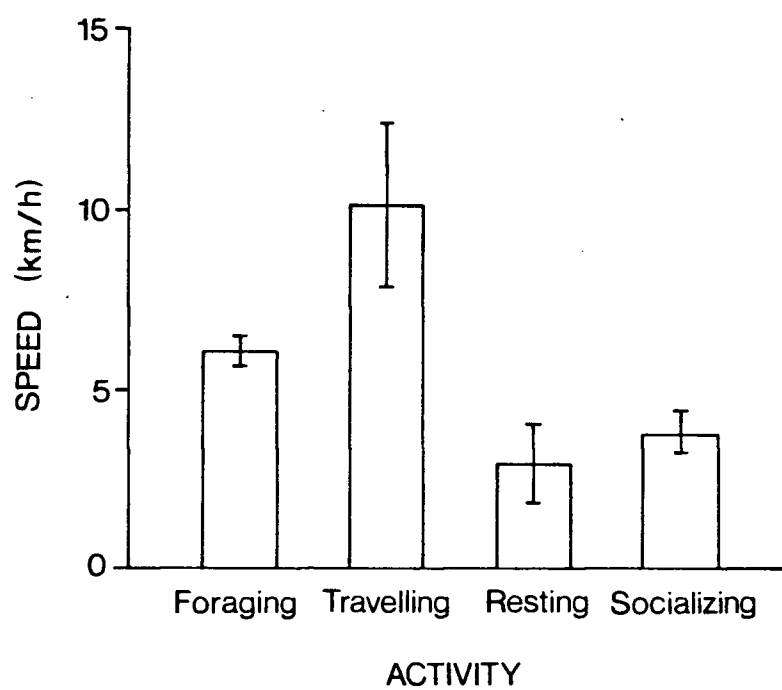
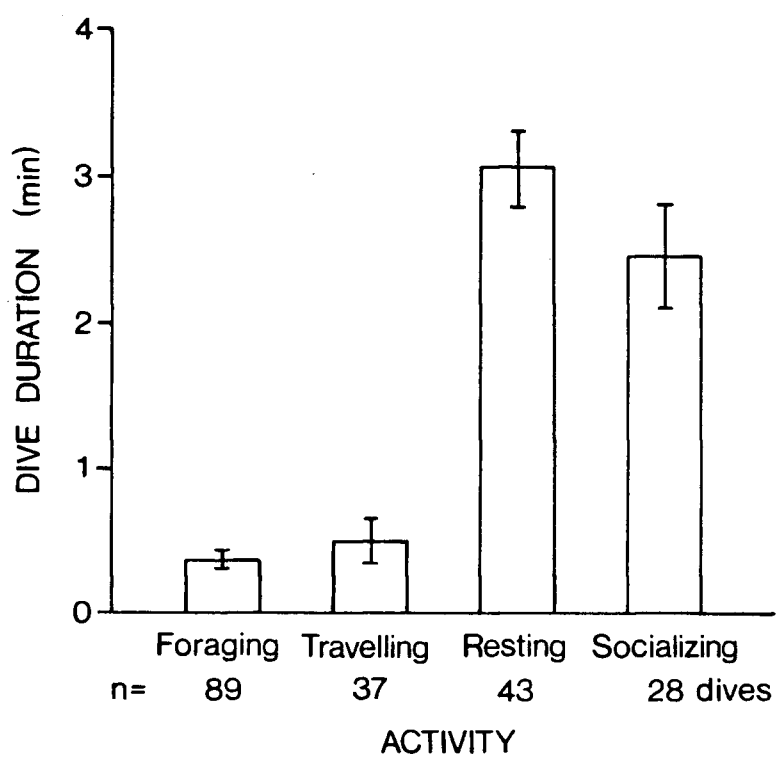


Figure 6. Durations of dives for northern-community resident whales in different activity states. Bars represent means, lines above and below bars enclose 95% confidence intervals.



swimming.

Travelling was the least common activity of northern resident pods, representing only 4.19% of the observed time (Fig. 3). Bouts of travelling were typically brief, averaging 0.92 h (range = 0.25-2.0, sd = 0.61, n = 19; Fig. 4). Distances of 2.0 to 6.7 km were covered (mean = 8.6, sd = 4.71) at speeds averaging 10.4 km/h (range = 6.5-20.4, sd = 3.7), significantly faster than foraging ($p < 0.001$, Scheffe's test; Fig. 5).

C) Group-Resting

Killer whales rest either in groups or individually. Group-resting accounted for 13.2% of the 416 h observation period. When group-resting, all members of a pod join together in a tightly-knit group, usually with animals lined up abreast. Dives and surfacings become highly regular and coordinated in the group. Long dives (mean = 3.07 min, range = 1.73-4.95, sd = 0.713, n = 43; Fig. 6) are interspersed with shorter periods at the surface (mean = 1.72 min, range = 1.07-2.97, sd = 0.41, n = 35). During each surface period the whales make between 2 and 5 respirations and shallow dives. Although the entire pod is generally underwater or at the surface together, members of maternal subgroups maintain close physical association and tend to coordinate their movements.

Bouts of group-resting in pods lasted from 0.5 to 7.5 h (mean = 2.1, n = 26). Progression tends to be very slow (Fig. 5). Typically, the whales travel less than 150 m during each long dive. Overall rate of travel during resting was 2.96

km/h (range = 0.93-6.4, sd = 1.41). On occasion, pods break their diving pattern and remain at the surface for as long as 15 min, slowly milling about.

D) Socializing

Socializing whales group together and engage in a variety of physical interactions and aerial activities. Animals chase each other, roll and thrash at the surface, and occasionally swim upside down. Sexual interactions are common, and erections are often visible among both subadult and adult males. Aerial behaviours are frequent, and may include breaches, spyhops, bellyflops, tailslaps, flipperslaps, dorsal-finslaps, and diverse forms of acrobatic leaps. Individuals may also play with inanimate objects such as floating kelp, and surf in the wake of passing vessels.

Most of these activities are especially prevalent and vigorous among younger whales. Adults often mill slowly or rest individually in the vicinity of frolicking juveniles. When resting, individuals stop swimming and lie quietly at the surface, usually for brief periods of < 2-3 min. During this time they breathe slowly and gradually sink. Once its blowhole passes beneath the surface, a resting whale will start moving once again.

Bouts of socializing lasted an average of 1.86 h (range = 0.25-5.25, sd = 1.23, n = 26), and accounted for 11.65% of the overall behaviour observations (Fig. 3). Many aspects of the group's spacing and movements are similar to group-resting.

Socializing whales usually coalesce into a single group and dive together for relatively long periods (mean = 2.45 min, sd = 0.52, n = 28; Fig. 6). Group progression is usually slow, (mean = 3.80 km/h, sd = 1.5, n = 26 bouts), but occasionally speeds of 10-15 km/h are attained in highly active pods. Socializing occurs periodically in subgroups of pods engaged in foraging, travelling, or beach rubbing behaviour.

E) Beach Rubbing

Beach rubbing was observed regularly among pods of the northern resident community, representing 4.5% of the group activities. This behaviour was seen primarily in the Johnstone Strait area (Fig. 12, Part II), where pods frequently interrupt foraging sessions with visits to a specific 0.5 km section of shoreline on Vancouver Island in order to rub. This area is comprised of two small beaches and an underwater shelf some 3-6 m deep. The beaches and the shelf are covered in small (1-5 cm) smooth pebbles, which are relatively uncommon in the region. Rubbing was observed occasionally at other gravel beaches (see also Thomas 1970), but only sporadically.

Animals rub by diving to the bottom and rolling their lateral, dorsal and ventral surfaces against the pebble shelves for approximately 0.25-1.5 min before surfacing again. Large bursts of air are often released during dives, probably to reduce buoyancy. Rubbing may be accompanied by individual resting and socializing among nearby animals. Periods of rubbing varied from several minutes to as long as 1.5 h (mean =

0.62 h, $sd = 0.4$, $n = 30$ bouts, Fig. 4).

Beach rubbing is common among northern-community resident pods, especially for pods A1, A4, and A5. However, resident whales in the southern community have never been observed beach rubbing, despite many hours of intensive observation (R. Osborne, Moclips Cetological Society, pers. comm.; M. Bigg, pers. comm.; this study).

3. Sounds Produced During Different Activities

The following section describes the patterns of occurrence of the major sound categories (introduced above) among resident killer whales engaged in the activities outlined above. The context and use of specific discrete call types is discussed in Section 4.

A) Foraging

Sounds produced by foraging killer whales include echolocation-type clicks, whistles, and both discrete and variable pulsed calls.

'Echolocation' clicks are produced commonly during foraging activity, presumably to locate and catch food. Normally, several simultaneous click series, each at different repetition rates, can be heard as a pod approaches. Click repetition rates are generally less than 25/s, but occasionally go higher, apparently when whales are scanning objects acoustically at close range (Norris et al. 1967). Intense click bursts

reaching repetition rates of 200-300/s were often recorded when animals approached to within a few m of the hydrophone.

Social signals produced by foraging killer whales are dominated by discrete pulsed calls. In recordings of northern resident pods A1, A4, and A5 while foraging, this sound category accounted for 95.2% of calls produced (Fig. 7). Of the remaining signals, 4.3% were variable pulsed calls and 0.5% were aberrant renditions of discrete call types. Whistles are given infrequently by foraging killer whales. However, they are heard, along with variable and aberrant calls, when socializing occurs within subgroups of foraging pods.

The rate of calling is highly irregular during foraging. Calls may be produced rapidly at rate of 25-50/min, or sporadically at rates of < 5 /min. Periods without calling may prevail for a few min to > 1 h. It is often very difficult to predict from the surface behaviour of foraging animals when they will be calling and, if so, at what rate. Whales foraging quietly may abruptly begin calling for several minutes then subside into silence once again, all without any obvious change in behaviour. The rate of calling varies to some extent with the number of whales in the area. Small pods (< 10 members) foraging alone usually call intermittently at rates of < 15 calls/min and often spend the majority of time in silence. Aggregations of several pods (> 30 animals) tend to call more consistently and at higher rates.

Changes in the direction of progression of a foraging pod often occur quickly and involve all members of the group. These

Figure 7. Frequency histogram of discrete, variable and aberrant call occurrence during four activity states of pods A1, A4 and A5. Significant differences determined from ANOVA with Scheffe's test as follows:

Discrete Calls:

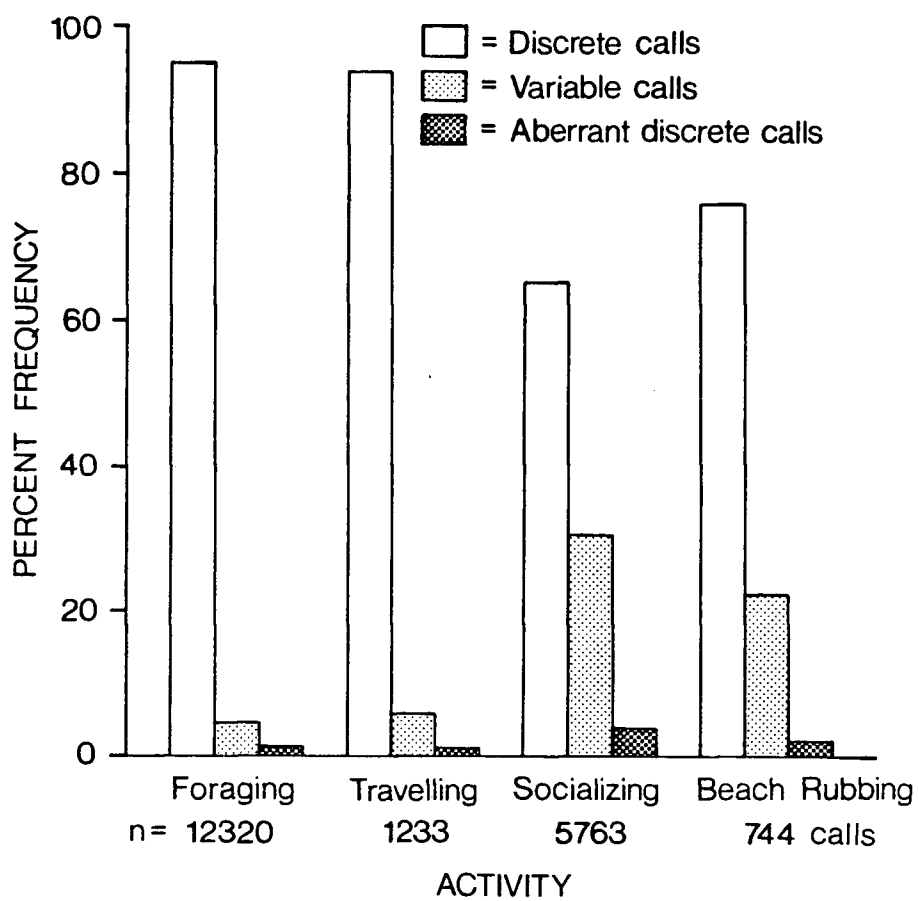
Foraging and travelling > socializing ($p < 0.001$)
Foraging and travelling > beach rubbing ($p < 0.05$)

Variable Calls:

Socializing and beach rubbing > foraging ($p < 0.001$)
Socializing > travelling ($p < 0.001$)
Beach rubbing > travelling ($p < 0.05$)

Aberrant Calls:

Socializing > foraging and travelling ($p < 0.001$)



turns are typically accompanied by calling. Some synchronous turns were observed immediately following the onset of calling after an interval of silence. Others took place during periods of constant calling, with no increase or decrease in call rate apparent either before or after the turn. A few turns were carried out in the absence of any detectable calls.

Bouts of calling within a foraging pod appear to represent exchanges of signals among its scattered members. Often, calls in a series are heard at widely different intensities and with different reverberation patterns, suggesting the involvement of several animals at different locations. Stereophonic recordings reinforced this impression.

A number of instances of individual whales and subgroups taking salmon were observed and monitored acoustically at close range. In each case, the animals were silent while pursuing the fish, except for periodic bursts of echolocation-type clicks. The whales generally resumed calling only after making the kill.

B) Travelling

Vocalization usually occurs at high rates while travelling. Rates in excess of 50 pulsed calls/min were recorded from pods A1, A4 and A5 while travelling together. Complete silence was observed on a few occasions when a pod was travelling rapidly as a compact group, diving and surfacing simultaneously.

The proportions of different pulsed sound types did not differ significantly from those in foraging contexts (Fig. 7). Overall, 94.0% were discrete calls, with the remainder made up

of variable (5.8%) and aberrant (0.2%) calls. The latter two sound types, along with whistles, were heard only when socializing activities accompanied travelling behaviour.

C) Group-Resting

Group-resting behaviour is generally accompanied by low levels of vocal activity. In most cases, resting whales become completely silent, except for sporadic clicks. On other occasions, almost continuous low-level whistling can be heard from resting pods, but only within 100-200 m of the group. At times, discrete calls are given, generally at low rates of < 20/min, in addition to quiet whistling.

Sound production during group-resting varies with the animals' state of arousal. Fully resting whales, grouped tightly and diving as a single unit, are most often silent. Whales that are resting "lightly", or are at somewhat higher levels of arousal, are more likely to emit whistles and calls. Spatial cohesion is looser at such times, but pod members still tend to synchronize dives and surfacings. As will be shown in Section 4, certain discrete call types predominate in, but are not exclusive of, these low-arousal contexts.

Group-resting bouts terminate with either abrupt or gradual transitions into other activity categories. Protracted changes into socializing are accompanied by increases in whistling and variable and aberrant call production. Foraging behaviour often develops slowly from group-resting as pod members scatter and become asynchronous in their diving. Concurrent vocal behaviour

at such times shifts from silence or low-arousal discrete calls to call types typical of foraging activity. Abrupt transitions from group-resting to foraging were always accompanied by the sudden onset of vocalization involving a variety of discrete call types.

D) Socializing

Whales tend to be very vocal while socializing. Periods of silence are both brief and infrequent. Variable calls and aberrant versions of discrete calls and whistles are used more often during socializing activities than while foraging or travelling (Fig. 7). Variable calls comprised 30.5% of social signals given by socializing A-pods, compared to 4.3% and 5.8% during foraging and travelling, respectively. The proportion of variable calls reached almost 100% for brief (< 5 min) periods during intense socializing. Aberrant calls, relatively uncommon in any context, were significantly more frequent during socializing (4.0% of calling) than foraging (0.5%) and travelling (0.2%) (Fig. 7). Whistles are abundant throughout most socializing bouts. Often, they are the only signals produced while a socializing pod is underwater. Calling with pulsed signals resumes once the whales return to the surface.

E) Beach Rubbing

Sound production during beach rubbing activities is similar to that in socializing contexts, although the rate of calling tends to be more variable. Whales often lapse into silence

while slowly rubbing, or emit occasional low-arousal discrete calls and whistles. When animals are rubbing vigorously, call rates increase to levels comparable to other activities.

As in socializing, the use of variable pulsed calls is greater than in foraging and travelling (Fig. 7). Aberrant calls appear to be more frequent, although not to a statistically significant extent, and whistles are also common. Loud, broadband sounds caused by animals pushing and sliding through the loose pebbles are heard throughout rubbing episodes.

The above analyses indicate that the abundance of variable calls, aberrant calls, and whistles is directly related to the degree of social activity within pods. Highly social behaviours such as beach rubbing and the various interactions during socializing bouts are accompanied by the greatest incidence of these sound types. Such signals are rarely heard from foraging or travelling groups unless some animals (often juveniles) are physically interacting or playing nearby. As the proportion of members engaged in social activities increases, so too do these sounds.

4. Correlation of Discrete Call Types with Activity Context

Although most resident pods have quite different repertoires of discrete calls (Part II), the manner of call use by these groups is, in most cases, very similar. Three pods, A1, A4 and A5, were selected from the 16 resident pods recorded for detailed analysis of correlation between discrete call occurrence and behaviour. These pods were the most commonly

observed and recorded in this study, accounting for 234 (54.9%) of the 426 resident pod encounters. Examples are also drawn from the acoustic behaviour of certain other resident pods.

The following description includes all five major activity categories discussed above, as well as three additional contexts not previously defined. These are (1) large aggregations of pods, (2) instances of pods meeting, and (3) cases of very high arousal or excitement.

The Call Repertoire of the A-pods:

Pods A1, A4 and A5 contained 14, 7 and 12 individuals, respectively, in 1983. Details of age and sex compositions are given in Part II. The three groups are very closely associated. On the 110 days that one or more of the A-pods were encountered, all three were present on 43 occasions (39.1%), two were together on 25 days (22.7%), and on 42 days (38.2%) only a single A-pod was present. This close association is reflected in their very similar repertoires of discrete calls. The three pods together share 10 call types, N2, N3, N4, N5, N7, N8, N9, N10, N11 and N12. Pods A1 and A4 produce a further call, N1, which is not given by A5, while A4 and A5 share call N13, not produced by A1 pod. Pods A4 and A5 each have an additional pod-specific call type, N19 and N17, respectively. Finally, two more calls, N27 and N47, are given by A1 pod alone. For descriptions and illustrations of these and other resident pod call types, as well as an explanation of the call numbering system, see Part II.

Based on comparisons of calls given in a standard foraging context, I determined that pods A1, A4 and A5, in addition to having pod-specific calls, differ significantly in their frequency of use of 6 of the 10 shared call types (Part II). For this reason, only those encounters where all three A-pods were present were used in the call occurrence versus activity analyses. Calls N13, N17, N19, N27 and N47 were excluded from statistical comparisons owing to their low rate of occurrence in any context.

Call Repertoires of Individual Whales:

From field recordings using a single, omni-directional hydrophone, it is difficult to determine which animals are producing sounds. One of the main questions which arose early in the study was, does each member of a pod produce the entire repertoire of discrete calls that is recorded in the presence of the group? Calls recorded from individuals travelling and vocalizing at some distance from their pod suggested that this is the case. For example, one short recording of an adult male, B2, swimming alone contains all but one call type in the 10-call repertoire of B pod - the missing call (N20) is uncommon, comprising only 4.1% of the call production of the pod (Part II).

Further evidence is contained in recordings of 6 captive killer whales, provided by M. Dahlheim and D. Bain. These whales, 4 females and 2 males, were taken from 2 captures in 1968 and 1969, at Pender Harbour, B.C. The 1969 capture is

known to have involved A5 pod (Bigg 1982), but there is no photographic documentation of the pod taken in 1968. However, judging from calls produced by individuals from the earlier capture, A5 pod was involved in this case as well.

The calls given by the 6 captive whales are listed in Table I. A total of 10 calls was recorded, but not all were present in the short samples available for each individual. All 10 call types are commonly given by all three A-pods, but structural variations in call N9 (see Part II) are typical of A5 pod alone. Calls N13 and N17, two uncommon calls which amount to 1.4% and 2.8%, respectively, of A5-pod's recent call production (Part II), were not given by any of the 6 whales. The important feature to note, however, is that no call in Table I was given exclusively by one sex.

A) Foraging

The frequency of occurrence of all 16 discrete call types during foraging contexts was determined from 67 10-min periods sampled from 27 encounters with the three A-pods between July, 1978, and August, 1981. Frequencies were calculated independently for each sample time-period, and the descriptive statistics of these values are listed in Table II.

Five call types, N2, N4, N5, N7 and N9, were consistently the most abundant, being present in all 67 sample time-periods. Of these five calls, which together comprised 78.5% of overall call production, call N4 was the most common (31.2%) and N5 the least (9.2%). Of the remaining 11 calls in the repertoire, 4

Table I. A-pod call types produced by captive whales. Recording of "Bonnie" provided by D. Bain. All others provided by M. Dahlheim. Whales were sampled from two captures, March, 1968, and December, 1969, at Pender Harbour, B.C. The second capture was determined by Bigg (1982) using photographic evidence to have involved A5 pod.

Name	Sex	Capture	Oceanarium*	Call									N12
				N2	N3	N4	N5	N7	N8	N9	N10	N11	
Orky	M	1968	ML	X	X	X	X	X	X	X	X	X	
Bonnie	F	1968	MW	X		X		X	X	X	X	X	X
Kianu	F	1968	MW	X	X	X		X	X				
Corky	F	1969	ML	X	X	X		X	X	X	X		
Yaka	F	1969	MW	X	X	X	X	X	X	X			X
Nepo	M	1969	MW	X	X	X		X	X	X			X

* ML = Marineland of the Pacific, California
 MW = Marine World Africa U.S.A., California

Table II. Frequency of occurrence of discrete call types produced by pods A1, A4 and A5 while foraging. Sample size (n) is number of 10-min sample periods containing one or more examples of each call, out of a total of 67 time periods. Descriptive statistics based on proportions calculated independently for each sample period.

Call	n (%)	Mean	SD	Min	Max
N1	62 (92.5)	4.15	3.62	0	17.90
N2	67 (100)	12.24	5.80	2.25	40.98
N3	40 (59.7)	3.14	4.72	0	27.06
N4	67 (100)	31.21	9.31	9.09	54.54
N5	67 (100)	9.21	4.70	1.61	21.81
N7	67 (100)	11.12	5.58	1.63	24.18
N8	63 (94.0)	4.40	2.90	0	13.75
N9	67 (100)	14.73	6.64	0.82	34.17
N10	61 (91.1)	2.67	2.05	0	10.91
N11	37 (55.2)	1.86	1.51	0	6.34
N12	62 (92.5)	4.31	3.20	0	14.92
N13	40 (59.7)	0.81	1.08	0	5.64
N17	28 (41.8)	0.94	1.73	0	7.73
N19	19 (28.4)	0.27	0.63	0	3.16
N27	13 (19.4)	0.22	0.51	0	2.24
N47	41 (61.2)	1.79	2.87	0	16.48

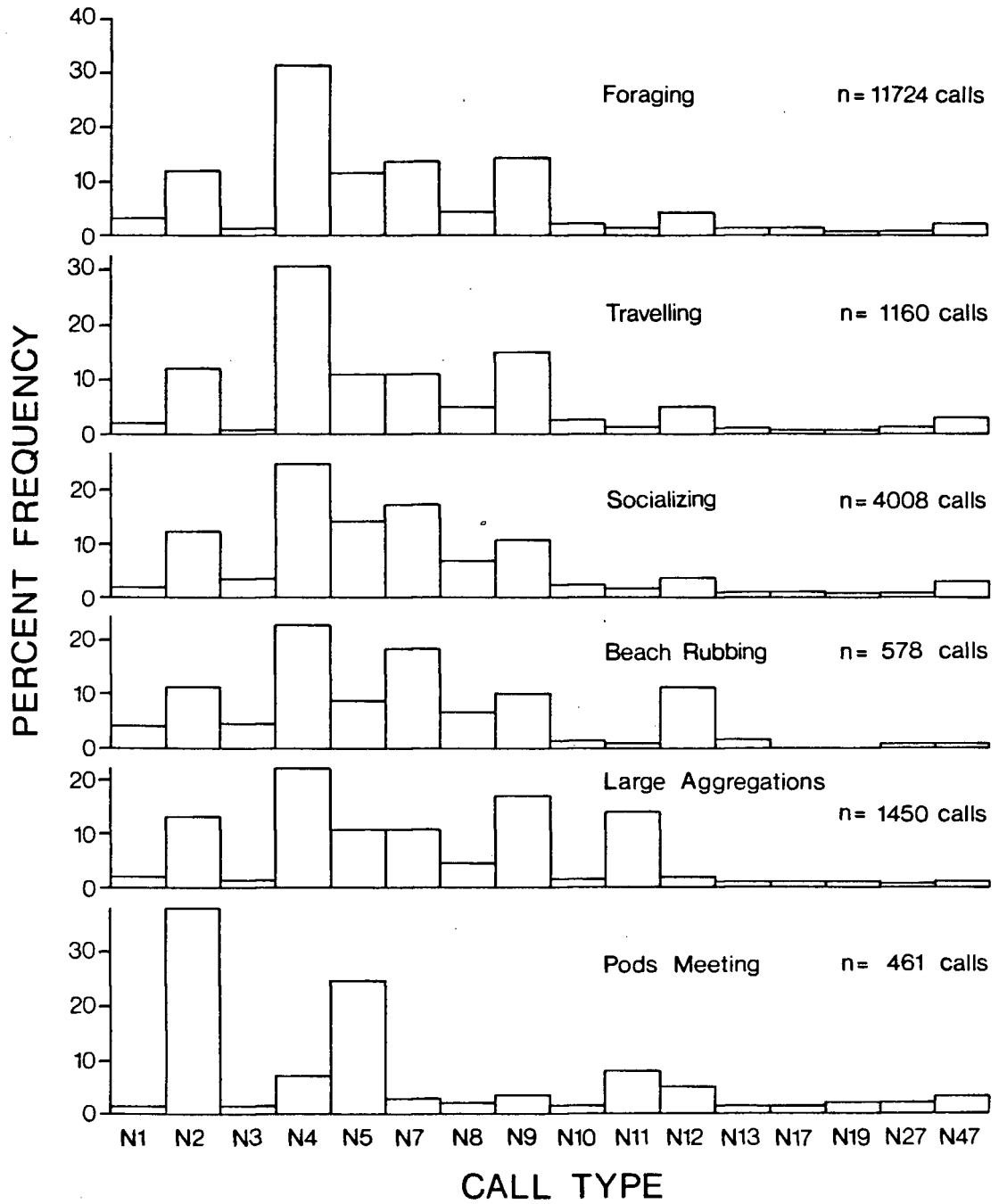
(N1, N8, N10 and N12) were recorded in > 90% of the time periods, while only 3 calls (N17, N19 and N27) were represented in < 50% of the samples.

B) Travelling

Five 10-min time periods, containing 1160 calls, were sampled from travelling episodes involving pods A1, A4 and A5. The frequency distribution of these calls is shown in Fig. 8. There were no statistically significant differences in the occurrence of call types between foraging and travelling contexts (Table III).

In contrast to this situation, however, pods J and L of the southern resident community appear to change markedly the nature of discrete call use when travelling. Pod J, for example, has a total repertoire of 17 call types (see Part II for a description of these calls). During foraging, exchanges were dominated by call S1 (52.4%), followed by S4 (16.6%) and S7 (6.2%). While travelling, however, S2, S44 and S42 became the predominant calls, comprising 38.3%, 19.2% and 14.5% of the total, respectively. Analyses of variance were applied to proportion data for calls S1, S2, S3, S4, S7, S42 and S44 to determine the significance of these differences (other call types occurred too infrequently in one or both contexts to warrant analysis). A total of 30 10-min time periods was sampled from foraging bouts and 9 time periods from episodes of travel. All 7 call types differed at the $p < 0.001$ level. The reason for this difference in the patterns of vocal activity between southern and northern

Figure 8. Frequency histograms of discrete call types produced by pods A1, A4 and A5, during different activity states. Group resting is not shown because of near total reliance on the N3 call category during vocal bouts. Significant differences in call occurrence between pairs of activities shown in Table III.



communities is not known.

C) Group-Resting

As mentioned previously, group-resting whales are either silent, or produce whistles and discrete calls. In the case of pods A1, A4 and A5, these discrete calls consist almost entirely of call N3, with occasional use of N12, a call related in structure to N3. Bouts of exclusive N3 calling extend into other contexts with low-arousal levels. An example is when pods cruise slowly in what appears to be a state intermediate between resting and foraging. N3's are also heard from subgroups resting in the presence of active whales, especially during socializing activities. It should be noted that N3 calls are given occasionally in apparent high-arousal contexts such as active foraging and travelling (Fig. 8).

Low-arousal, or resting calls are produced by most resident pods. Usually only 1 or 2 different call types are used, but in the case of 3 acoustically-similar pods G, I11 and I31, a total of 6 calls occur predominantly in low-arousal contexts. At the opposite extreme, no calls characteristic of resting were identified for J pod of the southern resident community. On the 7 occasions group-resting was observed in this pod, the animals were silent. Similar observations were made by Hoelzel and Osborne (in press) and R. Osborne (pers. comm.) for resting in southern pods.

D) Socializing

As described previously, only 65.5% of the social signals given by the A-pods while socializing were discrete calls, with the remainder made up of variable and aberrant calls. An examination of the distribution of discrete call types from 23 10-min time periods sampled from socializing contexts (Fig. 8) reveals several significant differences (Table III). Calls N3, N5, N7, N8 and N11 were given more frequently than during foraging, and of these, N3 also occurred more often than while travelling.

E) Beach Rubbing

Of the signals present in 5 10-min time periods recorded during beach rubbing, 75.8% were discrete calls. Call type occurrence did not differ from foraging, travelling, or socializing, with the exceptions of N3 and N12. Call N12 comprised 10.9% of the total, higher than in any other context (Fig. 8), although the differences were significant only for foraging, socializing and large multi-pod aggregations (Table III). Call N3 was more common during beach rubbing than during foraging or travelling.

F) Other Contexts

Table III. Differences in call occurrence during activity categories. Significance levels based on one-way ANOVA with Scheffe's pair-wise comparison of means.

F = Foraging
T = Travelling
S = Socializing
BR = Beach Rubbing
LA = Large Multi-Pod Aggregations
PM = Pods Meeting

Call	Significance level		
	p < 0.001	p < 0.01	p < 0.05
N1	---	---	---
N2	PM > S	PM > F PM > LA	PM > BR PM > T
N3	---	---	S > F S > T BR > F BR > T
N4	---	F > PM	T > PM
N5	---	---	PM > BR
N7	---	---	S > F S > PM
N8	---	---	S > F
N9	---	---	LA > PM
N10	---	---	---
N11	LA > BR LA > F LA > S LA > T	S > F	PM > F
N12	BR > LA	---	BR > F BR > S

Large Aggregations:

To examine the effect of large multi-pod aggregations on call production of the A-pods, samples were drawn from 3 encounters where 5 or more additional pods were present in the immediate area. These encounters included representative pods from the two other main dialect groups of the northern resident community (see Part II). On one of the three occasions, 7 pods accompanied the A-pods, creating an assemblage of more than 100 whales. At such times, vocal activity was intense and call identification was made difficult due to frequent overlapping of calls.

The distribution of 1450 A-pod calls identified in 11 10-min time periods is generally similar to those described above for other activities (Fig. 8). A major difference, however, can be seen in call N11, an uncommon call in most contexts, which comprised 14.1% of the total calls produced during large-aggregation contexts. This is significantly greater ($p < 0.001$) than all contexts except pods meeting, described below. The only other difference seen is in call N9, which occurred more frequently ($p < 0.05$) than during the pods-meeting context (Table III).

Pods Meeting:

On occasion, pods or groups of pods which had been travelling independently approached and met each other, with a wide range of behavioural responses. Often one of the two groups changed its course and joined the other, sometimes

changing its activity to that of the pod it was joining. Meetings among the three closely-related A-pods usually occurred with little change in group activities or level of arousal. However, meetings between the A-pods and other northern resident groups were often accompanied by a dramatic change in behaviour and high levels of excitement. Sounds were sampled from one of these active meetings to investigate the A-pods' call use in this context.

The meeting analyzed here involved the A-pods and B pod, a fellow northern resident group of 8 whales. It can be considered representative of a high-arousal meeting. Calling was extremely intense throughout the meeting, at times reaching rates of 90-95 calls/min. The frequency distribution of A-pod discrete calls recorded during two 10-min samples from this meeting are shown in Fig. 8. Call N2 was by far the most abundant call, comprising 38.2% of the total. This proportion was significantly greater than in any other activity category (Table III). Calls N5 and N11 were also relatively abundant during the meeting context. Discrete calls produced during high-arousal meetings and excited contexts in general (see below) tend to be emitted rapidly (i.e., shorter duration) and at higher pitches (Fig. 9). Frequency and duration measurements for call N2 during excited versus foraging contexts are described in Table IV. Most duration measurements are significantly shorter in the excited versions and sideband intervals (directly related to pitch) are higher.

Figure 9. Examples of calls N2 and N16 given in typical and excited forms.

A = Call N2, produced by pods A1, A4 and A5

B = Call N16, produced by B pod

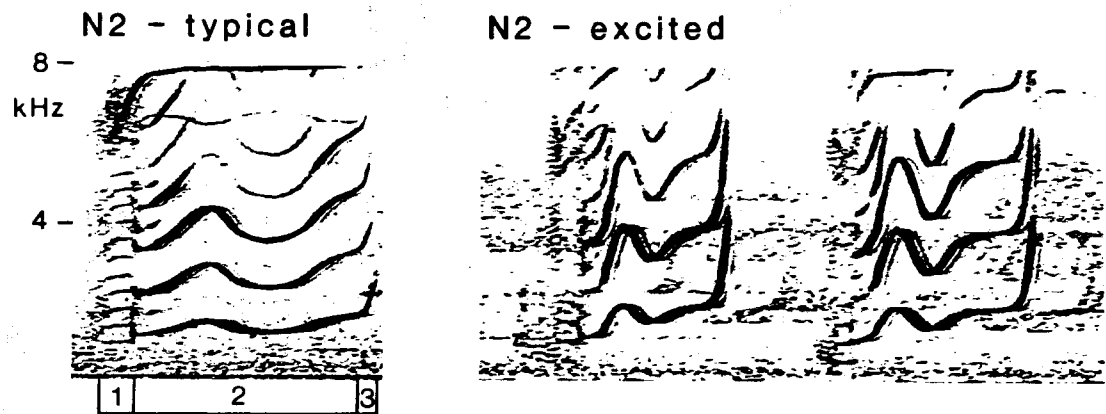
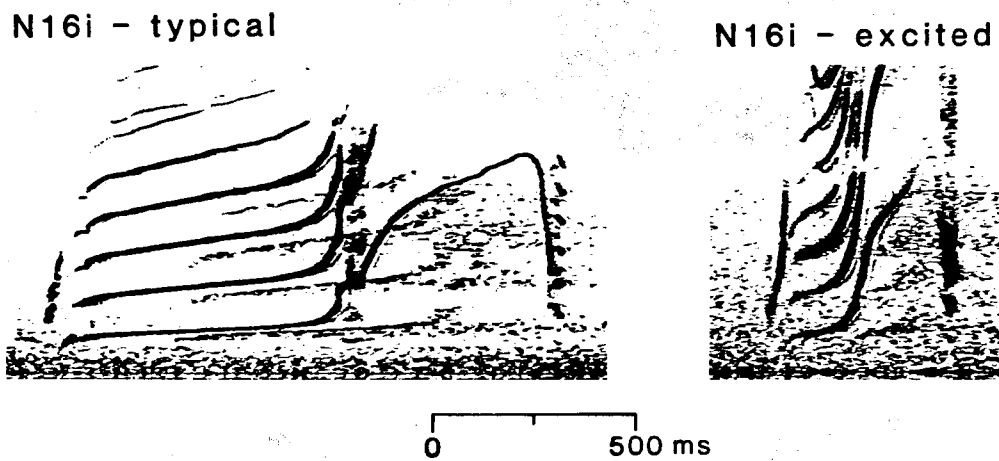
A.**B.**

Table IV. Comparison of call N2 structure during normal versus excited contexts. The different subdivisions, or 'parts' of the call are identified in Figure 9.

Abbreviations:

Nor = normal renditions sampled from pods A1, A4 and A5.

Exc = excited renditions from encounter with same pods.

SBI = sideband interval

f = frequency

Measurement	Type	Mean	C.V.	Min	Max	n	p
Duration (ms)	Nor	680	19.4	468	1066	86	<0.001
	Exc	424	13.3	315	502	30	
<u>Part 1:</u>							
Dur (ms)	Nor	58	34.5	16	395	86	ns
	Exc	50	32.4	19	81	30	
SBI (Hz)	Nor	481	13.1	291	611	71	ns
	Exc	471	11.4	355	562	30	
<u>Part 2:</u>							
Dur (ms)	Nor	612	19.9	415	1001	86	<0.001
	Exc	374	17.1	259	470	30	
SBI, start (Hz)	Nor	1099	10.2	830	1419	86	ns
	Exc	1088	7.2	873	1246	30	
SBI, 1st peak (Hz)	Nor	1567	11.8	1179	2098	86	<0.001
	Exc	1971	9.1	1747	2350	30	
SBI, end (Hz)	Nor	1819	16.5	1418	2766	85	<0.001
	Exc	2419	32.2	1695	4951	30	
time to 1st peak (Hz)	Nor	138	34.6	56	265	86	ns
	Exc	110	13.2	64	148	30	
<u>Part 3:</u>							
Dur (ms)	Nor	63	32.9	27	127	60	<0.05
	Exc	52	23.8	28	71	22	
f, SB2, end (Hz)	Nor	6389	8.4	4825	7544	82	<0.001
	Exc	7429	12.0	6051	9861	22	
<u>Tone:</u>							
f, start (Hz)	Nor	6389	8.4	4825	7544	82	ns
	Exc	6148	12.2	3448	7058	25	
f, midpoint (Hz)	Nor	7609	13.2	2418	8081	65	ns
	Exc	8126	2.4	7794	8712	22	

Excitement:

Conditions of intense arousal or excitement were observed occasionally during all activity categories. Most cases involved sudden physical interactions between animals, often subadults, both at the surface and underwater. Individuals were seen to chase or lunge at each other, and collisions and slapping were also noted. Very likely many of the fresh body wounds and healed scars that are obviously made by killer whale teeth result from such apparent altercations or rough play.

Discrete calls, given in short and high-pitched forms as described above, were frequent during heightened excitement. Equally characteristic, however, were distinctive series of intense signals with rapid up and down pitch modulations (Fig. 10). These "excitement calls" generally contained from 1 to 20 modulations in series. In a sample from the A-pods, modulations lasted an average of 180 ms (sd = 55.4, n = 15) and were separated by brief gaps of 15-132 ms (mean = 60 ms, sd = 40.8, n = 15). Each modulation began at an average pulse rate of 700 Hz (sd = 155.0, n = 30) which increased rapidly to a peak of 1150-2910 Hz (mean = 1854 Hz, sd = 527.7, n = 30), then fell off again to a mean of 650 Hz (sd = 105.83, n = 18).

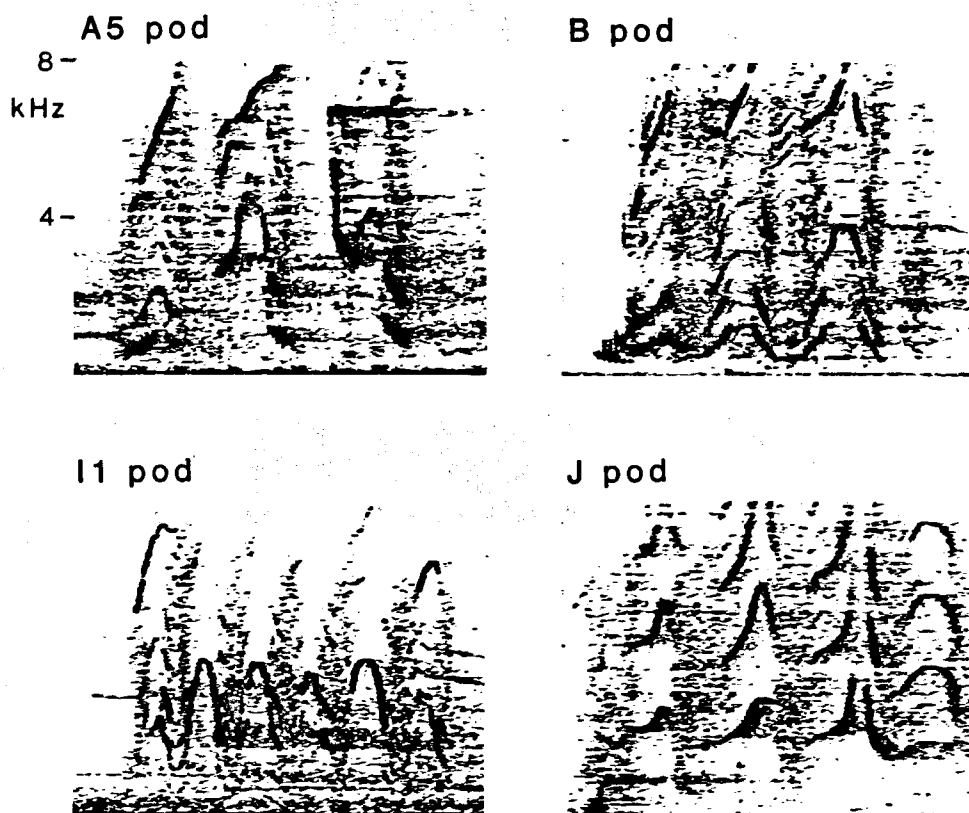
Excitement calls with similar structure were recorded from many pods, including members of both resident communities. At times, rapid series of short discrete calls graded into excitement calls through intermediates that contained characteristics of both signal types (Fig. 10). This was noted both in field encounters and recordings of captive animals.

Figure 10. Spectrograms of "excitement calls" and call type N1iv modified by high arousal.

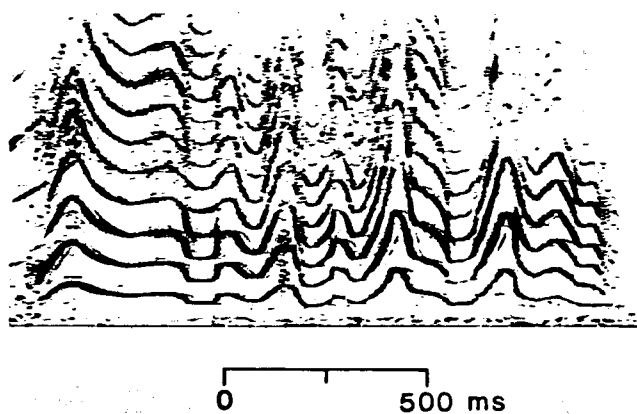
A = Excitement calls produced by northern resident pods A5, B, and I1, and southern resident pod J.

B = Call N1 produced by H pod, grading into an excitement call.

A. Excitement calls



B. Call N1iv, grading into excitement call



Excitement calls were heard occasionally during episodes of rapid travelling and during violent physical interactions between individuals.

5. Patterns of Discrete Call Occurrence

From preliminary analysis of recordings, it became clear that discrete calls often occur in repetitive series and that at least some call types tend to be given in close association by individuals (Ford and Fisher 1983). A complete understanding of call production patterns is confounded the difficulty of identifying individuals making sounds from omni-directional recordings. At any given time, one generally hears several different call types being produced and, apparently, responded to by an unknown number of whales in unknown positions. Thus, accurate description of the manner in which calls are exchanged within a pod must await recordings which allow accurate location and identification of sound sources (e.g., Clark and Clark 1980).

To examine further the associations of call types, a transition analysis was performed on sequences of calls recorded from the A-pods while foraging. This analysis is complicated by the same factors described above. A recorded sequence of calls is likely to include simultaneous call exchanges within several subgroups of whales. The animals may be engaged in different behaviours or may be at different levels of arousal. Because of this lack of stationarity in the data, the analysis was restricted to first-order transitions only (Slater 1973).

Contingency table analysis of the transitions among 9 common calls recorded from the A-pods are presented in Table V. Calls N3, N11, N13, N17, N19, N27, and N47 are not included due to their low frequency of occurrence. A test of overall heterogeneity of the transitions revealed that there are highly significant dependencies among the calls ($G = 2867.9$, $df = 64$, $p < 0.001$). Table V shows two clear trends among the transitions. First, a given call type is most likely to be followed by a repetition of the same call. Thus, calls tend to occur in series. This is true for all calls except N8, which shows no significant positive or negative tendency to occur repetitiously. Second, calls N7 and N8 are closely associated in that N8's both follow and precede N7's more often than expected. This reflects the fact that N7's and N8's are generally given together by individuals, with N8's following N7's by an average of 2.1 s (Ford and Fisher 1983). Not all N7's are followed by N8's, but N8's never occur without first being preceded by one or more N7's. The significantly higher incidence of N8 to N7 transitions (Table Vb) results from the frequent simultaneous (but asynchronous) emission of N7/N8 pairs by several animals.

To further investigate the interrelationships of different call types, transitions between repetitions of the same call (the descending diagonal in Table Va) were eliminated to remove the strong influence of these transitions on other interactions (Slater 1973, 1983). This test demonstrated that associations among the nine calls examined are highly significant (chi-square

Table V. Contingency table analysis of transitions between common call types of pods A1, A4 and A5.

A. Transition frequency matrix for 9698 call transitions.

B. Transition matrix showing significant departures from a random model at the $p < 0.05$ level of significance (contingency table analysis using the G-statistic) for the data above.

+ = observed > expected

- = observed < expected

ns = no significant difference

A.

		FOLLOWING CALL									
		N1	N2	N4	N5	N7	N8	N9	N10	N12	
PRECEDING CALL	N1	88	33	104	35	37	6	47	12	4	366
	N2	45	361	365	95	148	26	156	30	35	1261
	N4	111	360	1486	302	289	47	404	73	126	3198
	N5	38	117	262	278	90	11	116	20	32	964
	N7	24	117	228	67	292	365	111	14	46	1264
	N8	11	51	113	47	107	32	64	8	30	463
	N9	46	138	425	110	134	19	522	43	56	1493
	N10	9	23	78	26	19	1	32	41	12	241
N12	11	41	124	24	80	3	49	8	108	448	
		383	1241	3185	984	1196	510	1501	249	449	9698

B.

		FOLLOWING CALL								
		N1	N2	N4	N5	N7	N8	N9	N10	N12
PRECEDING CALL	N1	+	-	ns	ns	ns	-	ns	ns	-
	N2	ns	+	-	-	ns	-	-	ns	-
	N4	ns	-	+	ns	-	-	-	ns	-
	N5	ns	ns	-	+	-	-	-	ns	-
	N7	-	-	-	-	+	+	-	-	ns
	N8	ns	ns	-	ns	+	ns	ns	ns	ns
	N9	ns	-	-	-	-	-	+	ns	ns
	N10	ns	ns	ns	ns	ns	-	ns	+	ns
	N12	ns	ns	-	-	-	-	-	ns	+

= 2415.1, $df = 55$, $p < 0.001$). All transitions were again tested for departure from randomness by reducing the matrix to a 2x2 contingency table about each pair. These analyses (Table VI) show that 17 of the 72 transitions (23.6%) were significantly more common than expected and 21 (29.2%) were less common (all at $p < 0.01$ or less). As expected, there is a tendency for many call types both to precede and follow N4's, the most abundant call in the repertoire (Fig. 8). The close association of N7's and N8's also affects the probability of transitions of these calls with others in the repertoire.

Another appraisal of call associations was obtained by summing preceding/following transitions for each call pair (Table Va) and calculating an index of association on the basis of this value (as described in Materials and Methods). These indices (Table VII) reflect the tendency for calls to occur together regardless of the order in which they are given. This analysis shows that calls N7 and N8 have the highest transition probability with an index value of 0.304, closely followed by transitions between repetitions of N4 at 0.303. These "self transitions" tend to have the highest association indices, as do transitions between most calls (except N7 and N8) and the common call N4.

The data in Table VII were used to create a cluster diagram of associations between different call types (Fig. 11). This again shows that N7 and N8 are strongly associated and that, to a lesser extent, calls N2, N4, N5 and N9 tend to occur together. Calls N1, N10, and N12 are weakly associated with other calls.

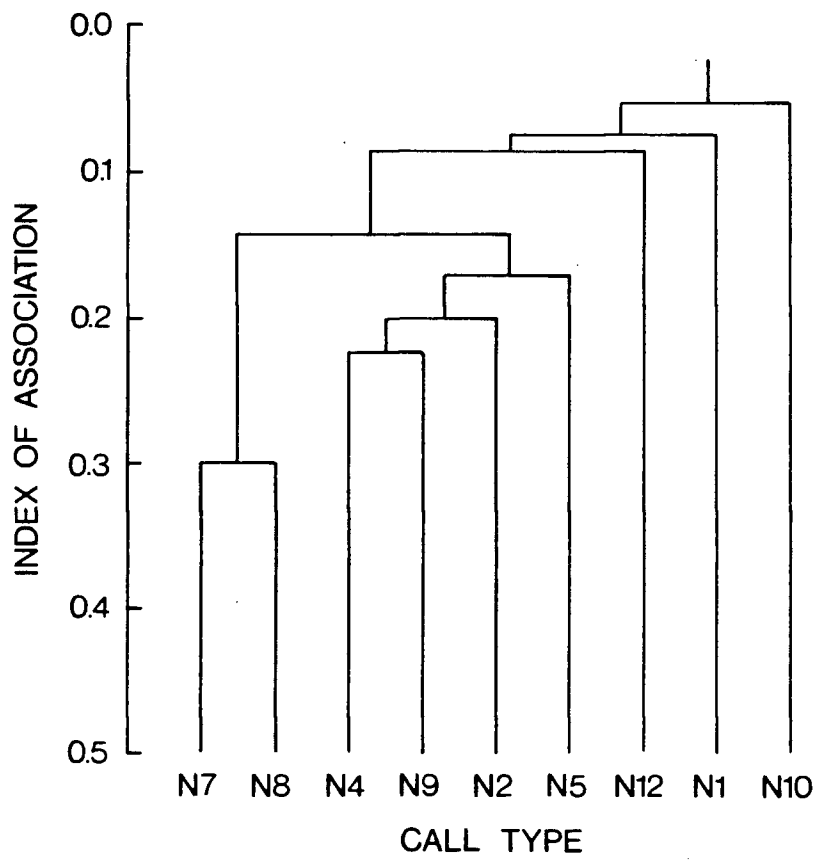
Table VI. Transition matrix of common A-pod calls showing significant departures from a random model. Analysis similar to that in Table VIb, except "self transitions" (the descending diagonal in Table IVa) is excluded, and each transition pair was tested using chi-square with significance level set at $p < 0.01$, as recommended by Chatfield and Lemon (1971).

		FOLLOWING CALL								
		N1	N2	N4	N5	N7	N8	N9	N10	N12
PRECEDING CALL	N1		ns	+	ns	ns	-	ns	+	-
	N2	ns		+	ns	ns	-	ns	ns	ns
	N4	+	+		+	+	-	+	+	+
	N5	ns	ns	+		ns	-	ns	ns	ns
	N7	-	-	-	-		+	-	-	-
	N8	-	-	-	ns	+		ns	-	-
	N9	ns	ns	+	ns	ns	-		ns	ns
	N10	ns	ns	+	ns	-	-	ns		ns
	N12	ns	ns	+	-	+	-	ns	ns	

Table VII. Indices of association of common A-pod calls based on transition frequencies. See text for additional explanation.

		CALL								
		N1	N2	N4	N5	N7	N8	N9	N10	N12
CALL	N1	.133								
	N2	.056	.169							
	N4	.077	.206	.303						
	N5	.063	.111	.172	.167					
	N7	.043	.123	.146	.082	.135				
	N8	.021	.050	.055	.044	.304	.034			
	N9	.059	.127	.225	.109	.106	.049	.211		
	N10	.038	.041	.056	.043	.025	.013	.051	.091	
	N12	.021	.052	.088	.046	.085	.038	.064	.032	.137

Figure 11. Cluster diagram of associations among common call types produced by pods A1, A4 and A5. Diagram is based on indices of call association given in Table VII.



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DISCUSSION

Many parallels exist between the social behaviour of odontocete cetaceans and terrestrial social mammals, especially the ungulates and primates (Tayler and Saayman 1972; Wursig 1978; Saayman and Tayler 1979; Wells et al. 1980). This may also be true of their social signalling. The complex communication patterns of the higher primates have been the subjects of much recent research, and there is now a good understanding of some of the major roles played by acoustic signalling within natural primate societies (Green 1975a; Seyfarth et al. 1980; Byrne 1982; Robinson 1982; Waser 1982). It is evident that there are many similar trends in the acoustic behaviour of primates and killer whales. In the following discussion, these similarities are explored in an attempt to provide a broader perspective and interpretation of the killer whale communication system.

Potential Communicative Roles of Pulsed Calls and Whistles

The sounds of killer whales are correlated with the animals' activity and social contexts. An examination of these patterns provides clues about the communicative functions and evolutionary implications of their vocalizations. One clear trend in the social signalling of killer whales concerns the use of discrete calls versus variable calls and whistles in different contexts. When individuals or subgroups are dispersed and out of sight of one another, their calling consists almost entirely of discrete calls. This situation prevails during

foraging and travelling activities. Whenever animals join together and interact socially, there is an associated production of variable pulsed calls, aberrant versions of discrete calls, and whistles. These types of sounds are generally heard in direct proportion to the amount of socializing activity in a pod.

A similar differential use of discrete versus variable or "graded" calls in different contexts has been observed in many primate species (Marler 1965, 1968, 1972, 1973, 1976; Struhsaker 1967; Gautier and Gautier 1977; Oppenheimer 1977; Byrne 1982). In general, discrete calls tend to be used in situations involving long-range communication in habitats where vision is limited by foliage or other obstructions. Graded signals, on the other hand, are exchanged among closely-spaced animals.

The distinctive "loud calls" used in maintenance of territorial boundaries or in intergroup spacing of non-territorial primate species are structurally specialized for unambiguous identification and localization over long distances (Marler and Tenaza 1977; Waser 1977, 1982; Brown 1982). "Contact" or "coherence" calls are used to keep troop members in touch while out of sight of each other, and to coordinate intragroup spacing and movements. Although these calls are less elaborate in structure, they also tend to be discretely distinct (Marler 1968, 1973; Byrne 1981, 1982; Robinson 1982). In a number of species, inter- and intragroup calls have been found to contain features that are consistently unique to individuals (e.g., Marler 1973; Marler and Hobbett 1975; Waser 1977, 1982).

Experimental studies have demonstrated that conspecifics can perceive these minor variations and use them to identify different callers (Waser 1977; Snowdon and Cleveland 1980; Cheney and Seyfarth 1980).

Unlike long-range calls, acoustic signals exchanged among primates in close-knit groups where visual or physical contact is maintained do not require such structural distinctiveness and stereotypy. Factors such as signal degradation and noise masking have less effect over short distances, and information can be conveyed simultaneously (and redundantly) via visual or tactile, as well as auditory, signalling. Close-range calls tend to be much more variable or graded in structure and, as a result, have the potential to convey more subtle and complex information, especially when used in concert with visual displays (Marler 1965; Green 1975a). Graded vocal systems are especially prevalent among primates that form large, often non-territorial groups and reside in open habitats where vision is unrestricted (Green 1975a; Marler 1976). Species with graded calling also tend to have more complex social organizations (Gautier and Gautier 1977).

Underwater vocalization appears to be the best means of interindividual communication available to killer whales for most of the time. Although vision in the species is good (White et al. 1974), water clarity is generally so poor in the study area that visual contact between animals would not be possible beyond ranges of 10-20 m. Vision would, of course, be even less effective at night.

It seems most probable that discrete calls of killer whales serve a similar purpose to the contact calls and loud calls of arboreal primates. In addition to keeping individuals in touch while the pod is dispersed, the calls may coordinate spacing and the direction and rates of group progression.

Killer whale discrete calls share many features with the calls used by dispersed primates. They often contain complex structural components with abrupt shifts in pitch and wideband energy content, both of which enhance their recognizability over long distances and background noise, as well as their potential for accurate localization (Brown 1982). As in primate contact calls (Marler 1968; Gautier and Gautier 1977; Byrne 1982; Robinson 1982), killer whale calls are produced frequently during periods of activity. Also, the spontaneous emission of a call by one whale often triggers calling from other group members, but otherwise the calls elicit little overt behavioural response.

Whether killer whale discrete calls convey information about the caller's identity is not yet known, but it appears likely. Individual-specific differences could account for a portion of the structural variability within each call category. In a study of the sounds of captive killer whales, Dahlheim and Awbrey (1982) describe apparent individual differences in rather broad signal categories. However, their analyses involved animals taken from a variety of locations and pods, and therefore are complicated by overriding group-specific differences (see Part II). Hoelzel and Osborne (in press) noted

differences in the renditions of one call by three members of J pod in the southern resident community which may represent individual "signatures". However, larger samples from several different encounters would be required before other factors which might affect call structure, such as differing motivational levels, can be ruled out. Signature function has been suggested for many of the stereotyped signals of several odontocete species recorded both in captivity and in the wild (see review by Herman and Tavolga 1980).

Unlike primate signals, many of the discrete calls of killer whales contain consistent group-specific structural variations (Part II). With information about group and, possibly, individual identity, discrete calls have an even greater potential function as effective cues for coordinating group activities and maintaining pod cohesion.

Variable and aberrant calls and whistles given by killer whales may be functionally analogous to the graded vocalizations of primates. In both groups, the signals are associated with close proximity between individuals and social interaction; in killer whales, such contexts occur during socializing and beach-rubbing behaviour. These activities may be a means of re-establishing social relationships within the group following periods of dispersion or separation. This function has been suggested for similar behaviours in a variety of terrestrial mammals (e.g., Gautier and Gautier 1977; Marler and Tenaza 1977; Smith et al. 1982). Whales often mill quietly or rest close to one another, engage in physical and sexual interactions, and

carry out a variety of aerobatics. During such times, signalling is probably accomplished through the simultaneous use of visual, tactile, and auditory channels, allowing the communication of subtle variations in arousal or other circumstances related to the interactions. The resting, or low-arousal calls given frequently by most resident killer whale pods during group-resting, socializing, and beach rubbing contexts (e.g., call N3, described previously) resemble the "quiet" calls used during play and affiliation in some primates (Smith et al. 1982). The production of relatively high-pitched whistles during these contexts also parallels the trend apparent in many birds and mammals towards the use of high-frequency, pure tonelike sounds in "friendly" social circumstances (Morton 1977).

Information Content of Discrete Call Types

As discussed above, one primary function of discrete calls may be to maintain contact among individuals and to preserve the overall cohesion of the pod. However, this is probably not the only potential function of the calls for two reasons. First, discrete calls are often produced when pods form compact groups, such as during socializing. The requirement for interindividual contact and localization at such times would be expected to be reduced, but calling often continues at relatively high rates. Second, intragroup contact and coordination of movements could be accomplished with the use of one or two call types, as in many primates (Gautier and Gautier 1977; Byrne 1981; Robinson

1982). The 16 resident pods, however, each have an average of 10.7 discrete call types.

Assuming that discrete calls contain additional information beyond contact and localization of individuals, what might be their function? The acoustic signals of mammals are often considered to be direct expressions of the vocalizing individual's internal motivational state or level of arousal (Smith 1977; Gould 1983). This is especially true of species with comparatively simple social organizations and vocal repertoires. Socially-advanced mammals such as primates have more complex acoustic repertoires which vary in structure and pattern of use according to the animal's demeanor or "mood", a reflection of the underlying internal state of the vocalizer modified by the specific social circumstance or context eliciting the vocalization (Green 1975a; Byrne 1982; Robinson 1982). Recently, increased attention has been given to the possibility that "semantic" signals which refer to or symbolize external features of the environment may be more widespread, at least among primates, than previously thought (Seyfarth et al. 1982; Marler 1983; Dittus 1984).

The examination of discrete call occurrence in different contexts may shed some light on the potential function of specific signals. However, this task is difficult in practice owing to the inability to observe the details of many behaviours and interactions underwater. For this reason, call-type versus behaviour correlations are limited to rather broad activity contexts. One clear correlation is evident in the use of

certain calls in group-resting and other apparent low-arousal situations. It is interesting, however, that some resident pods, such as A1, A4, and A5, produce only a single resting-type call (N3), while other pods give as many as six different calls (pods G, I11 and I31) or, apparently, none (J pod), in similar situations. As was pointed out earlier, resting calls also occur in what appear to be moderate or even high arousal contexts, such as rapid travelling, pod meetings, or large multi-pod aggregations. Thus, these calls may not be simply generalized expressions of low-arousal states, but perhaps instead are correlated with some form of social circumstance which occurs most frequently, but not exclusively, during periods of rest or low-activity levels. Why some pods have several such calls while others have one or none is unknown.

With the exception of group-resting, discrete call production in most resident pods is consistent throughout the major activity categories, foraging, travelling, socializing, and beach rubbing. Detailed examination of calling by the three A-pods revealed little significant variation in occurrence patterns in these contexts. All call types were recorded during each activity, and in relatively few cases did the proportions of different call types vary. The only significant differences were in the use of calls N5, N7, N8 and N11, all of which tended to be more frequent in socializing contexts, and N12, which was more common during beach rubbing. More pronounced differences were evident during large multi-pod aggregations and meetings of pods. Call N2 was produced abundantly during the pods-meeting

context, as was N5 and N11. Call N2 was also strongly associated with other occasions of extreme excitement during social interactions within the A-pods, and occurred intermixed with the "excitement calls" described earlier. During multi-pod aggregations, call N11 comprised 14.1% of discrete calls, compared to < 2% in most activity contexts. There was no obvious correlation with the occurrence of other calls in the repertoire.

From this comparison, it is apparent that call use by the three A-pods varies to some extent with context. It is noteworthy, however, that all call types were given in all activity contexts. Given this general consistency in the A-pods' repertoire, it is interesting how dramatically call use changes with activity levels in the southern resident pods. In J pod, for example, calls which were heard rarely or not at all during foraging became predominant during episodes of rapid travelling and high arousal. This difference in patterns of call occurrence between the two resident communities is surprising and its cause unknown, but it is consistent with other fundamental acoustic differences in both call structure and use (e.g., the lack of resting calls in the southern residents).

Although the analysis of transition frequencies between call types demonstrates that call occurrence is non-random, it does little to reveal the functions of the different signals. There is some association of call types in the repertoires of all resident pods, usually evident in more frequent transitions

than expected by chance.

While the abundance of some discrete call types may be related to arousal, variation in motivation can strongly affect the manner in which calls are produced. Calls given during heightened social excitement, for example, tend to be shorter and higher in pitch. This was demonstrated earlier using measurements of call N2, but high arousal appears to affect many call types in a similar way. It has been shown that gradations within call categories of primates are related to both arousal and the social context, and that these variations have meaning to fellow group members (Byrne 1982).

In summary, although levels of arousal may affect the frequency of use and structure of some calls in a pod's repertoire, few calls are tied exclusively to any particular circumstance that I could identify in this study. Does this mean that the use of most discrete calls is independent of context? This question cannot be addressed adequately using the field observations in this study, but some clues can be obtained from whales in captivity. As reported earlier (Table I), captive individuals taken from A5 pod produced many of the calls in their pod-specific repertoire. Even though these whales were in an unnatural setting, they were usually with other whales and had the opportunity to interact and communicate socially, which might account for the occurrence of different calls. The same cannot be said for the whale "Namu", a mature bull captured in 1965 at Namu, B.C., and maintained alone in a net-pen for several months before being joined by "Shamu", a female taken

from a southern resident pod (see Part II). Despite the absence of any social interaction or normal environmental stimulus, the whale "Namu" produced all but 2 of the 10 discrete calls typically used by C pod of the northern resident community. "Namu" is known to have been removed from C pod from photographs taken at the time of capture (Bigg, pers. comm.). In addition to having essentially the same structure, the calls were given in remarkably similar proportions to those on tapes made in 1964, apparently in the presence of C pod, and to tapes obtained from the pod recently in the course of this study. The two calls not recorded from "Namu" represent only 2.2% of the calls used by C pod today (see Part II).

The pattern of calling by the whale "Namu" raises the possibility that many discrete call types may not be tied to any particular social context or external referent. Different calls may still reflect variation in arousal, but this too is open to question when one considers the marked differences in call structure that exist within a community of pods. If discrete calls are controlled by basic emotive states, variability of call structure would presumably be limited by genetic constraints to rather conservative levels. This may be the case for the "excitement calls" given in states of extreme arousal, which seem to have essentially the same form regardless of pod or community affiliation. However, as shown in Part II, discrete call types of pods which associate together differ in such fundamental ways that it is often difficult to identify potentially homologous calls in separate pods. Vocal variation

on this scale might typically be expected between species, but not among local groups.

An alternative explanation for the function of call repertoires in killer whales may be found in the unusual group-specific dialect system which exists in the B.C. population. It is possible that discrete calls serve as contact or cohesion calls, but the actual call types used are irrelevant for this purpose. Arousal or motivational cues may be conveyed in structural variations within the call category and perhaps by calling rate, but the call type used may be less important. Instead, discrete call repertoires may function primarily as indicators of kinship, and thus be involved in determining social organization and distribution within the population. A large repertoire of calls that vary among pods could allow the encoding of detailed information concerning relatedness. Among the potential selective advantages of such a system would be the avoidance of excessive inbreeding, or possibly the tolerance of related pods during feeding or foraging associations. A similar hypothesis has been proposed to explain repertoires and dialects in bird song by Treisman (1978), but it is not supported by recent field studies on several bird species (Krebs and Kroodsma 1980; McGregor and Krebs 1982). The social system and dialects of killer whales are quite different from any bird, however, and the kin-recognition hypothesis may be more valid in this species. Further evidence and ideas related to the hypothesis are given in Part II.

PART II

DIALECTS AND CALL TRADITIONS IN RESIDENT KILLER WHALES

INTRODUCTION

Geographically-related variation of vocalization is much less common in mammals than in birds, where it is a well-known and widespread phenomenon. Regional differences in birdsong occur at two major levels, (1) as 'geographic variation' between isolated populations, and (2) as 'dialects' among neighbouring groups which can potentially mix and interbreed. Geographic variation is considered to result from acoustic adaptations to differing environmental conditions at each site, or to represent functionless cultural or genetic divergence caused by isolation. Dialects which develop among local populations, on the other hand, have generally been thought to have some adaptive significance (Krebs and Kroodsma 1980; Payne 1981; Baker 1982; Mundinger 1983). Recent studies on some species, however, suggest that these too may be byproducts of vocal learning, patterns of dispersal or some other factor (Mundinger 1983; Payne 1983; Trainer 1983; Slater et al. 1984).

The only true dialects documented in wild mammals occur in killer whales (Ford and Fisher 1982, 1983). Earlier reports of dialects in the threat calls of the northern elephant seal (Mirounga angustirostris) (LeBoeuf and Peterson 1969) involved short-lived phenomena caused by population expansion and colonization of new rookeries (LeBoeuf and Petrinovich 1974). These variants no longer exist today (Shipley et al. 1981). Variations described as "dialects" have been reported for several mammalian species, including pikas (Ochotona princeps) (Somers 1973), black-tailed prairie dogs (Cynomys gunnisoni)

(Slobodchikoff and Coast 1980), and humpback whales (Megaptera novaeangliae) (Winn et al. 1981). In each case, however, the vocal differences described were between populations isolated by geographic barriers or long distances, and therefore are correctly defined as geographic variations (Nottebohm 1969, 1972; Grimes 1974; Conner 1980; Ford and Fisher 1983; Payne and Guinee 1983).

An unusual case of locale-specific variation has been reported in calls which developed and spread within three isolated troops of Japanese monkeys (Macaca fuscata) as a direct result of artificial feeding (Green 1975b). Dialects apparently do not occur naturally in the species, nor have they been recorded in the vocalizations of any other non-human primate. Indeed, the calls of primates are so consistent over wide geographic areas that they are often used as taxonomic markers (e.g., Marshall and Marshall 1976; Hodun et al. 1981; Newman and Symmes 1982; Waser 1982; Oates and Trocco 1983).

The existence of group-specific vocal dialects in killer whales on the coast of British Columbia was first described in preliminary reports by Ford and Fisher (1982, 1983). The vocalizations produced within killer whale pods consist predominantly of repetitious, discrete pulsed calls. Analyses of recordings made during repeated encounters with photographically-identified pods demonstrated that each has a limited repertoire of discrete call types which is constant over a number of years. Some pods share call types, while others have entirely different repertoires.

In this chapter, a description is given of the call repertoires of all 16 pods which comprise the resident population in B.C. coastal waters. The description is based on recordings made between 1978 and 1983, as well as a number of historical recordings made by others of both wild and captive whales. Call repertoires are compared to the geographical distribution and social associations of pods. Finally, I discuss hypotheses to account for the formation and maintenance of group-specific call traditions and dialects in killer whales.

MATERIALS AND METHODS

1. The Study Animals

The data in this study result primarily from behavioural observations and recordings of vocalizations from a population of about 280 killer whales along the coasts of British Columbia and Washington State. The abundance, movements and life history of this population has been studied intensively since 1973. (Bigg et al. 1976; Balcomb et al. 1980; Balcomb et al. 1982; Bigg 1982). These studies were based on observations of individual whales identified photographically by unique natural markings on the dorsal fin or lightly-pigmented dorsal 'saddle'. The following summary of killer whale distribution and social organization is based on these studies and on data collected during this investigation.

The primary social unit of killer whales in British Columbia waters is the pod, a stable association of mixed ages and sexes. Pod members remain together throughout the year, and have done so over the years from 1973 to 1983. Pods generally contain from 5 to 20 individuals, with a range of 1 to 50. On average, pods are composed of about 1/4 mature males, 1/3 mature females, and the remainder juveniles and calves. Most pods contain several females and their offspring of various ages. These maternal associations usually travel as distinct subgroups when the pod is dispersed. Whether different breeding females in a pod are related is unknown. There is considerable evidence

that young animals remain with their mothers and the pod into maturity. No permanent dispersal from or exchange between pods has been observed. However, different pods or subgroups may travel together for periods of up to several weeks.

Low mortality and birth rates contribute to the long-term stability of the pod. Longevity is estimated to be 50 years for bulls and 75-100 years for cows. The minimum calving interval for breeding cows is 3 years. However, a substantial proportion of females in the population give birth rarely. Some cows, likely post-reproductive, have not been seen to give birth since 1973. Hence, the average calving interval is about 10 years.

A total of 33 pods occur off British Columbia. These pods are of two distinct types, "resident" and "transient", which differ in movements, pod size, behaviour and feeding habits. Resident pods are commonly seen in predictable locations during the summer months and a few have been sighted in these same locations at other times of the year, despite low observer effort. Transient pods have less predictable movements and are seen relatively infrequently. Resident pods typically have 5 or more members (mean = 13.4, $n = 16$) while most transient pods contain 5 or less (mean = 3.2, $n = 17$). Resident pods travel only with other residents and transient pods with other transients. The two types of whales do not interact when in the same area.

While foraging, members of resident pods tend to disperse widely and move rather predictably at constant speeds (see Part I). Transient pods, in contrast, remain together and usually

meander along the shoreline (Part III). The main diet of resident whales during the summer appears to be fish, while transients seem to prey selectively on marine mammals.

The resident pods are divided into separate "northern" and "southern" communities with different distributions, as shown in Figure 12. Pods from one community are rarely sighted within the range of the other. No pod appears to have an exclusive home range, nor is there any evidence of mobile territoriality or group-spacing, such as in wolves (Canis lupus) (Harrington and Mech 1983). Pods frequently associate with others within their community, but no intermixing occurs between the two communities.

Table VIII shows the size and composition of resident pods. The alphanumeric designation of Bigg (1982 and pers. comm.) is used to name pods. Pod names were assigned arbitrarily and do not imply degrees of association or relationship. The northern resident community contains 13 pods, totalling about 150 whales. The southern resident community is comprised of three pods, with a total of approximately 80 whales. The transient community, consists of 17 pods with about 50 whales. Transient pods travel throughout both resident community ranges. The transient community is discussed in detail in Part III.

Figure 12. Map of the known distributions of the northern and southern communities of resident killer whale pods, and place names mentioned in the text. Data from M. Bigg (1982 and pers. comm.).

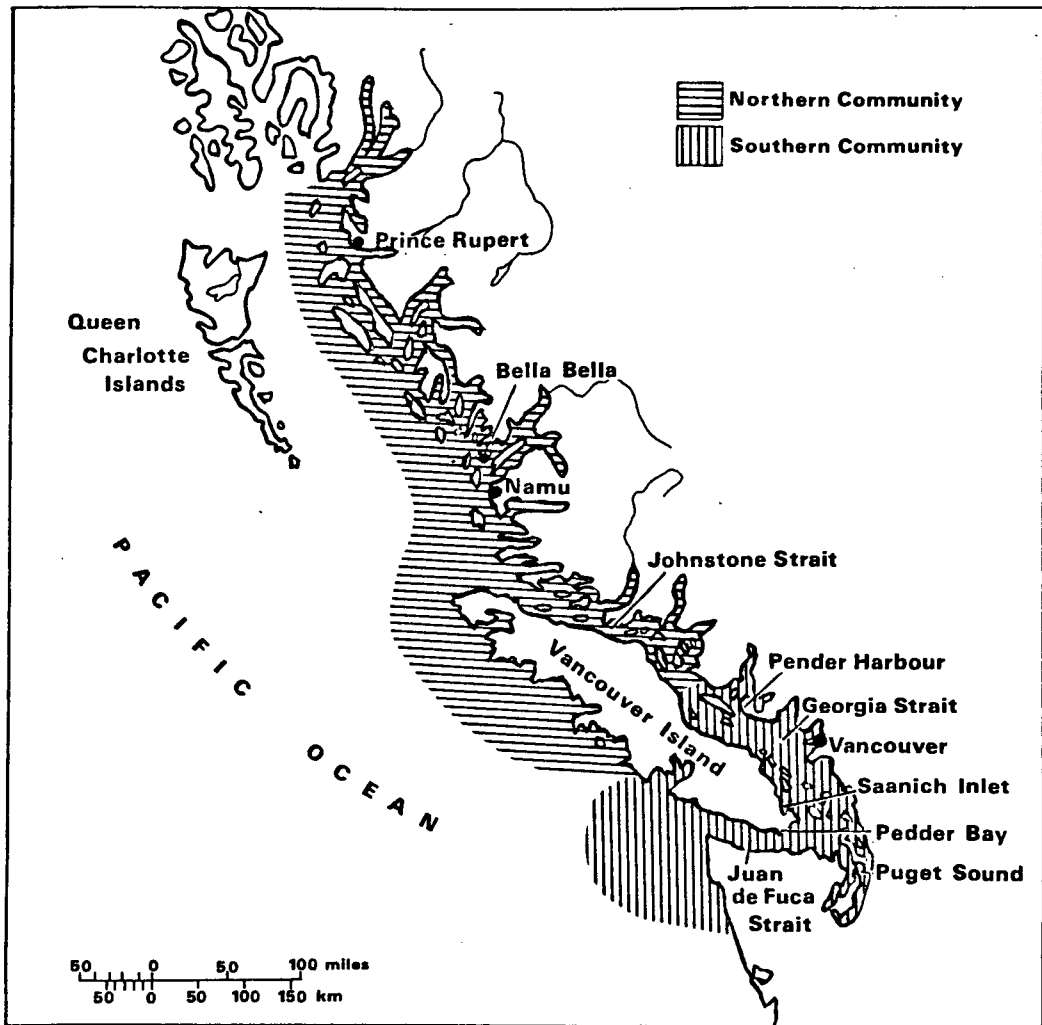


Table VIII. Size and composition of resident pods identified off Vancouver Island. Pod sizes considered exact, except those marked by *, which are probably accurate to within one individual. Data from M. Bigg (1982 and pers. comm.).

Pod	Size	No. of bulls	No. of cows	No. of juveniles	No. of of calves
Northern Resident Community:					
A1	14	5	4	5	0
A4	7	1	3	2	1
A5	12	1	4	6	1
B	8	5	1	2	0
C	9	4	3	2	0
D	10	4	2	4	0
G	19*	4	5	11	1
H	6	1	2	3	0
I1	16*	4	5	6	1
I11	6	0	3	3	0
I31	5	1	2	2	0
R	19*	3	?	?	1
W	4	2	2	0	0
Southern Resident Community:					
J	19	3	8	7	1
K	10	2	5	3	0
L	50	9	16	24	2

2. Field Observations And Recordings

Between July, 1978, and October, 1983, I studied resident killer whales at a variety of locations in the waters to the east and south of Vancouver Island, British Columbia. Whales were encountered on 154 days during this period, mostly in June to September. All 16 resident pods known to occur in the area were encountered and recorded acoustically. A total of 426 "pod encounters" was made with residents (one pod encounter is the interception and identification of one pod on one day), for an average of 2.76 pods per observation day (range = 1-10). The dates, locations and pods involved in each encounter are summarized in Appendix I.

In addition, I examined 43 recordings of captive and wild killer whales made by other individuals, mostly prior to the onset of this study. The early field recordings and their sources are listed in Appendix II.

Whales were located either by patrolling waters known to be frequented by pods or with the help of volunteer observers who telephoned when they saw whales. Upon receipt of a call, interception of the group was attempted. All field work was carried out from a 5-m, outboard-powered boat. The identification of the pods present was determined from photographs or visually. About 7500 photographs were taken. Equipment used was a 35 mm single-lens-reflex camera with a 300 mm lens mounted on a shoulder brace, and Kodak Tri-X film taken at ISO 1200 or 1600. Identifications of individual whales in the photographs were made by M.A. Bigg and G. Ellis (Pacific

Biological Station, Nanaimo, B.C.).

Acoustic recordings were made with a variety of equipment, mainly a Nagra IV-SJ instrumentation recorder fitted with a specially-designed preamplifier/filter unit and a single Celesco BC-10 or BC-50 hydrophone. Frequency response of this system varied with tape speed. Tapes made at the maximum speed of 38 cm/s (15 i/s) were flat (\pm 3 dB) from 100 Hz to 35 kHz. Cassette recorders (Sony TC-D5M and Superscope C-205) were used exclusively during 1982-83. These systems had flat responses from 100 Hz to 14 kHz. Some stereophonic recordings were made using a VHF radio-linked hydrophone deployed from a second boat or from shore, and another hydrophone on the recording boat.

3. Sound analysis

Most killer whale social signals, or calls, can be classified by ear into discrete categories based on distinctive structural characteristics. For initial classification, sounds were transcribed using symbolic notations which reflect the pitch and temporal patterning of the calls. Later, clear examples from each category were selected and analyzed on a Kay 7029A spectrum analyzer. Most spectrograms were made using an 80-8000 Hz frequency range with a narrow 45 Hz filter bandwidth. These analyses served to clarify call classifications, and permitted quantitative definition and comparisons of call types.

Discrete Call Classification:

Discrete calls of killer whales are made up of rapidly emitted pulses which, to the ear, have a tonal quality. The repetition rate of these pulses, reflected in the harmonic or sideband interval (SBI) seen in spectral analysis, is usually modulated over the call's duration. Many calls contain several abrupt shifts in pulse repetition rate, which allow division of the call into different parts. Sound patterns on spectrograms were measured using frequency and duration variables appropriate to the structure of each call type. For simple, one-part calls, the overall duration and minimum and maximum sideband intervals were measured. In the more complex calls, duration and SBI measurements were made for each separate part, and other components, such as simultaneous pure tones, were also measured.

An average of 8.4 variables (range = 2-17) per call were measured from about 3600 calls. These measurements were made digitally using an Apple Computer Graphics Tablet. Means, ranges, and coefficients of variation (c.v. = standard deviation x 100/mean) were calculated for each variable. Comparisons of measurements were carried out using analysis of variance (ANOVA) with Bartlett's test of homogeneity of variance's and Scheffe's pair-wise comparison of means (Sokal and Rohlf 1981).

Discrete calls were classified alphanumerically. Numbers were assigned in the order that calls were identified, regardless of which pod was responsible for their production. Call numbers are preceded by a letter indicating whether they

were recorded from northern (N) or southern (S) community residents.

Most discrete call types are shared by a number of pods. However, shared calls are often rendered in consistently different forms specific to each pod or to groups of pods. Some of these call-type variants are so modified that they were initially given separate call numbers. Eventually, however, they were proven to be homologous from subtle structural clues or from patterns of call association. Structurally-unique variants of a discrete call were distinguished by different lower-case Roman numeral suffixes. An example of a typical call type is N9, shared by three pods, A1, A4 and A5, of the northern resident community, but given in a slightly different manner by each pod. These subtypes are identified as N9i, N9ii, and N9iii, respectively.

A quantitative measure of similarity of call repertoires for each pair of pods was obtained by calculating an index from the degree of call sharing. This index is based on Dice's coefficient of association (see Morgan et al. 1976), which normalizes the data to account for differences in repertoire size:

$$\text{Index of Similarity} = \frac{2(N_c)}{r_1 + r_2}$$

where N_c is the total number of call types and subtypes shared and r_1 and r_2 are the repertoire sizes of the pod.

These values were then used to calculate a hierarchical structure of acoustic similarity, displayed in the form of a

dendrogram by means of single-link cluster analysis (Morgan et al. 1976).

Patterns of Call Occurrence:

To examine the frequency distribution of call types and their patterns of occurrence, continuous sections of tapes were divided into 10-min time periods. Proportions for each call type in each time period were calculated. These were transformed using the arc sine square root, and used as replicates in an analysis of variance with Scheffe's test for determining the significance of differences among means. This technique was chosen over analysis of frequencies since it more accurately reflects the variability in the data.

Associations of different call types were examined by calculating the preceding and following transition frequencies for calls within each min of the 10-min time periods. The transition frequencies for each call combination were summed and used to calculate an index of association, described in Part I. These indices were then arranged in a hierarchy and displayed using single-link cluster analysis.

RESULTS

1. Recording and Identification of Call Repertoires

Recordings used to describe the call repertoire of each pod were made under the following circumstances. First, the pod was recorded while travelling either alone or at a sufficient distance from other groups so that the calls could be attributed unequivocally to that pod. Second, the recordings chosen were made in social and activity contexts that were as similar as possible, so as to avoid potential complicating effects of context-related variation in call use or structure (Part I). Foraging, the most common activity of resident killer whales, was selected as the standard context from which samples were drawn.

All recordings meeting the above criteria were used to describe the typical pattern of call use for the pod. Also, representative samples of each call type for quantitative structural analysis were drawn from these tapes. Although most pods were encountered and recorded alone on several occasions, some common groups were seldom found apart from other whales, and other pods were simply rare in the study area. Pod A4, for example, was encountered a total of 62 times, but was alone on only 3 of those occasions. In contrast, R pod was encountered on only 3 days, each time in the presence of 7 or more additional pods. Despite the limited samples available for some groups, it is very likely that most, and in many cases all, call types in each pod's repertoire have been identified and their

relative frequency of use correctly determined. The majority of calls in a pod's repertoire can be heard in one or two 10-min sample periods (Part I). Tapes made prior to 1978 are, unless otherwise mentioned, attributed to certain pods on the basis of the call types recorded since no photographic evidence of the pods present was available. These early recordings were made in the same locations as those in this study. In all cases, pods presumed to be present in the older tapes were also recorded recently in the same area. All call repertoires present in pre-1978 tapes were also recorded during 1978-83.

In the following sections, the discrete calls of resident pods are illustrated, and their frequency of occurrence in each pod's repertoire is described. Descriptive statistics of the frequency and duration measurements for each call type, and results of ANOVA's comparing these variables are listed in Appendix III.

2. Dialects of Northern Community Resident Pods.

All 13 pods in the northern resident community were recorded acoustically between 1978 and 1983 off northeastern Vancouver Island. Certain pods share call types yet have no calls in common with other pods in the community. I have termed each distinct acoustic association a "clan", defined as a set of pods which shares one or more discrete call types. This term was chosen since it implies that member pods are part of a common lineage, a notion which, as will be discussed later, is not proven but can be considered probable. The northern

resident community is comprised of three clans, the A-clan, G-clan and R-clan.

A. A-Clan

The A-clan is comprised of eight pods, A1, A4, A5, B, C, D, H and I1, all of which share a portion of their call repertoires. The 19 A-clan call types and the pods observed to produce them are summarized in Table IX. All eight pods share a minimum of four call types, N3, N7, N8 and N12. A further three calls, N1, N5 and N11, are produced by all but one or two of the groups. The clan is clearly divided into two major dialect groupings on the basis of the remaining call types. The first, referred to as the "A-group", consists of pods A1, A4 and A5. These pods share four unique call types, N2, N4, N9 and N10, as well as several additional group-specific call types. The second, or "B-group", contains pods B, C, D, H and I1, all of which produce call N16. These two groups can be further subdivided according to the call types shared or absent in the repertoires of certain pods, as well as in the different renditions of shared call types.

I) Call characteristics

Calls shared by most A-clan members: Calls given by representatives of both the A- and B-groups of pods include N1, N3, N5, N7, N8, N11 and N12. Most occur in a number of different variant forms, or subtypes (Table IX).

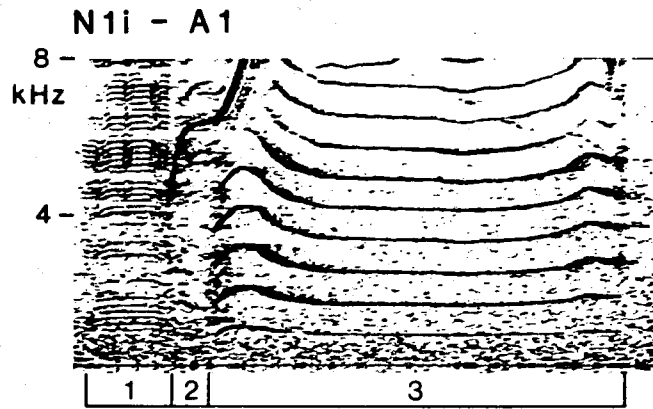
Call N1 is given by all A-clan pods with the exception of

Table IX. Call types and subtypes produced by pods of the A clan in the northern resident community.

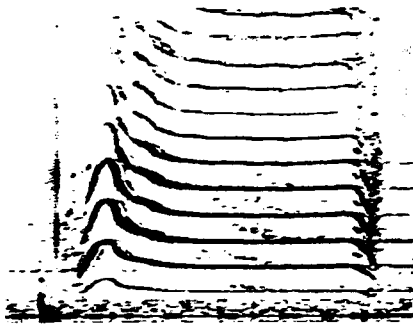
Call	Pod							
	A1	A4	A5	B	C	D	H	I1
N1 — i	X							
ii				X				X
iii					X	X		
iv							X	X
v		X						
N2	X	X	X					
N3	X	X	X	X	X	X	X	X
N4	X	X	X					
N5 — i	X	X	X	X			X	X
ii				X			X	X
N7 — i	X	X	X					
ii	X	X	X				X	X
iii				X				X
iv					X	X		
N8 — i	X	X	X				X	
ii					X	X		
iii				X				X
iv				X				X
N9 — i	X							
ii		X						
iii			X					
N10	X	X	X					
N11 — i	X	X	X	X				
ii				X	X	X	X	
N12	X	X	X	X	X	X	X	X
N13		X	X					
N16 — i				X				
ii					X	X		
iii							X	X
iv								X
N17			X					
N18				X	X			
N20				X	X	X		X
N21				X				
N27	X							
N47	X							
Total	14	14	13	14	9	8	9	13

A5 pod. There are five distinct subtypes of the call, shown in Figure 13. N1 is a three-part signal which begins typically with a low-pitch pulse burst having a sideband interval (SBI) of 25-100 Hz (part 1). This short component (average durations 80-220 ms) is followed by part 2, a brief gap (generally < 100 ms) in the pulsed signal during which a narrowband tonal component begins at a frequency of 2500-4500 Hz and increases rapidly to > 8000 Hz for the remainder of the call. The final portion of the call, part 3, is the longest, consisting of a pulsed signal which reaches an early peak in pitch, then drops off for the rest of the call. In subtype N1i, given by A1 pod, part 1 is strongly emphasized and relatively long in duration compared to other renditions, and part 3 ends with a distinct upsweep in pitch. Subtype N1iii, shared by pods C and D, is similar to N1i, except parts 1 and 2 and the terminal upsweep of part 3 are less pronounced. In N1i, part 3 ends at an SBI of > 800 Hz, while in N1iii the upsweep SBI is < 800 Hz. Subtype N1iii is given in very similar manner by C and D pods, differing only in that the peak SBI in part 3 reaches a higher frequency in D's version ($p < 0.01$). Pod A4 also makes a distinct version of call N1 (N1v), distinguished by a consistently high SBI throughout the middle 'plateau', or portion of constant pitch, of part 3 (> 900 Hz in N1v, < 900 Hz in other subtypes). Subtype N1ii, shared by pods B and I1, differs from N1i, N1iii and N1v in that the call terminates with a slight downsweep, rather than upsweep, in pitch. The renditions of this subtype differ between B and I1 pod in a number of ways. In the B's

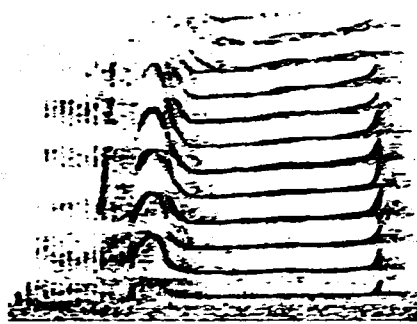
Figure 13. Spectrograms of A-clan call type N1. The three structural subdivisions, or 'parts' of the call type are marked on bottom of call N1i (A1 pod). In this and other figures showing sample spectrograms of call types, subdivisions are indicated only if they are referred to in the text. Descriptive statistics of structural variables for all call types are given in Appendix III.



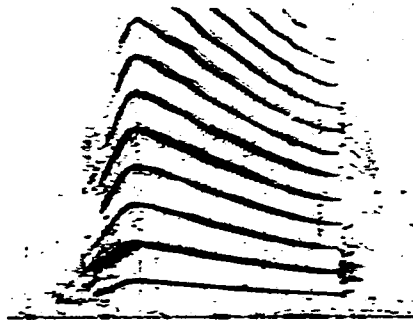
N1ii - B, I1



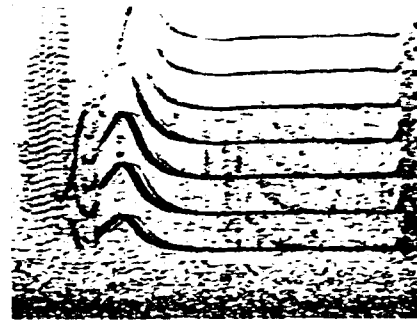
N1iii - C, D



N1iv - H, I1



N1v - A4



0 500 ms

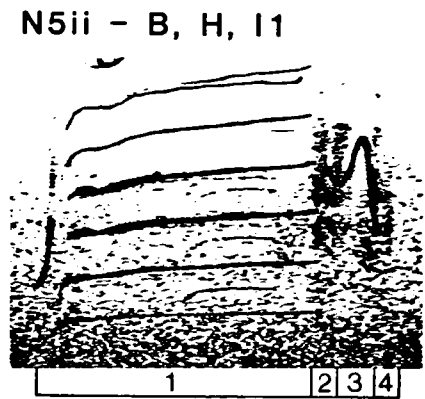
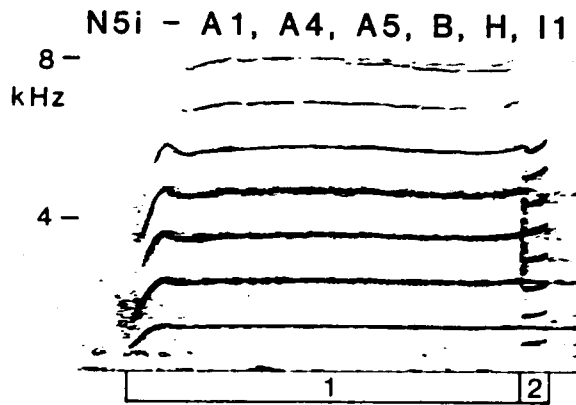
version, parts 1 and 2 are shorter ($p < 0.001$ and < 0.01 , respectively) and higher in pitch ($p < 0.001$), while the middle plateau of part 3 is lower and the tonal component higher in frequency (both $p < 0.001$).

Pod H produces the most unique form of call N1, subtype N1iv. Unlike other versions of the call, there is no portion of constant pitch following the early peak in part 3. Instead, the SBI decreases gradually over the remainder of the call, resulting in a very distinctive sound. Indeed, N1iv is so unusual that its homology with other N1 subtypes would be doubtful were it not for the diagnostic parts 1 and 2. These, however, are very much reduced in N1iv, and the tonal component is absent in about half of those sampled (12 of 25). In addition to H pod, this subtype is made rarely by I1 pod.

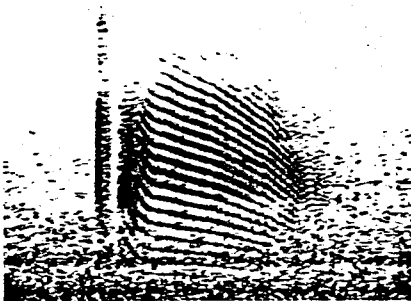
Call N3 is a short, simple three-part call produced by all A-clan members. The call occurs in each activity category, but it is rather uncommon in all except low-arousal contexts, when it predominates (Part I). Most of the B-group of pods give an additional call, N20 (described below), during these contexts. An example of call N3 is shown in Figure 14. Adequate samples of the call could not be obtained for all pods, hence group-specific differences could not be identified. However, comparisons of frequency and duration for the call as given by pods A1, A4 and A5 failed to detect any significant variation.

Call N5 is used by all A-clan pods except C and D. Two subtypes were identified, shown in Figure 14. Subtype N5i, produced by all pods making the call, is the simpler of the two.

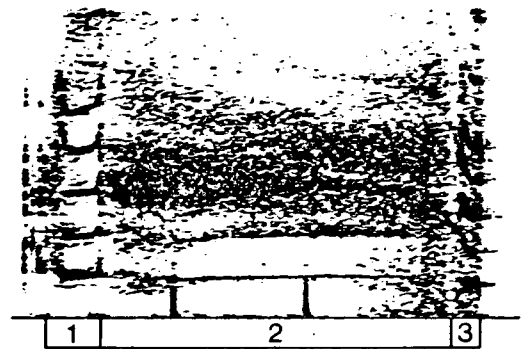
Figure 14. Spectrograms of A-clan call types N3, N5 and N11.



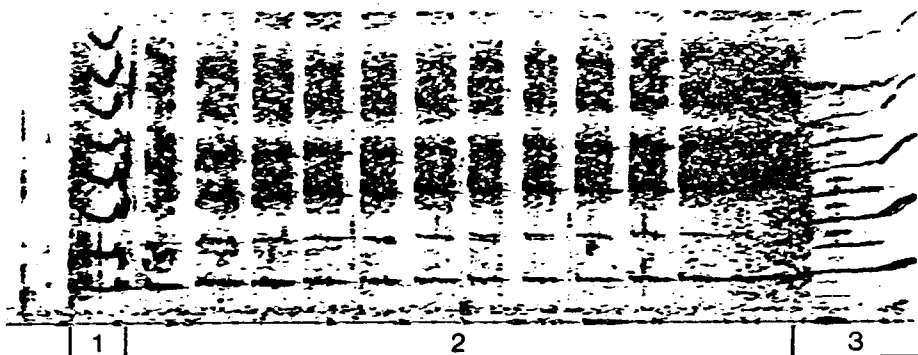
N3 - all A-clan pods



N11i - A1, A4, A5, B



N11ii - B, C, D, H



0 500 ms

It is a two-part pulsed signal often with a simultaneous narrowband tonal component. A number of pod-specific differences occur within subtype N5i (Appendix III). Overall duration, as well as duration of part 1, tend to be longer in the A-pods' versions than B, H and I1's. In many examples of N5i from the A pods and H pod, there is a peak in SBI early in part 1, after which the SBI quickly drops within 100 ms, then gradually increases once again until the start of part 2. Part 2 of N5i is given in a longer form by A5 pod than A1 or A4 ($p < 0.01$), while H pod produces a longer part B than any other pod ($p < 0.001$). The SBI of part 1 is quite uniform among the pods, while part 2 tends to be of a lower pitch in pods B and I1 compared to pods A1, A4, A5 and H (p 's < 0.01 or 0.001). Finally, the tonal component in part 1 is more prominent in pods B, H and I1 than the A pods, and its starting frequency is significantly lower ($p < 0.001$). In summary, pods A1, A4 and A5's renditions of N5i are relatively similar in most respects, as are those of B, H and I1 pods.

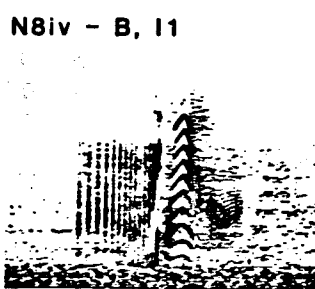
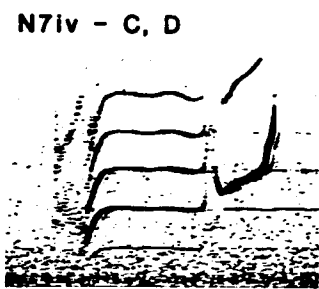
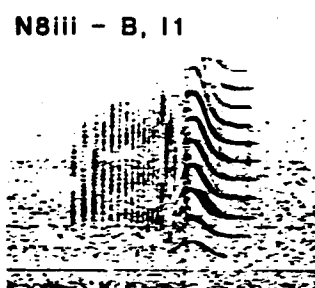
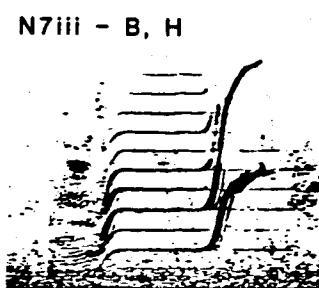
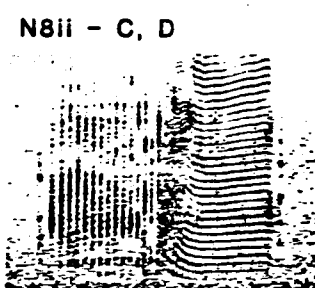
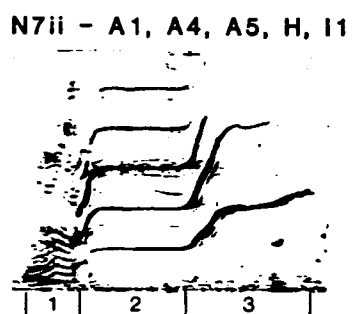
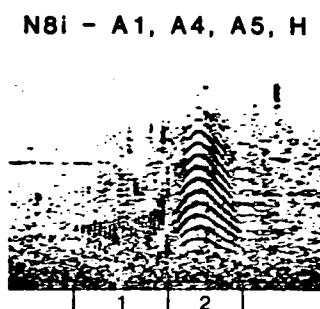
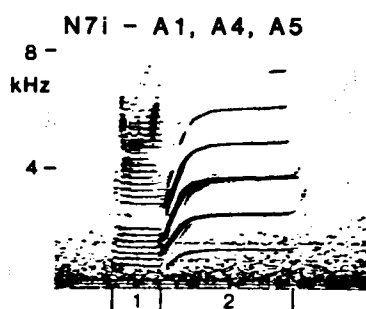
The second subtype, N5ii, has two additional components, parts 3 and 4, appended to the end of the N5i versions (Fig. 14). This subtype has been recorded only from pods B, H, and I1, and generally accounts for less than half of the N5 calls emitted by these pods. As in a proportion of H-pod's renditions of N5i, there is frequently an early peak in SBI at the start of part 1 in N5ii given by this pod.

Call N7 is a very common A-clan call type, used by all eight pods. There are four distinct subtypes of the call, shown

in Figure 15. Subtype N7i is given exclusively by pods A1, A4 and A5. It consists of two parts; part 1 is a low pulse-rate burst (generally < 300 Hz) of 100-250 ms duration, after which the SBI suddenly increases, typically over 50-100 ms, to about 1300-1400 Hz, which forms part 2. Subtype N7ii is very similar, except a third component, part 3, follows part 2. This part consists of a further upswEEP in SBI, starting at 1300-1400 Hz and increasing to levels of > 3500 Hz. Pods A1, A4, A5, H and I1 share this subtype; approximately one-third of N7 calls sampled from the A pods were N7ii, while H pod produces this variant exclusively. Pod I1 uses both N7ii and the third subtype, N7iii. This latter subtype, given only by B and I1 pods, is similar to the three-part N7ii, but part 2 has a much lower pitch. The SBI in this component of N7iii is < 800 Hz, while in N7ii and N7iv (described next), the SBI is > 1100 Hz. The final subtype, N7iv, is given exclusively by pods C and D. This three-part signal has an SBI in part 2 which is comparable to N7ii, but part 3 begins at an SBI generally > 1000 Hz higher in frequency. In addition, the variant differs from other N7 subtypes in that part 1 is very much reduced in intensity relative to other parts of the call. Within each N7 subtype, there are a number of pod-specific differences in call structure, listed in Appendix III.

As described in Part I, the occurrence of call N8 is closely tied to N7. N8's are produced by all A-clan pods, and in each case the call is never given without first being preceded 1 to 4 s earlier by an N7. Four subtypes of the call

Figure 15. Spectrograms of A-clan call types N7 and N8.



0 500 ms

were identified (Fig. 15). Subtypes N8i, N8ii and N8iii share a similar two-part format; part 1 consists of a pulsed component with a low repetition rate of < 50 Hz, while part 2 has higher pulsing rates of up to 900 Hz. Subtype N8i, emitted by pods A1, A4, A5 and H, has a rapid increase then gradual decrease of pulse rate in part 2. In H-pod's version, part 1 is brief compared to that of the A pods', while part 2 is longer (both $p < 0.001$). Also, the SBI in part 2 starts and peaks at higher frequencies in pod H than the A pods ($p < 0.001$). A variety of differences in the structure of N8i also occur within the A pods. Part 2 of the call tends to be longer in A5's versions ($p < 0.001$), while the peak SBI of the same component is lower in A1 than A4 or A5 ($p < 0.001$).

Subtype N8ii is, to the ear, quite different from other N8 variants and was only determined to belong to the call type from its association with call N7. Part 2 of the subtype has a pitch that, rather than increasing and decreasing as in other variants, is held relatively constant at SBI's of 200-300 Hz. N8ii is given exclusively by pods C and D, and the only pod-specific difference evident is in the terminal SBI of part 2, which is significantly higher in D pod ($p < 0.001$).

Subtypes N8iii and N8iv are both produced only by pods B and I1. N8iii is similar to N8i, except that following the SBI peak, the SBI decreases somewhat then is held at a relatively high 450-700 Hz for the remainder of the call. In N8i, the SBI continues to decline to levels of 100-400 Hz at the end of the call. N8iv differs from other variants in that the SBI in part

2 drops sharply following the peak, and then is maintained at low rates of < 50 Hz until the end of the call. This terminal component (part 3) averages about 115 ms in duration.

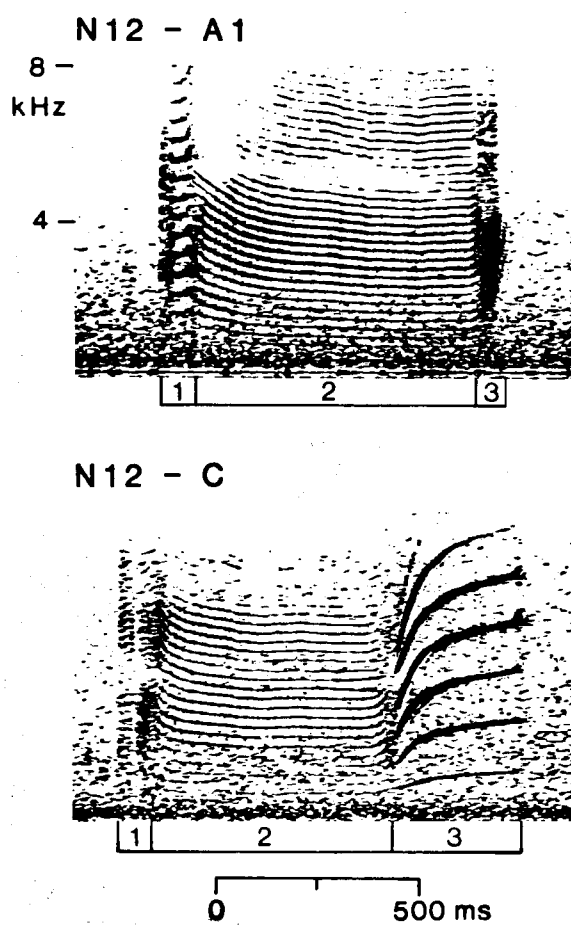
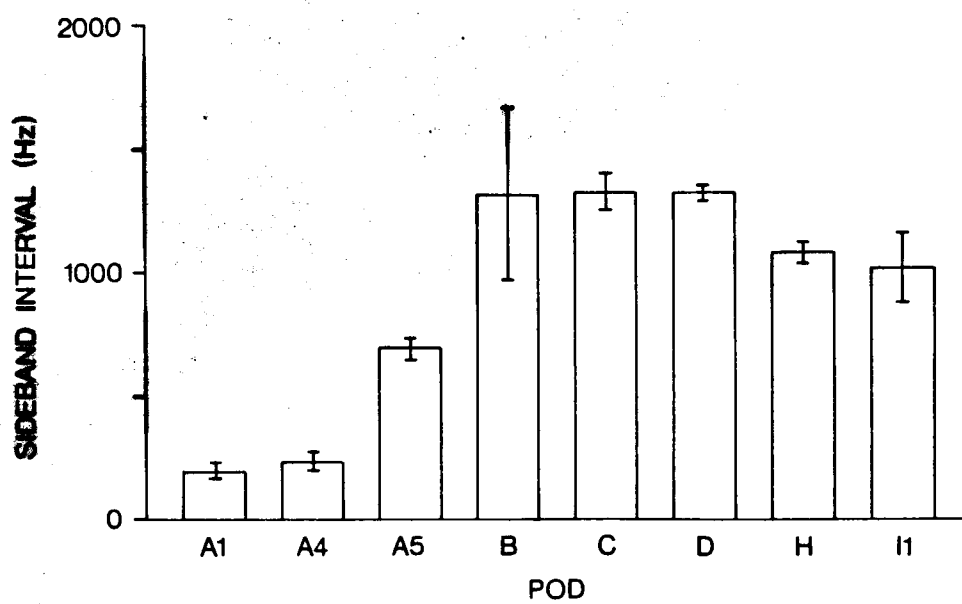
Call N11 is an unusual and, in most contexts, uncommon signal recorded from all pods of the A-clan except I1 - its absence in this pod may be a result of the short recording samples available. Two subtypes occur, both illustrated in Figure 14. N11i begins with an 80-200 ms component with an SBI of about 1500 Hz, followed by part 2, a longer noisy pulse-burst of 500 ms to almost 2.0 s duration in some samples. Part 3, terminating the call, is similar in structure to part 1. Subtype N11ii differs from N11i in part 2, which is broken up into a number of short (about 30-120 ms) bursts separated by gaps typically of 60 to 100 ms duration. Pods A1, A4 and A5 produce subtype N11i exclusively, while B pod makes both N11i and N11ii. Pods C, D and H, appear to use N11ii only.

Call N12 is another infrequently used call that is shared by all A-clan pods. Although no discrete subtypes are apparent in the three-part signal, much group-related variation occurs. As illustrated in Figure 16, the most pronounced differences are in the terminal upsweep of the call, or part 3. This component in the A pods reaches mean SBI's of < 700 Hz, while pods B, C, D, H and I1 have mean SBI's of > 1000 Hz. Within the A pods, A5 has a higher upsweep than either A1 or A4 ($p < 0.01$). There are no significant differences in this component within the B-group of pods, and all are significantly greater than the A-pods, with the exception of I1 compared to A5. Numerous less marked

Figure 16. Spectrograms and structural measurements of A-clan call type N12.

A = Examples of typical renditions of N12 by pods A1 and C.

B = Distribution of average sideband intervals (with 95% confidence intervals) at the termination of N12 calls sampled from A-clan pods.

A.**B.**

differences in other variables are listed in Appendix III.

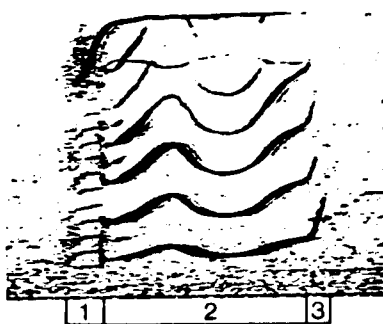
Calls Used by the A-Group of Pods Only: Pods A1, A4 and A5 share four call types, N2, N4, N9 and N10, which are given by no other pods. In addition, A4 and A5 pods share call N13, calls N27 and N47 are given by A1 alone, and N17 and N19 are used solely by A5 and A4, respectively.

Call N2 is one of the more common calls of the A-pods. It is a three-part call with an extremely distinctive structure and sound (Fig. 17). Part 1 is a short (means = 55-75 ms) pulse burst with SBI's of about 300-600 Hz. Part 2, the longest component, undergoes a smooth up-down-up pitch modulation at higher SBI's of 1000 to 2500 Hz. The call ends with part 3, a sharp upsweep usually < 100 ms in duration. In addition to these three parts, N2's have a distinct narrowband tonal component which begins at the start of the call at frequencies of 4800-7600 Hz, then rises quickly to 7400-8100 Hz, where it is held constant for the rest of the call.

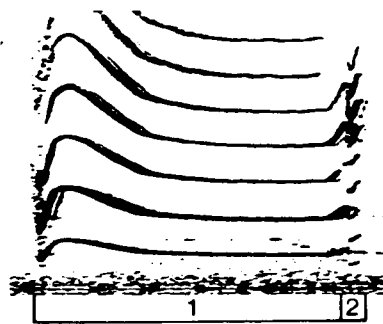
Pod-specific differences in call N2 occur mainly in parts 2 and 3. Pod-A1's versions of the call usually are lacking part 3 (in 24 of 31 samples, or 77.4 %), and when the component is present it is significantly reduced (maximum frequency reached by the second sideband is less than in A4 ($p < 0.01$) and A5 ($p < 0.001$)). Pods A4 and A5 tend to produce higher pitched N2's, reflected in the overall greater SBI's in part 2 (e.g. SBI, end of part 2: A4 and A5 > A1, $p < 0.001$) and the higher frequencies in part 3. In addition, the time interval between the start of part 2 and the SBI peak in the first pitch inflection is

Figure 17. Spectrograms of A-clan call types N2, N4 and N9.

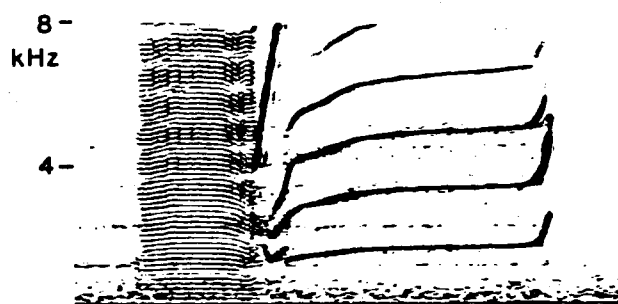
N2 - A1, A4, A5



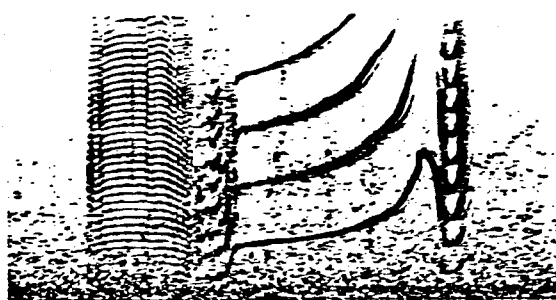
N4 - A1, A4, A5



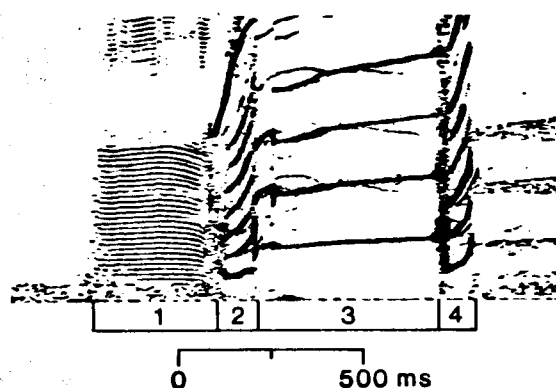
N9i - A1



N9ii - A4



N9iii - A5



consistently shorter in A1's renditions compared to A4's, which in turn are shorter than A5's (all $p < 0.001$).

Call N4 is consistently the most common call in the repertoires of pods A1, A4 and A5. It is a relatively simple two-part signal; part 1 is the longer, consisting of a pulsed component which rises rapidly in pitch to an early peak, then gradually declines and levels off until part 2, a short (means = 35-65 ms) lower-pitched component (Fig. 17). One major difference in structure of the call as given by the three pods is in the occurrence of a slight upsweep in SBI at the end of part 1, which occurs in the majority of samples from A4 and A5 (76.9% and 59.5%, respectively) but in only 17.9% from A1 pod. In addition, part 2 is absent in 66.7% of samples from A1 pod, compared to 5.7% in A4 and 4.7% in A5. When part 2 is present in A1-pod's N4 calls, it is of a significantly shorter duration ($p < 0.001$) than the counterparts from A4 and A5 pods. One final difference is in the peak SBI reached in part 1, which is higher in pod A4 than either A1 or A5 ($p < 0.001$ and 0.05 , respectively).

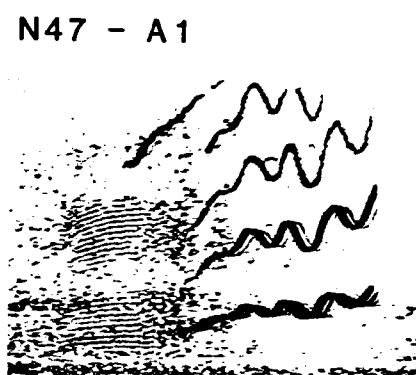
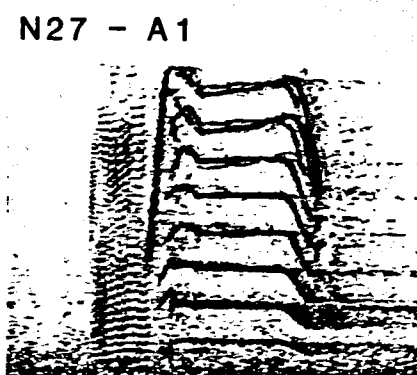
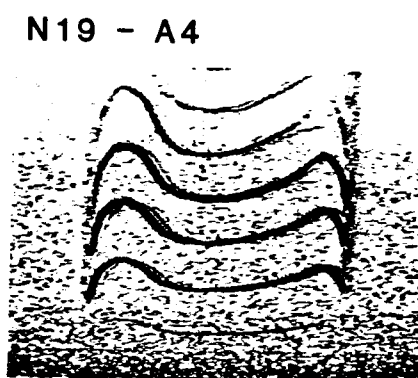
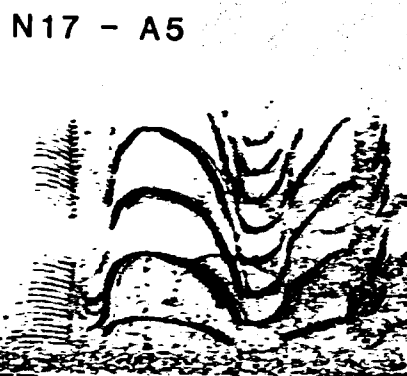
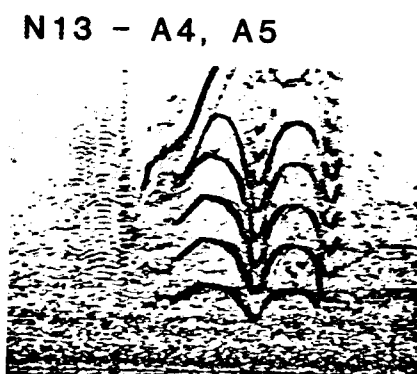
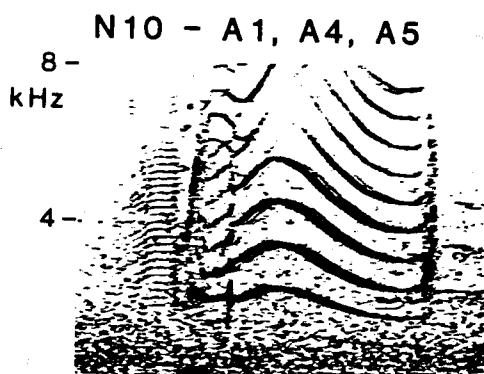
Call N9 is another very common signal of the A-pods. Each pod uses a similar four-part call format, but the pod-specific differences are so distinct that the call can be divided into three discrete subtypes (Fig. 17). Most differences occur in the third part of the call. This component starts with SBI's of 1100-1900 Hz which, in subtypes N9i and N9iii (pods A1 and A5, respectively), climb steadily to peaks of 1400-2100 Hz at the start of part 4. In A4 pod's version (subtype N9ii), the SBI

reaches higher peak frequencies (mean = 3058 Hz; $p < 0.001$), then drops sharply in the final 46 ms (range = 13-77 ms) before the start of part 4. A1-pod's subtype N9i, has a very short part 4, consisting of an upsweep averaging 900 Hz (measured on the second sideband) in ≤ 55 ms. In contrast, part 4 in A4 and A5 pod's renditions consist of a pronounced downsweep in pitch, with average durations of 94 and 108 ms, respectively. This component is significantly longer and higher in frequency in A5 pod compared to A4 (both $p < 0.01$).

N10, a fairly uncommon four-part call, is shared by all three A-pods. It has a very similar structure to N1i, given by A1 pod, except that the long plateau of constant pitch in part 3 of N1i is absent in N10 (Fig. 18). No subtypes of N10 were identified, and few group-specific differences were apparent. The most important of these is that part 4 of A5's version of the call is significantly longer than both A1's ($p < 0.01$) and A4's ($p < 0.05$).

The remaining five calls from the collective A-pod repertoire are emitted by only one or two of the three groups, and all are comparatively uncommon. Representative spectrograms of these signals are shown in Figure 18. Calls N13, shared by A4 and A5 pods, N17, produced by A5, and N27 and N47, given only by A1, are related in structure to N1, N9, and N10. All these calls begin with a similar low pulse-rate burst, followed by additional higher frequency components and a simultaneous narrowband tone which begins at a frequency of 3000-5000 Hz at the end of part 1, then increases to > 8000 Hz. Major

Figure 18. Spectrograms of A-clan call types N10, N13, N17, N19, N27 and N47.



0 500 ms

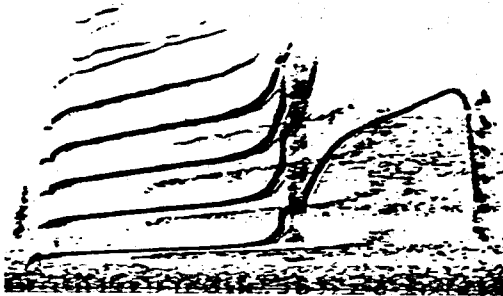
differences distinguishing the call types occur in the structure of parts 2, 3 or 4, where these parts are present. N47 appears to be closely related to N9, differing only in that N47 has a number of modulations in pulse rate in the equivalent of part 2 of N9. Call N19 was recorded only from A4 pod, and is similar to N4. It differs from the latter in that there is a significant peak in pitch towards the end of call, followed by another dip, and the terminal component (part 2) of N4 is lacking.

Calls Used by the B-Group of Pods Only: The B-group of pods, comprised of pods B, C, D, H, and I1, has a total of four call types, N16, N18, N20 and N21, which are not used by any other pods. Of these, N16 is the only call shared by all five pods, and it tends to be an important component in most repertoires. This distinctive signal occurs in four variant forms, illustrated in Figure 19. All share a common four-part format; part 1, the longest component, is a gradually rising tone with SBI's starting at about 1000 Hz and ending at 1500-2000 Hz. Part 2, a short lower-pitched pulse burst at SBI's of typically < 1000 Hz, is followed by a sudden shift in SBI to about 2500-3000 Hz. This increases to > 6000 Hz in many cases, then drops to 2500-4000 Hz, ending part 3. The terminal part 4 is another short component very similar to part 2. In addition to these four pulsed components, there is a simultaneous narrowband tone which begins at about 2000-3000 Hz at the start of the call, then increases quickly to > 8000 Hz.

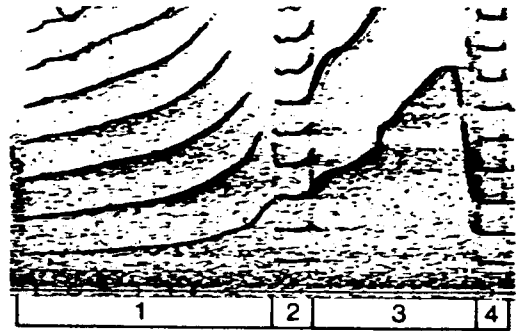
The most important distinguishing features of N16 subtypes

Figure 19. Spectrograms of A-clan call types N16, N18, N20
and N21.

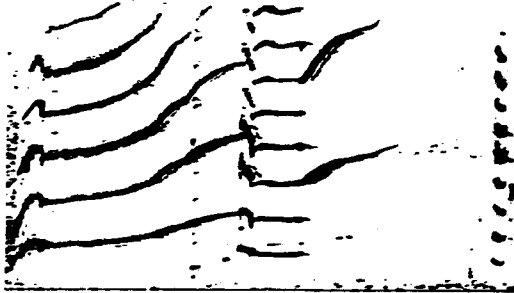
N16i - B



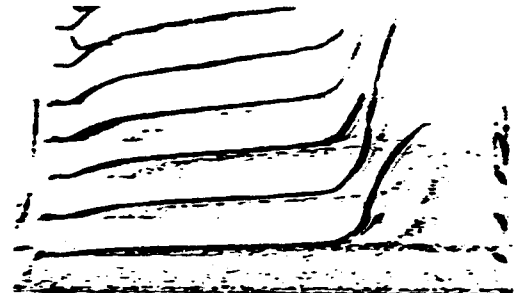
N16ii - C, D



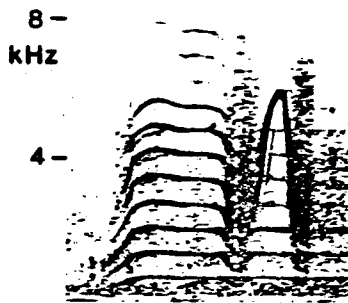
N16iii - H, I1



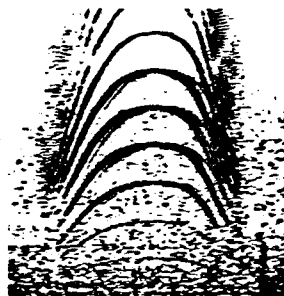
N16iv - I1



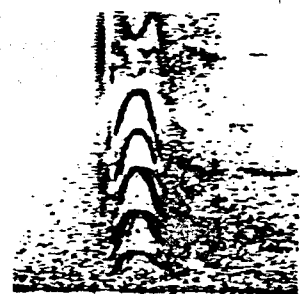
N18 - B, C



N20 - B, C, D, I1



N21 - B



0 500 ms

are as follows: N16i, emitted only by pod B, has a comparatively short part 2 (mean = 43 ms) with a noisy structure. Sidebands can be resolved in only 35.7% (10 of 28) of the sample spectrograms. Part 4 is also reduced, with a mean duration of 27 ms (range = 17-35 ms). In contrast, N16ii, made by C and D pods, has a longer part 2 (means = 63 and 68 ms, respectively) with distinct sideband structure. Part 4 of the subtype is similarly well developed, having mean durations of 61 ms (C pod) and 65 ms (D pod), more than double the mean duration of the same component in B's version. A gap of about 40-140 ms between the end of part 1 and the start of part 2 is evident in some 40 to 50% of N16ii's. This does not occur in any other N16 variants. The only difference apparent in C and D's production of N16ii is that the peak frequency reached in part 3 is significantly higher in D pod ($p < 0.01$).

N16iii, a subtype shared by H and I1 pods (used only rarely in the latter), has a well-defined part 2 (mean duration in pod H = 111 ms), but parts 3 and 4 are very much reduced. Although part 3 lasts an average of 430 ms in pod H's versions, the high pitch component ends after a mean of 173 ms, leaving the remaining 60% (on average) of the part with no sound. Part 4 is of a low relative intensity and brief duration (mean = 22 ms in H pod). Subtype N16iv, produced only by I1 pod, closely resembles N16iii in most respects except that part 2 is entirely absent. Instead, the SBI continues to increase steadily from part 1 into part 3. Three of the four N16 variants, N16ii, N16iii and N16iv, also occur in abbreviated forms which lack the

descending pitch-portion of part 3 and all of part 4.

Of the three remaining B-group calls, N20 is the only signal given by all the pods, with the apparent exception of H pod. Like call N3, N20's are heard predominately during low-arousal or resting contexts, although they are recorded infrequently during all major activities. It is a simple one-part call consisting of a pulsed tone which increases in pitch to a peak near the middle of the call, then returns to the original pitch at the call's end (Fig. 19). N20's given by pods C and D reach SBI peaks averaging 781 and 928 Hz, respectively, significantly higher than the 464 Hz reached on average by B pod's versions ($p < 0.001$). Only two samples are available for N20's produced by I1 pod, but they have a mean peak SBI of 484 Hz, similar to B pod. Calls N18 and N21 are relatively uncommon signals recorded from B and C pods, and B pod alone, respectively (Fig. 19).

II) Call use

The A-Group of Pods: The frequency of occurrence of discrete call types in the repertoires of pods A1, A4 and A5 during various activity contexts, and their pattern of use from transition analyses, are described in Part I. A number of early (pre-1978) recordings of calls made apparently by the A-pods were obtained and analyzed (Appendix II). The frequency distributions of call types recorded in these encounters, as well as those identified from recordings made of A1, A4 and A5 pods while foraging together during 1978 to 1981, are shown in

Figure 20. There is considerable consistency in call use from year to year. Analyses of variance with pair-wise comparisons for calls N1 through N12 among the samples for 1964, 1973, 1978, 1979, 1980 and 1981 revealed few significant differences. These consisted of a reduced occurrence of call N9 in 1964 compared to 1978 and 1979 (both $p < 0.01$), and the same comparing N9 in 1981 to 1978 and 1979 (both $p < 0.05$). The A-pod calls N13, N17, N19, N27, and N47 were recorded too infrequently to warrant statistical comparison; however, all are represented in recordings made as early as 1973. These calls may well have been used prior to that date but simply did not occur in the small samples available.

There is significant variation in the frequency of use of shared calls by the three A-pods (Fig. 21). Pod A4 tends to produce N4 and N12 calls proportionately more often than do A1 and A5, and calls N5 and N9 less often. Call N10 occurs more frequently in the repertoire of A5 pod than A1 or A4, and A1 uses call N1 more often than A4 pod. No differences were evident in the occurrence of calls N2, N3, N7, N8 and N11.

The frequency distributions of call types recorded during encounters with A1 pod alone are shown in Figure 22. The pre-1978 distribution is based on two short encounters combined. The first, made by P. Spong in the Johnstone Strait area on August 19, 1971, was recorded in the presence of a group containing a well-marked animal determined later to belong to A1 pod (Bigg et al. 1976). The second was recorded by E. Hoyt in Johnstone Strait on August 26, 1973; photographs taken by

Figure 20. Frequency distributions of calls produced by pods A1, A4 and A5 while foraging together. Pre-1978 samples are assumed to have involved the A-pods on the basis of call types recorded.

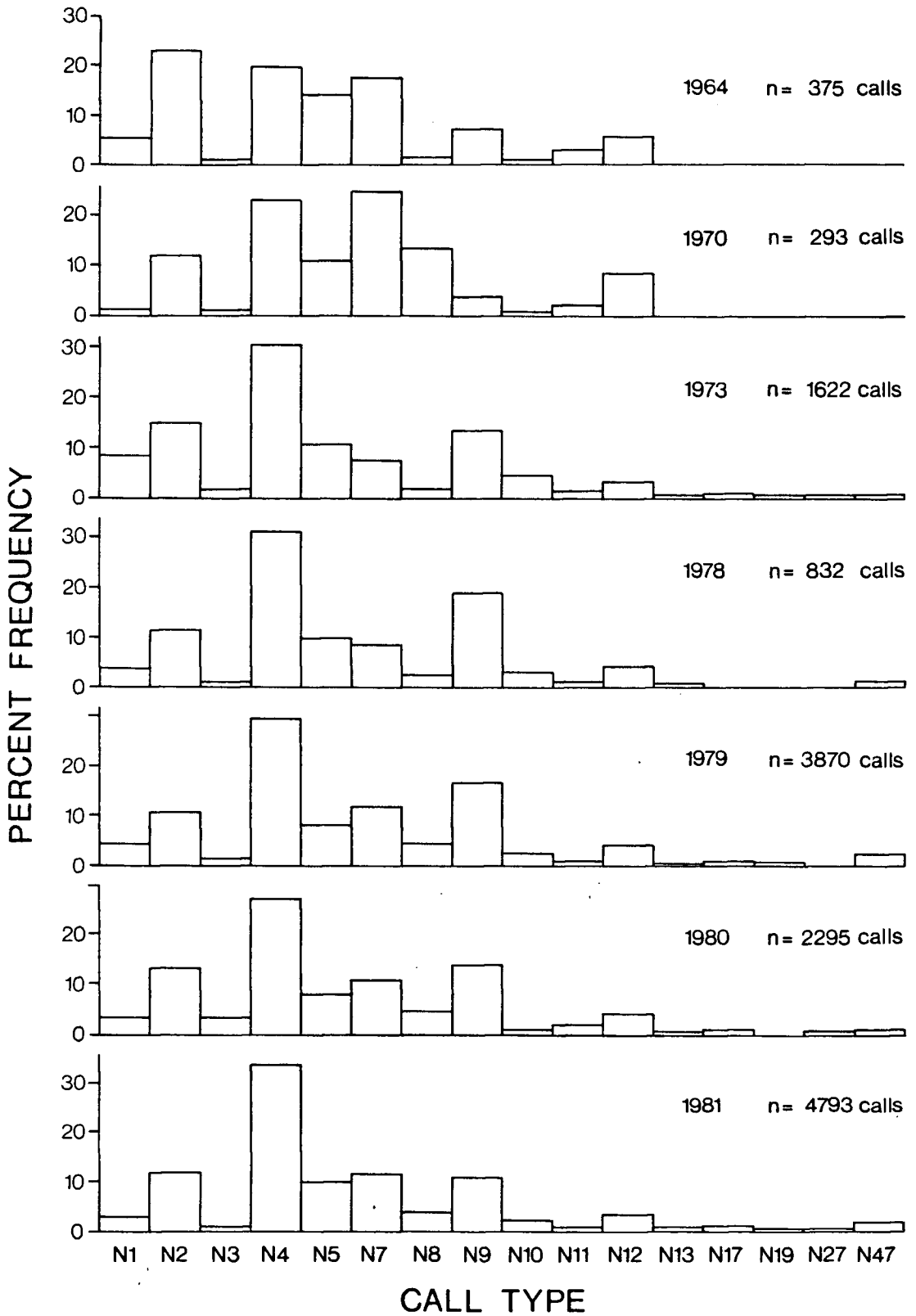


Figure 21. Frequency distributions of calls produced by pods A1, A4 and A5, during 1978-83 combined.

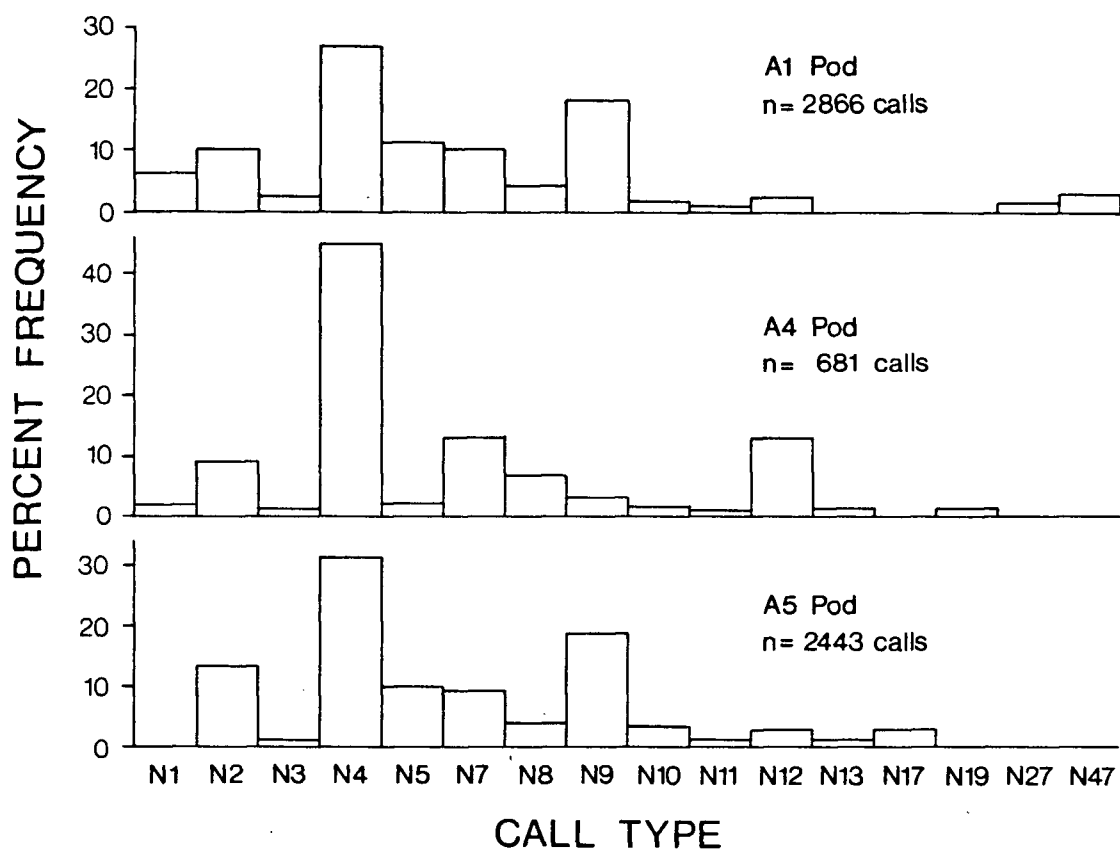
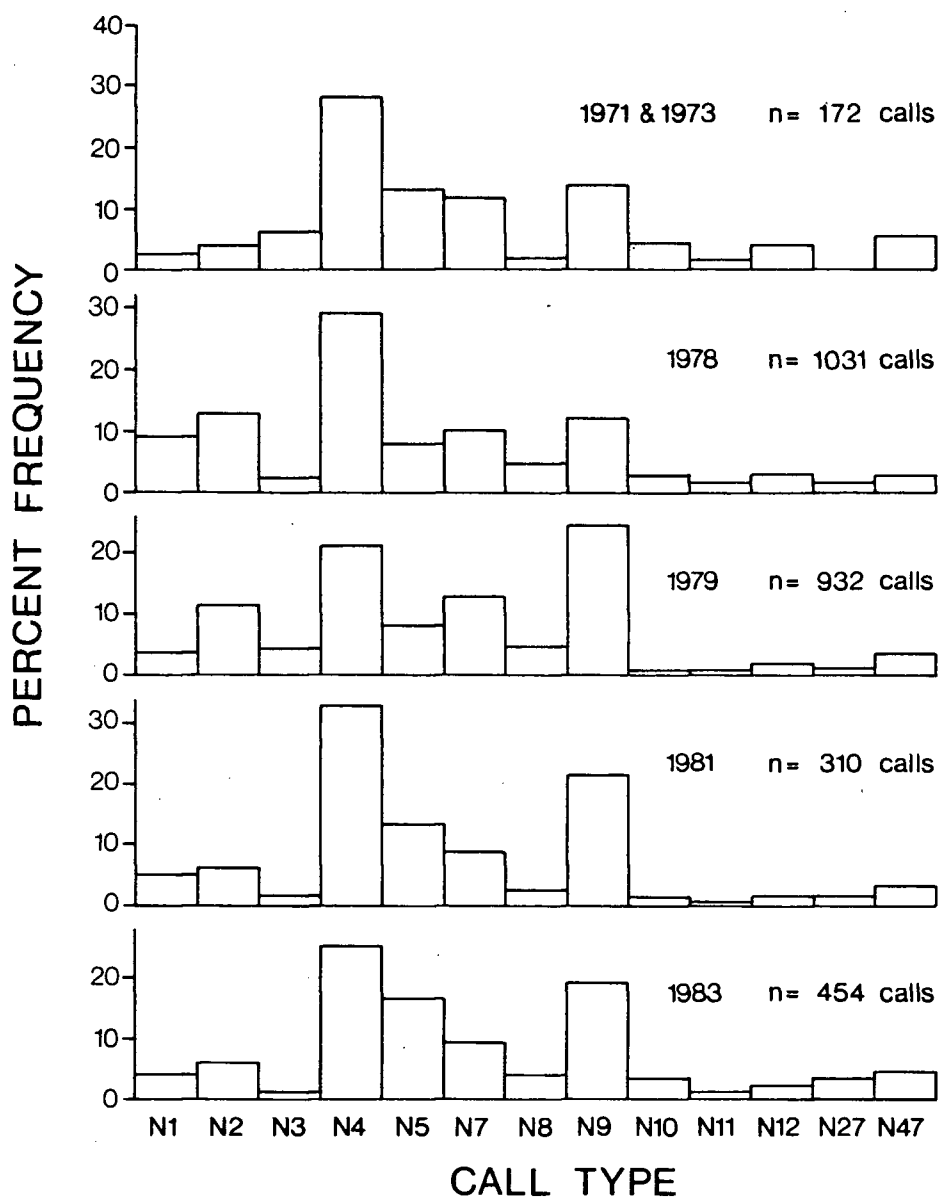


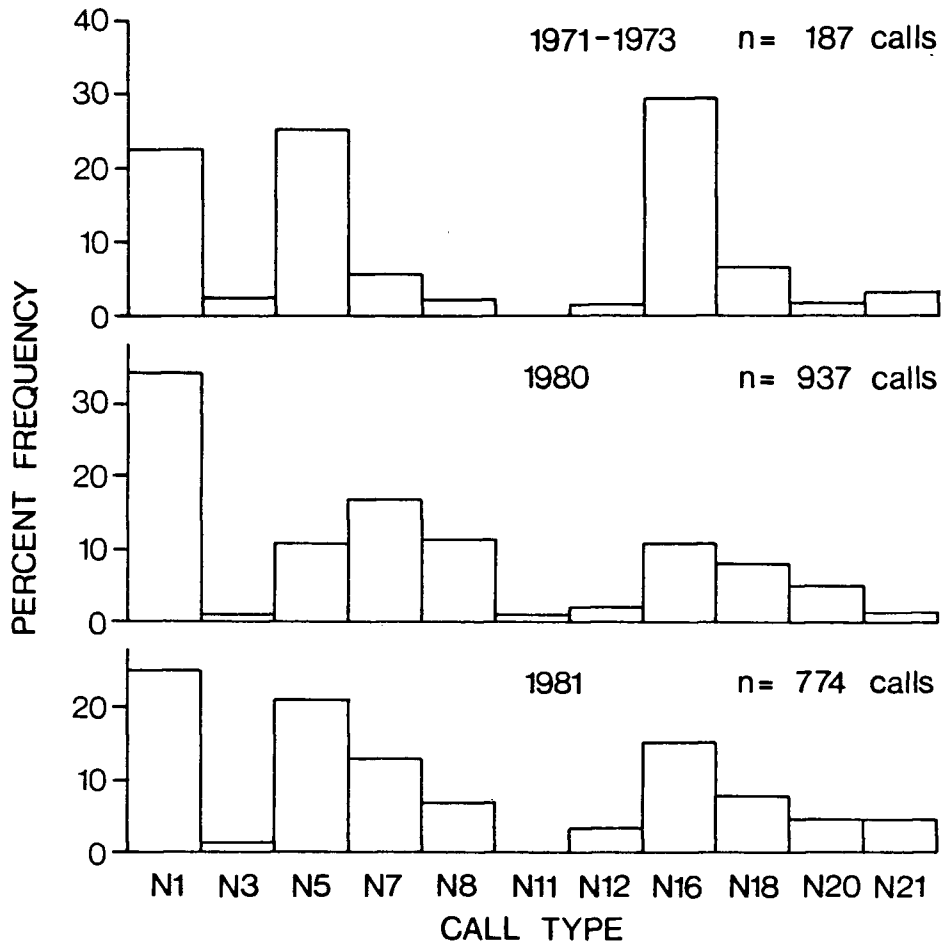
Figure 22. Frequency distributions of calls produced by A1 pod alone, 1971-1983. Recordings from 1971 and 1973 are known to have involved A1 pod from visual or photographic evidence.



M. Bigg and co-workers at this location on the same day contain A1 whales exclusively (M. Bigg, pers. comm.). Call types and variants recorded on both occasions are typical of A1 pod. Comparing the frequency of use for calls N1 to N12 and N47 in these early encounters and in A1 recordings made during 1978, 1979, 1981, and 1983 revealed no significant differences. The uncommon call N27 was recorded in the recent samples but not in 1971-73.

The B-Group of Pods: The five B-group pods can be divided into two subgroups based on call use; the first contains B, H and I1 which share call N5 and some subtypes of other calls, and the second contains C and D pods, which do not give N5 and share subtypes of other calls. The frequency distribution of B-pod calls during 1971 and 1973 combined, 1980 and 1981 are shown in Figure 23. The 1973 recording, made by E. Hoyt in Johnstone Strait on August 24, 1973, contained calls characteristic of both the A-pods and B. Identification photos taken independently at the same time and location by M. Bigg (pers. comm.) confirm that pods A1, A4, A5 and B were present in the area. All but the uncommon call N11 are present in the 1971/73 sample, and ANOVA comparisons of call occurrence among this early sample and those from 1980 and 1981 revealed no significant differences. Contingency table analysis of a preceding/following transition matrix for all calls in B-pod's repertoire except N3 and N21 indicate that call occurrence was highly non-random ($G = 850.5$, $df = 49$, $p < 0.001$). Cluster analysis of association indices calculated from this matrix

Figure 23. Frequency distributions of calls produced by B pod. Tapes from 1971-73 are assumed to have involved B pod on the basis of call types recorded.



(Figure 24) illustrate the very close association of calls N7 and N8, as described for the A-pods (Part I). Other than this pair, no calls show strong tendencies to occur together.

The distributions of calls produced by pods H and I1 are illustrated in Figure 25. Calls characteristic of H pod were present in two short samples from 1970 and 1974. Although too few samples are available for statistical comparison, the pattern of call use seems quite similar between these early tapes and those made during 1978-82. Calls N3 and N11, however, were not present in the older recordings. Pod I1's repertoire was not evident in any pre-1978 tape. Comparisons of frequency of occurrence of call N5 revealed no significant variation between pods B, H and I1, but all three groups produce the call more often than the A-pods ($p < 0.001$). B pod produces N1 less often than H pod ($p < 0.05$); neither pod differs from I1 pod in use of N1, but all produce the call more frequently than the A-pods. Occurrence of N7 is similar in B, H, I1 and the A-pods, but N8 is used less often by the A's ($p < 0.001$).

The considerable similarity in the structure of calls produced by pods C and D is paralleled, in most cases, in their use of those calls (Fig. 26). The principal difference lies in the production of the short and long versions of N16; in D pod, the short form represents 39.5% of total call use, significantly greater ($p < 0.001$) than the 12.9% in C pod. C pod's use of the long form amounts to 28.2% of all calls, in contrast to 3.9% in D pod ($p < 0.001$). The only other significant variation between samples of the two repertoires was in N20, which occurred more

Figure 24. Cluster diagram of call associations in the repertoire of B pod. Associations are based on an index derived from transition frequencies between call types. See text for further details.

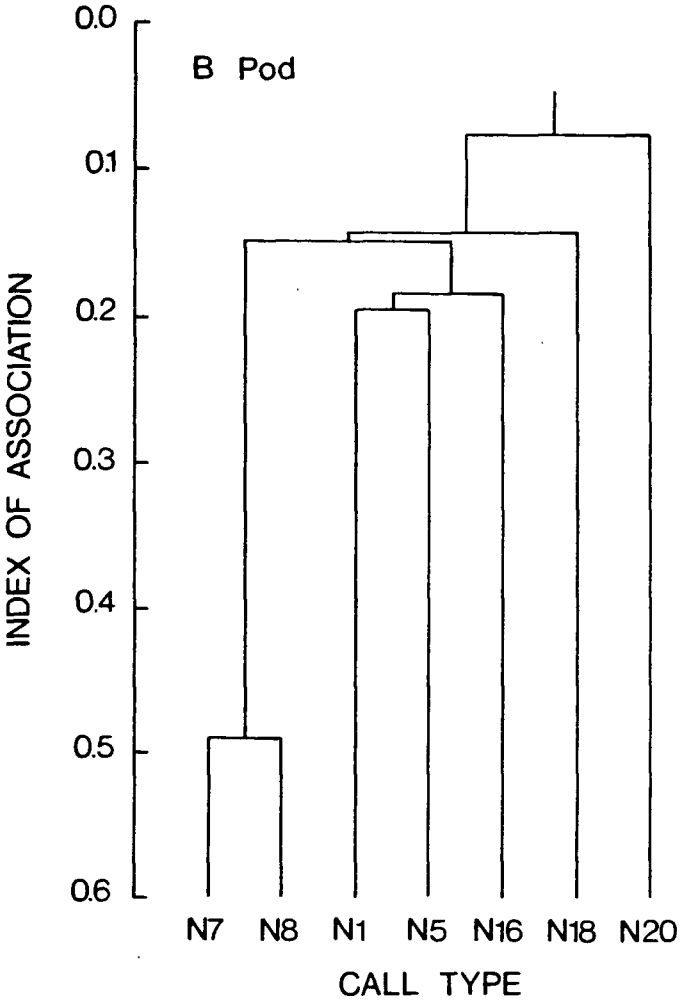


Figure 25. Frequency distributions of calls produced by pods H and I1. Tapes from 1970 and 1974 are assumed to have involved H pod on the basis of call types recorded.

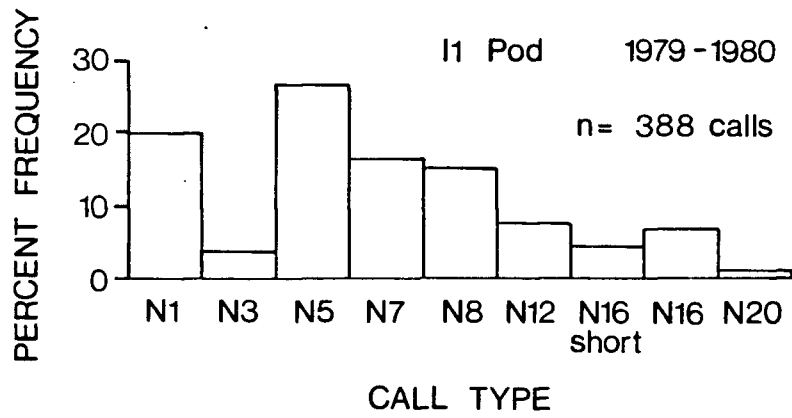
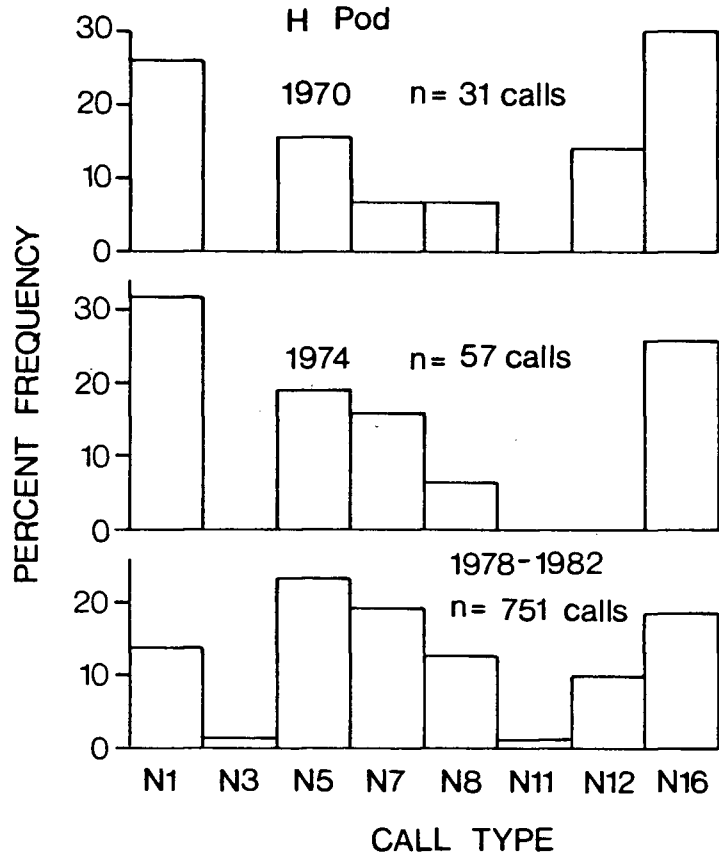
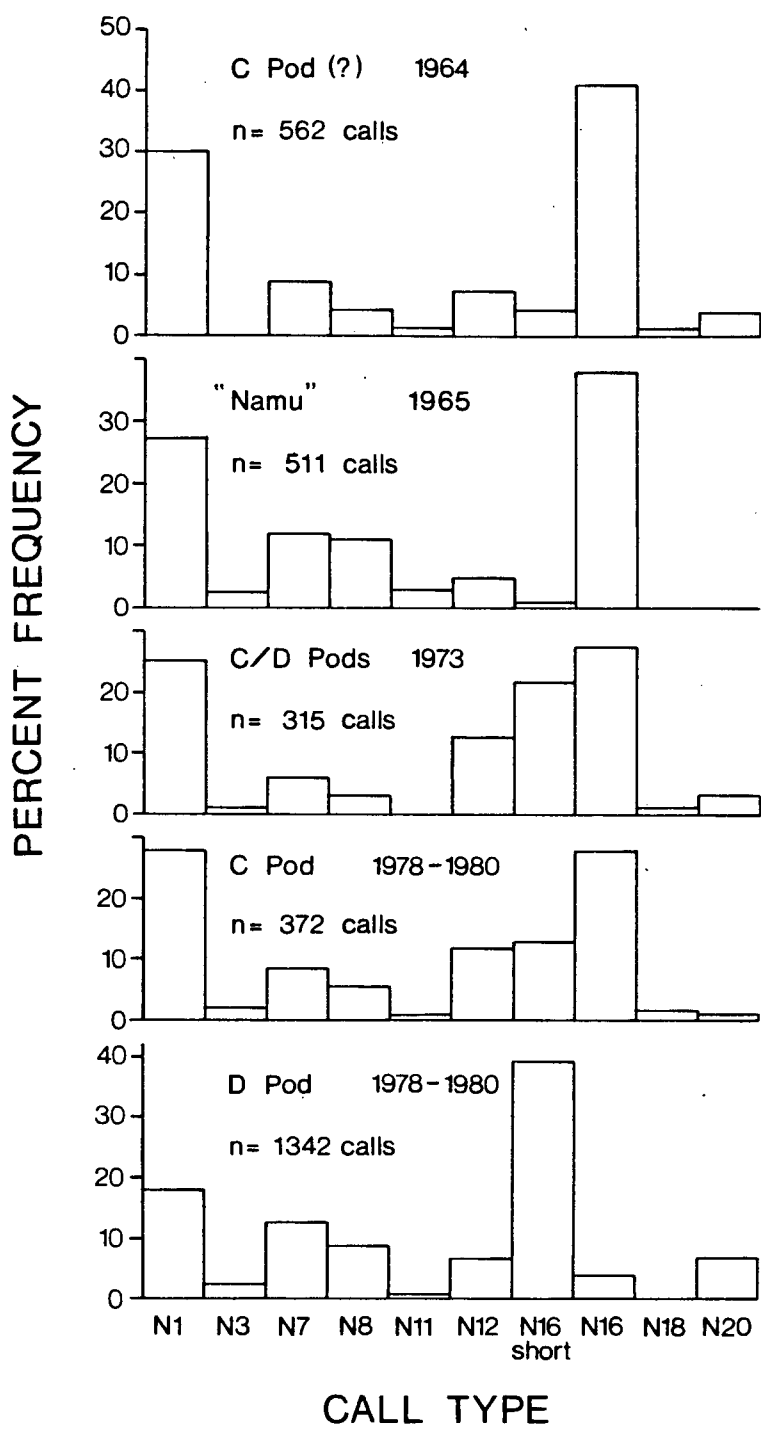


Figure 26. Frequency distributions of calls produced by C and D pods, and the captive whale "Namu". "Namu" was identified by M. Bigg (pers. comm.) as having been taken from C pod in June, 1965. Tapes from 1964 adn 1973 are assumed to have involved C and/or D pods on the basis of call types recorded.



often in the D pod recordings ($p < 0.01$).

There is a good deal of evidence to suggest that the repertoire of C pod has changed little since 1964. Recordings made apparently in the presence of the group in that year contain all but one (N3) of the calls used in recent years, and their frequency of occurrence differs only in the short form of call N16, which was significantly ($p < 0.05$) less common in 1964. Another indication of repertoire stability in the pod results from recordings of the whale "Namu", which was captured in 1965 from a group determined later by M. Bigg to be C pod. This animal produced all calls typical of the pod except the uncommon N18 and N20, and the frequency distribution of those calls differs only in the short form of N16, which again was less often used ($p < 0.001$). Cluster analyses of the transition associations of common calls of C pod and Namu show a similar pattern of call use (Fig. 27). There are significant differences in some structural variables of Namu's calls compared to C-pod's calls recorded during 1978-80 (Appendix III), but the overall forms of the signals are fundamentally the same. Sample spectrograms of two C-pod calls as they occurred in 1964, from Namu, and during 1978-80 are shown in Figure 28.

III) Summary of acoustic associations: A-clan

An appraisal of acoustic associations within the A-clan was obtained using an index of repertoire similarity for each pair of pods (Table X), and arranging these values into a dendrogram by means of single-link cluster analysis (Figure 29). The

Figure 27. Cluster diagrams of call associations in the repertoires of A), C pod, and B), the captive whale "Namu". See Figure 24 caption for details.

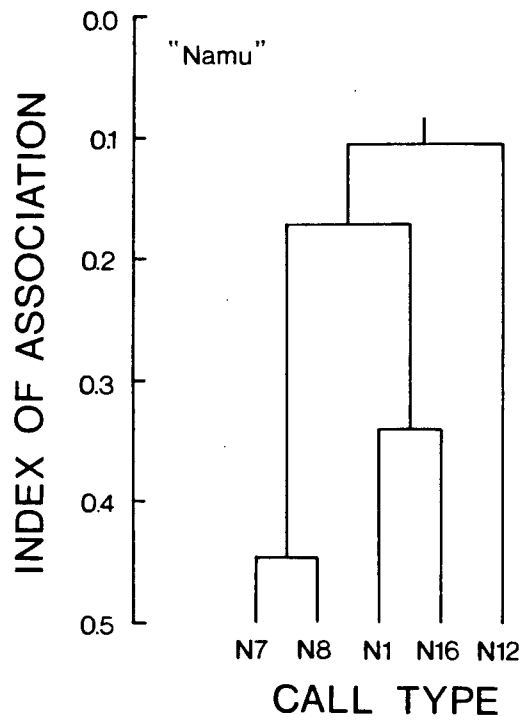
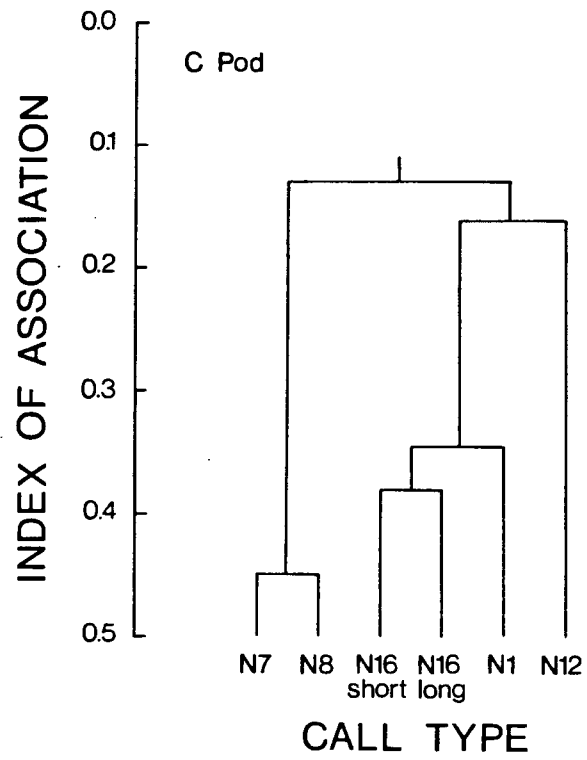
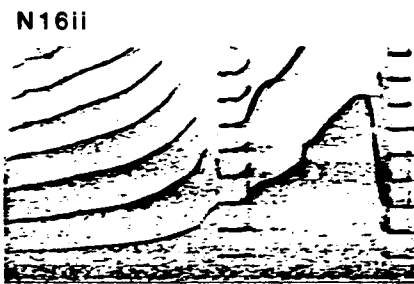
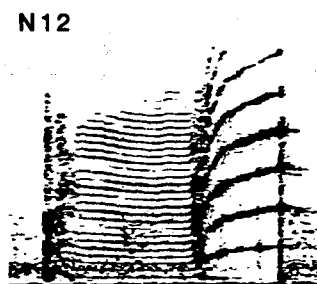
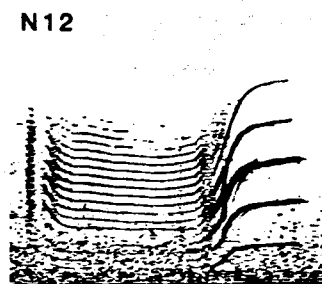
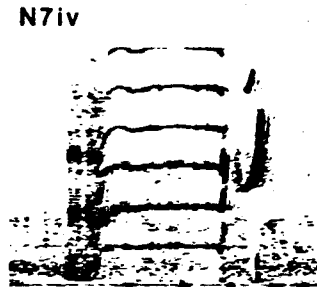
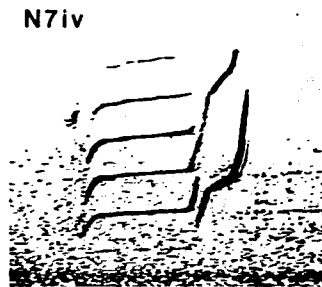
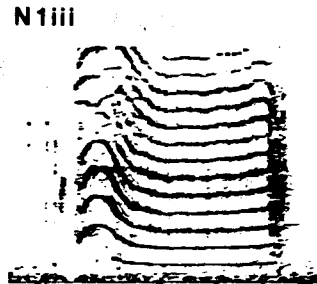
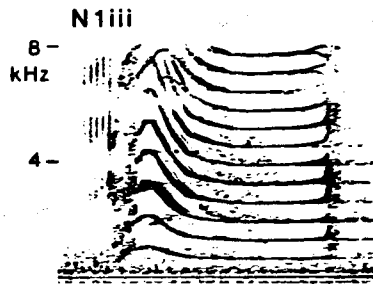


Figure 28. Spectrograms of selected C-pod call types produced in 1978-80 and by the captive whale "Namu" in 1965.

C POD - 1978-80

"NAMU" - 1965

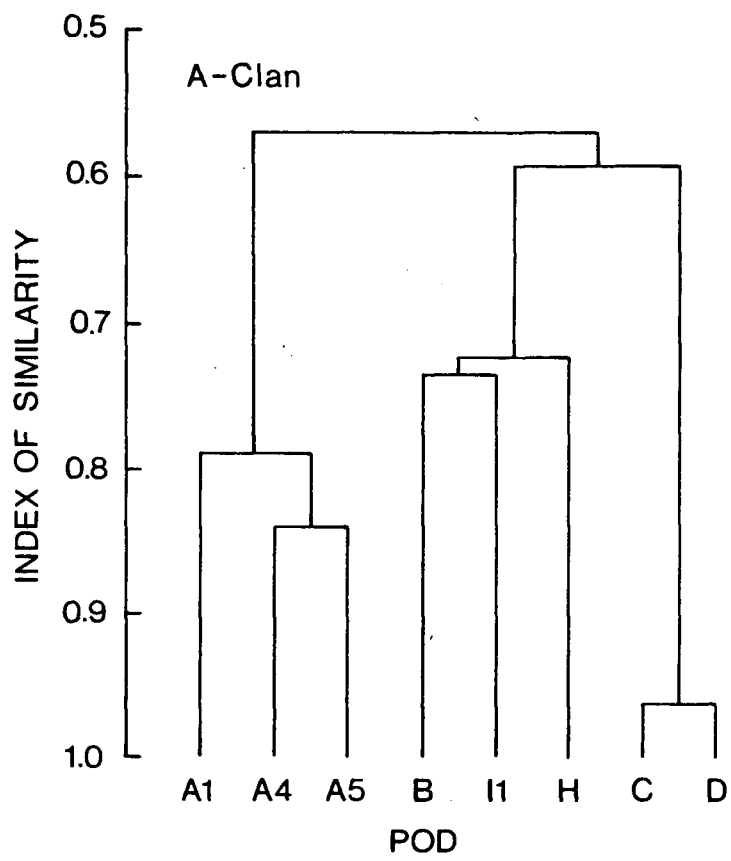


0 500 ms

Table X. Degree of similarity in dialects of A-clan pods. Values shown are the total number of call types plus the number of subtypes shared for each pair of pods, and, in parentheses, the index of similarity based on this number. See text for derivation of the index.

		POD						
		A1	A4	A5	B	C	D	H
POD	A4	15 (.750)						
	A5	15 (.789)	16 (.842)					
	B	9 (.450)	9 (.450)	8 (.421)				
	C	6 (.353)	6 (.353)	5 (.312)	10 (.589)			
	D	6 (.364)	6 (.364)	5 (.323)	9 (.545)	13 (.963)		
	H	10 (.571)	10 (.571)	9 (.545)	11 (.629)	8 (.522)	8 (.571)	
	I1	8 (.421)	9 (.514)	7 (.389)	14 (.737)	7 (.438)	7 (.452)	12 (.727)

Figure 29. Cluster diagram of acoustic associations of A-clan pods. Association is represented by an index of repertoire similarity based on the degree of call type and subtype sharing between pods. This index is described more fully in the text.



resulting diagram shows that within the A-group of pods, A4 and A5 tend to be more closely related acoustically than either is to A1 pod. Similarly, within the B-group, pods C and D form a distinct subgroup with a high level of similarity (0.963), and pods B, H and I1 form another subgroup with a somewhat lower degrees of homogeneity. It is noteworthy that I1 pod produces two versions of several call types. Some are unique to the pod, while others are shared with B or, more often, H pod. The A- and B-groups of pods are related at the 0.571 level of similarity.

B. G-Clan

The G-clan is comprised of three pods, G, I11 and I31, with a total of 37 members (Table VIII). The clan has a repertoire of 15 call types, one of which has two subtype forms. These calls and the pods observed to produce them are listed in Table XI. Four of the G-clan call types are used by all three pods. The remainder are made only by one or two of the pods.

I) Call characteristics

The most common call of the G-clan pods is N23, which occurs in two variant forms, N23i and N23ii (Fig. 30). N23i is shared by I11 and I31 pods and N23ii is given exclusively by G pod. It is a two-part signal with a distinctive, narrowband tone emitted simultaneously during part 1. Part 1 is similar in both subtypes, but significant differences in the structure of Part 2 distinguish the two subtypes. This component in N23i

Table XI. Call types and subtypes produced by pods of the G clan in the northern resident community.

Calls	Pods			Calls	Pods		
	G	I11	I31		G	I11	I31
N23		X	X	N40	X	X	X
i				N41	X	X	X
ii	X			N44	X		
N24		X	X	N45	X	X	
N25	X	X		N46		X	X
N26		X	X	N48	X	X	X
N28	X						
N29	X						
N30		X	X				
N38	X			Total	10	11	9
N39		X	X				

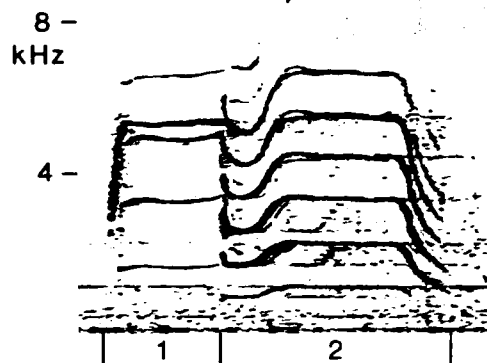
starts with an immediate drop in pitch to a mean of about 850 Hz, followed by an increase to approximately 1250 Hz, then a drop once again to about 400-475 Hz at the call's end. Part 2 in N23ii, on the other hand, maintains a nearly constant pitch of slightly more than 1000 Hz throughout, except for a slight drop to an average SBI of 726 Hz at the end of the call. Pod I31's versions of subtype N23i had a terminal downsweep which was reduced in both duration ($p < 0.001$) and drop in pitch ($p < 0.01$) compared to I11. As a result, the average duration of the call was almost 100 ms less in I31. Both subtypes of N23 are frequently preceded within 1 s by an 'introductory note' consisting of a short (< 150 ms) pulse burst with SBI's of 100-150 Hz.

Another call which shows considerable pod-specific variation is N25, used by pods G and I11, but not I31. The call has a fairly elaborate four-part structure, with an independent narrowband tone overlapping part 2 at about 7500 Hz (Fig. 30). Renditions of the call differ significantly in many structural variables (Appendix III), but most distinctively in the final part 4, which tends to be far shorter in most samples from G pod (means = 185 ms in G versus 637 ms in I11; $p < 0.001$). Despite this marked difference, overlap in the measurements of this component was noted, and hence the versions were not assigned to discrete subtype categories.

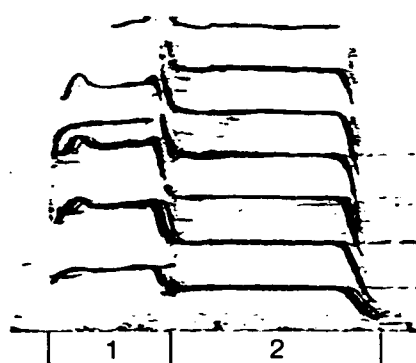
Calls N24, N26, N30 and N48, shown in Figure 31, are given exclusively by I11 and I31 pods, with the exception of N48 which has not been recorded from I31. N24 is a common call in both

Figure 30. Spectrograms of G-clan call types N23 and N25.

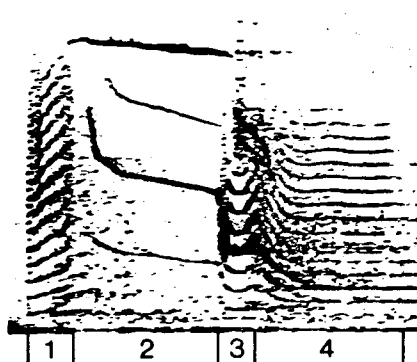
N23i - I11, I31



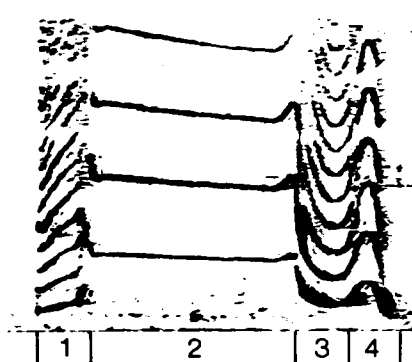
N23ii - G



N25 - I11

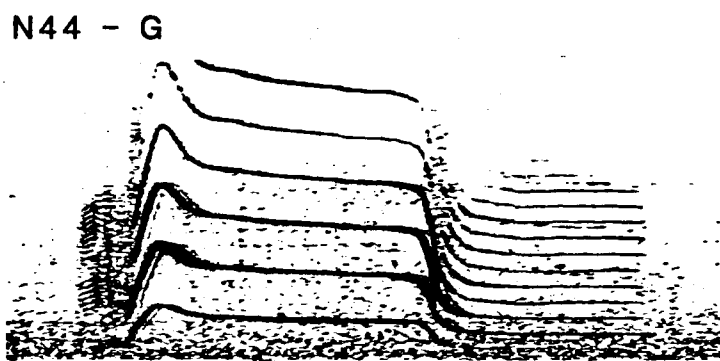
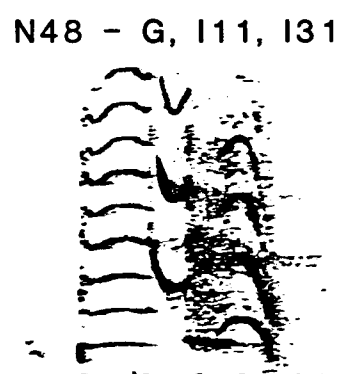
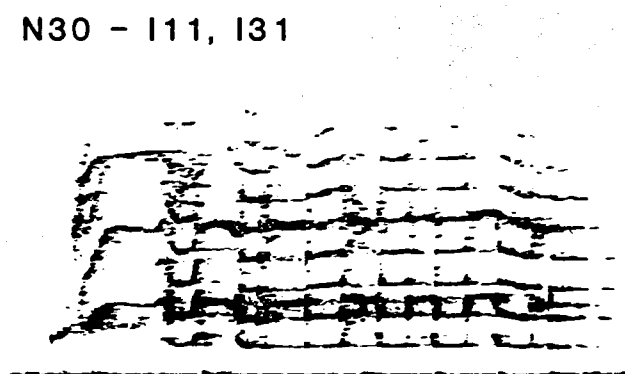
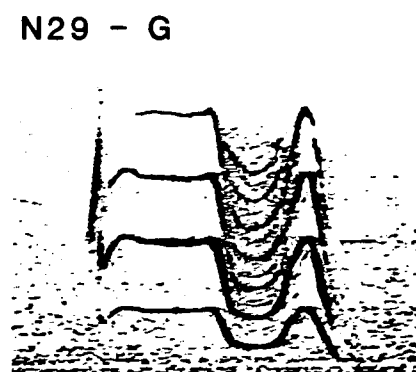
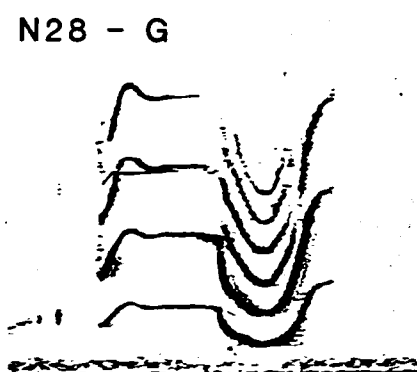
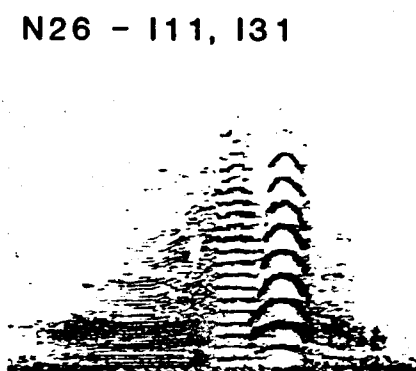
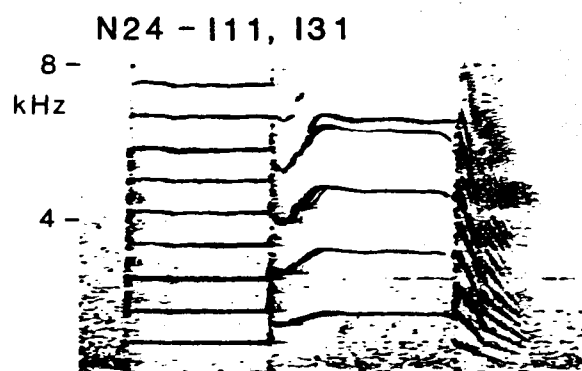


N25 - G



0 500 ms

Figure 31. Spectrograms of G-clan call types N24, N26, N28, N29, N30, N44 and N48.

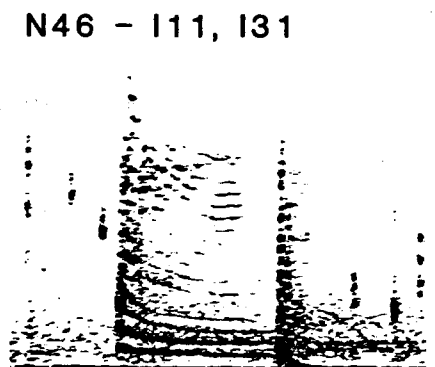
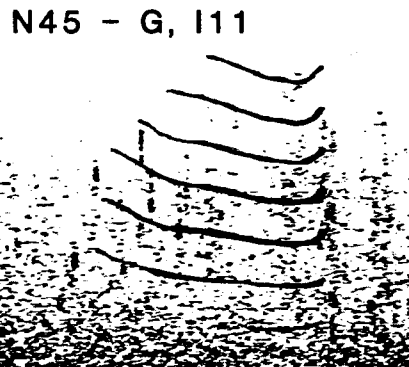
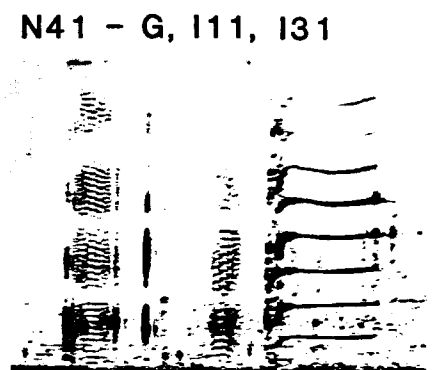
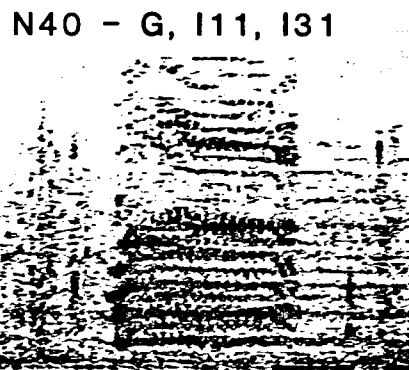
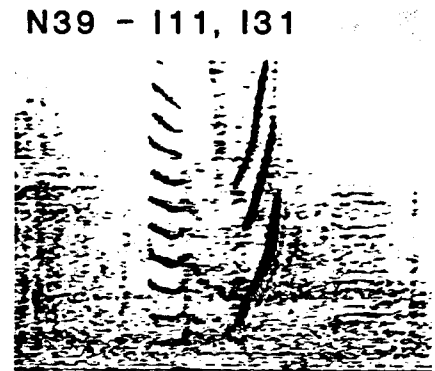
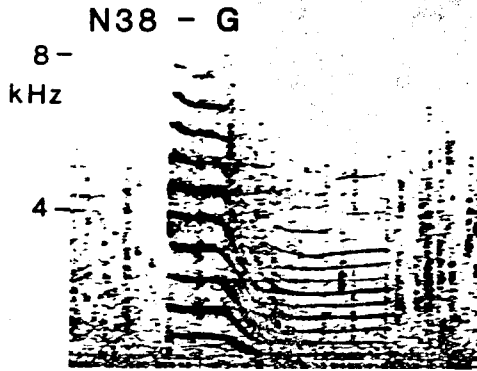


0 500 ms

repertoires and appears to differ in several aspects between the two pods. However, due to the small sample size for I31, the validity of these differences cannot be determined. Call N30 is an unusual call which often begins in the same manner as N23, but thereafter consists entirely of rapid alternations of high and low pitch pulse-bursts, both of which have consistently higher SBI's in I31 pod's versions ($p < 0.001$ and $P < 0.05$ in low and high pitched components, respectively).

Calls N28, N29 and N44 are given exclusively by G pod (Fig. 31). Both N28 and N29 appear to be closely related to N23 in the first part, but the remaining portions differ in each call. An introductory note, like that which precedes N23's, occurs frequently just prior to the emission of calls N28 and N29. The G-clan has a relatively large repertoire of six calls, shown in Figure 32, which are used mainly in low arousal contexts. However, not all of these are given by each pod (Table XI). All are short-duration signals and most have rather simple structures. An exception is N41, a call used by all three pods, which occurs generally in four parts, each separated by a short gap. Part 1 is very similar in structure to the introductory notes preceding many N23, N28 and N29 calls, and may have a comparable role since N41's occur occasionally without this component. Introductory notes without a following call are also heard during low-arousal contexts.

Figure 32. Spectrograms of G-clan call types N38, N39, N40, N41, N45 and N46.



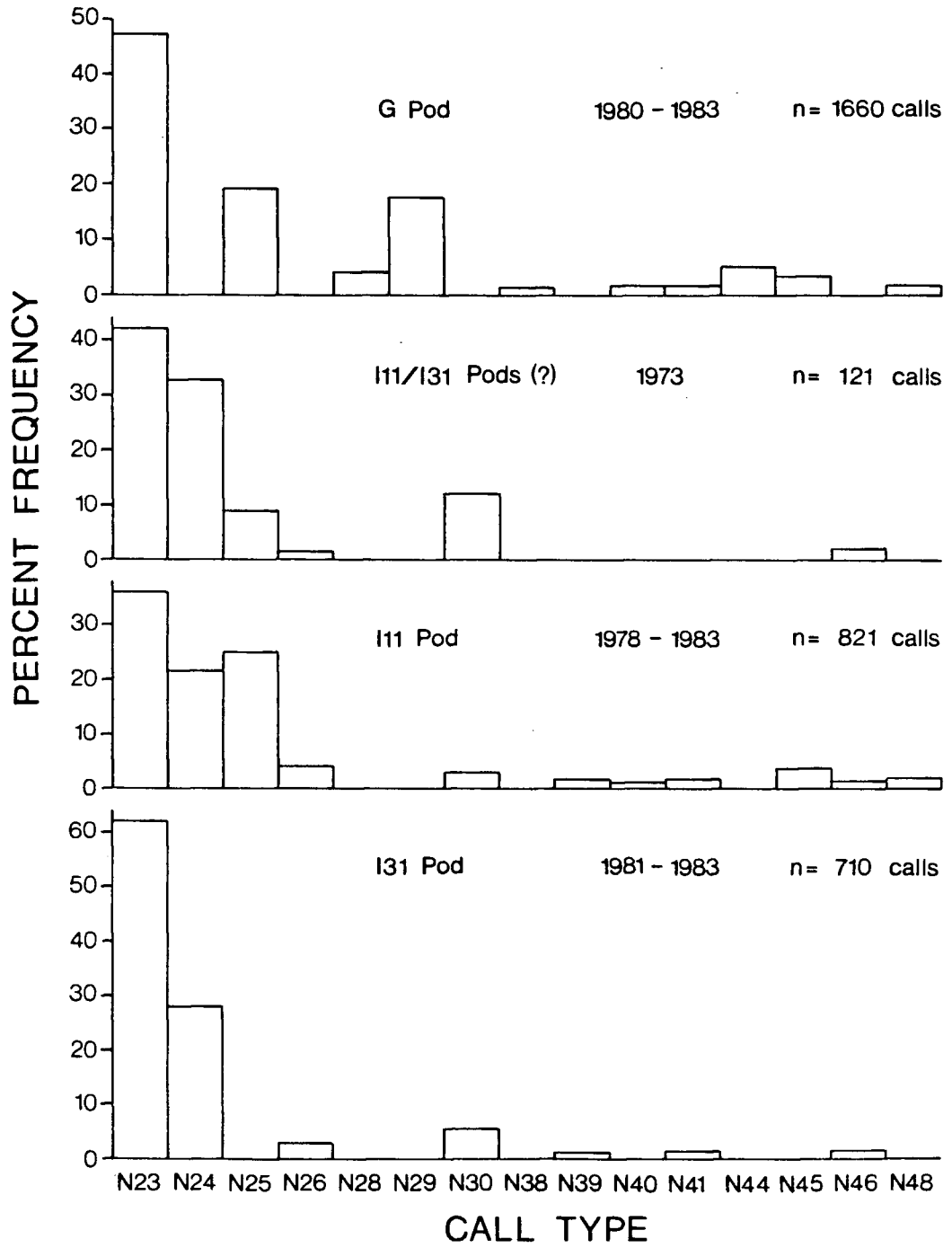
0 500 ms

II) Call use

Frequency distributions of calls produced recently by G-clan pods are illustrated in Figure 33, along with the distribution of calls in a tape recorded during 1973, apparently in the presence of I11 and, possibly, I31 pods. These show that there is a strong dependence on call N23 throughout the clan, especially in the case of I31 pod (61.8% of all I31 calls recorded during 1981-83). The occurrence of most of the remaining call types differs markedly among the three pods. Call N24 is the second-most abundant call in the repertoires of I11 and I31, representing 22.1% and 27.9%, respectively, of call use, but it is not used by G pod. N25 is important in the calling of G and I11, but it was not recorded from I31 pod. Although the sample for 1973 is small, the frequency distribution and structure of calls is similar to that recorded recently from encounters with I11 and I31 pods foraging together. No photographic evidence of the pods present on the single encounter in that year is available. Calls characteristic of G pod were not present in any pre-1978 tape examined.

There are limited data on each pod's use of resting or low-arousal calls. However, in several short encounters with a resting subgroup of G pod, N41 was the most common call representing 66.7% of the 78 calls recorded, followed by N40 (19.7%) and N38 (13.6%). Call N38 appears to be closely associated with N40, occurring typically within 1 or 2 s of the latter. In I11 and I31, call N46 is the most frequently used

Figure 33. Frequency distributions of calls produced by G-clan pods. Tape from 1973 is assumed to have involved I11 and/or I31 pods on the basis of call types recorded.



resting call, representing 43.8% of 160 calls recorded from the two pods together, followed by N40 (20.5%), N41 (18.8%), N45 (13.8%) and N39 (3.1%).

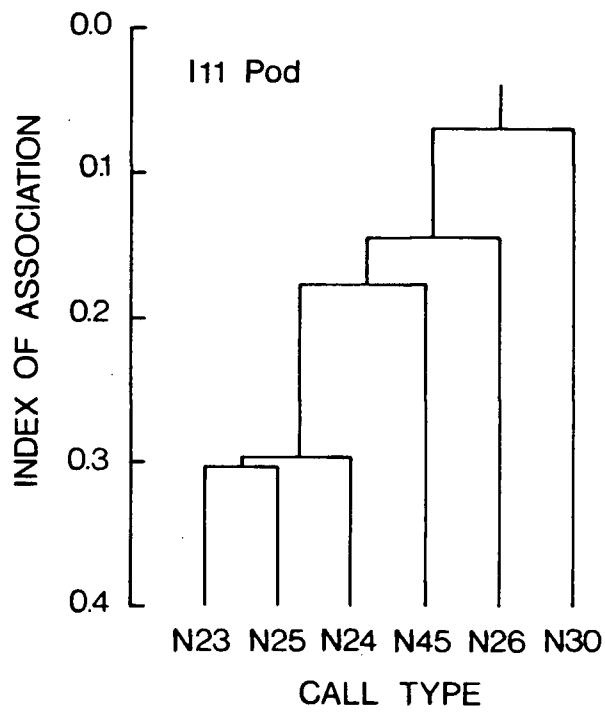
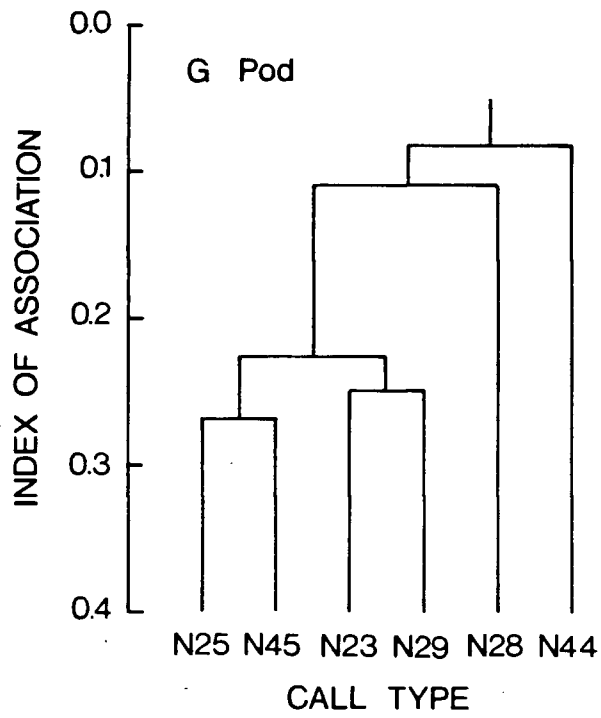
Examination of the associations of G-clan call types on the basis of transition frequencies revealed patterns of use similar to other clan repertoires. Calls are emitted typically in repetitive series, and within each pod's repertoire certain calls tend to occur together more often than by chance. In the repertoire of G pod, calls N25 and N45 are the most strongly associated, with an index of 0.269 (Fig. 34). This association results from the tendency for N45's to be given immediately prior (< 2 s) to the emission of an N25. Although many N25's were heard without an introductory N45, few N45's occurred alone. Calls N23 and N29 often occur together, but N28 and N44 are not strongly associated with any particular call.

Calls N25 and N45 are also related in the same manner in I11's repertoire, but N45's are also given commonly without a following N25, primarily during low-arousal activities. Thus, the N25/N45 association is not as clearly evident in the diagram of I11 call relationships. As might be expected, the common calls N23, N24 and N25, which dominate calling in the pod, frequently occur together (Fig. 34).

III) Summary of acoustic associations: G-clan

It is clear that repertoires of pods I11 and I31 are more similar to each other than either is to that of G pod. Indices of similarity based on sharing of call types indicate that I11

Figure 34. Cluster diagrams of call associations in the repertoires of pods G and I11. See Figure 24 caption for details.



and I31 are highly related acoustically with an index of 0.909. Pods G and I11 have a lower similarity level of 0.522, and G and I31 have an index of only 0.381.

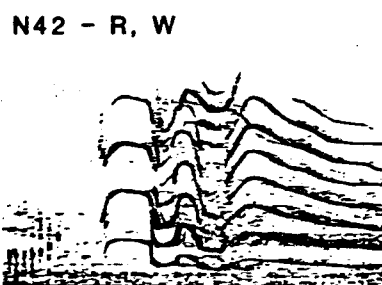
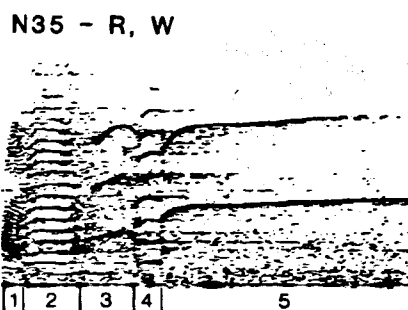
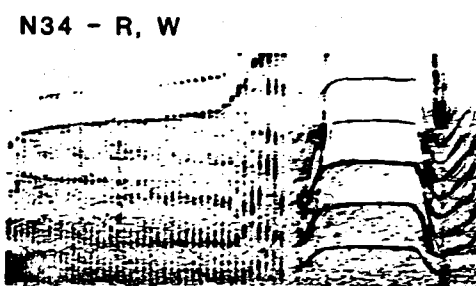
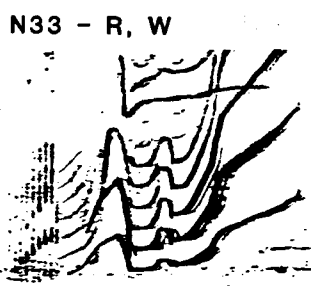
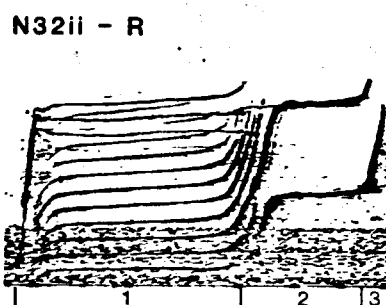
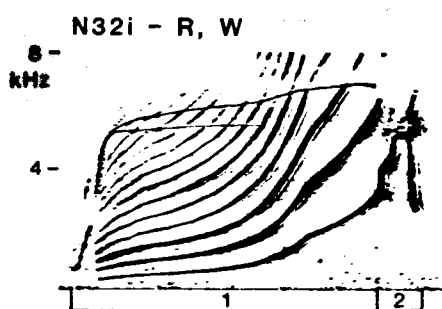
C. R-Clan

The R-clan is a small acoustic association of two pods, R and W, which had 19 and 4 members, respectively, in 1982. The clan has a total repertoire of 8 call types, N32, N33, N34, N35, N42, N43, N50 and N51, all of which are used by both pods. Call N32 occurs in two subtype forms; N32i is produced by both pods, but N32ii appears to be made by R only.

I) Call characteristics

The call repertoire of R-clan pods is illustrated in Figure 35. The two most common calls, N32 and N33, are similar in general structure, except N33 has a series of rapid modulations in SBI before terminating in the same manner as N32. In subtype N32ii, the pitch is constant or increases slightly over the first half of the call, then shifts suddenly to a higher SBI, in contrast to the steady increase seen throughout N32i. Pod R's version of N32i appears to be consistently longer in duration than W's ($p < 0.05$) and reaches a higher pitch in part 2 ($p < 0.01$). Of 17 frequency and duration variables measured for call N33, only one differed significantly between the two pods; the duration of the low pitch modulation following the first peak in part 2 was lower in R (mean = 54 Hz) than W (mean = 195 Hz) ($p < 0.001$).

Figure 35. Spectrograms of R-clan call types N32, N33, N34, N35, N36, N42, N43, N49, N50 and N51. Call N49 was recorded only in tapes made during August, 1964, apparently in the presence of R and/or W pods.

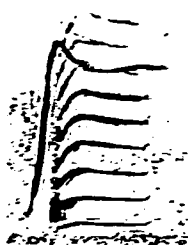


N36 - R, W

N49 - 1964

N50 - R, W

N51 - R, W



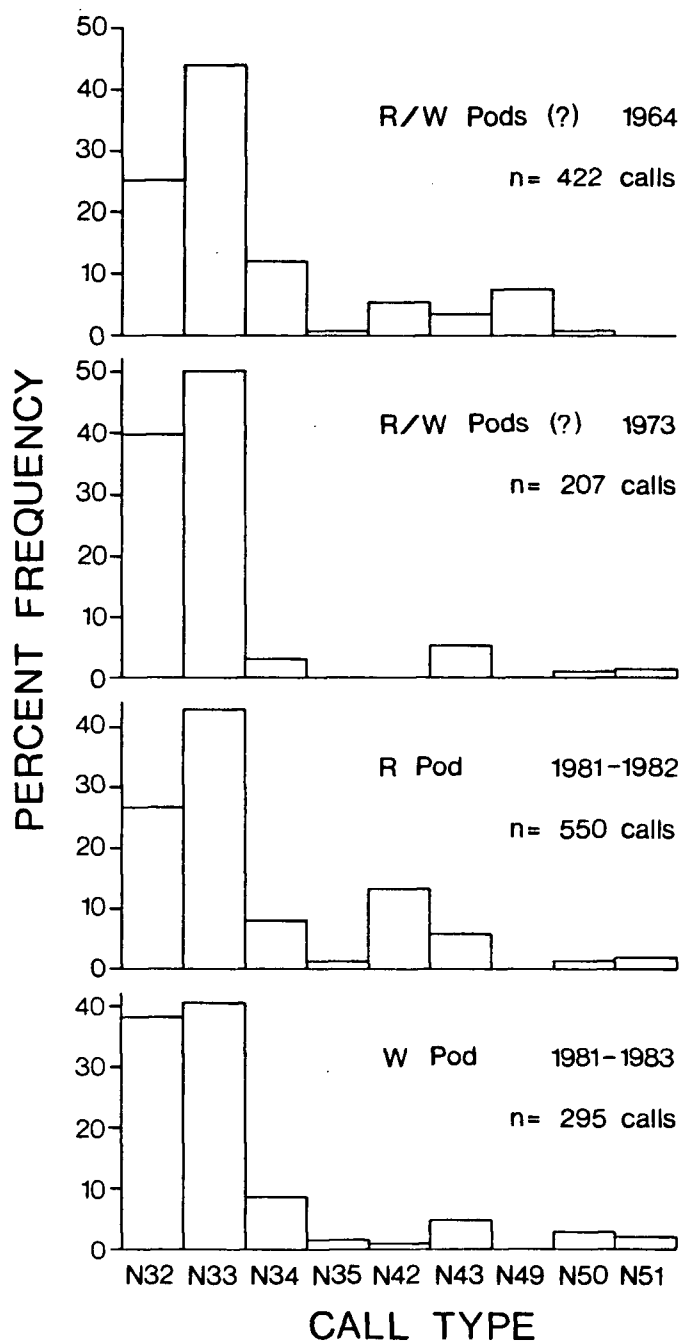
0 500 ms

Of the remaining R-clan calls, only N35 shows consistent pod-specific variation. In samples of this five-part call, parts 1, 2 and 4 are significantly shorter in W pod's version, resulting in overall durations averaging 1056 ms in R pod compared to 612 ms in W ($p < 0.001$). The structures of R-clan calls recorded in 1964 and 1973 were examined and found to be similar to those obtained from R and W pods recently. Although too few samples suitable for statistical analysis were obtained for most call types, N33 and N34 were well represented in the early tapes. A number of N33 variables differ significantly between 1964, 1973, and 1981-83 recordings of R and W pods, but there is no obvious trend of change in any component over the 19 year period between the earliest and most recent samples. In the case of N34, no significant differences are apparent in 1964 versus 1981-83 samples from R or W pods. Call N49 (Fig. 35) was present only in the 1964 recordings.

II) Call use

The frequency distributions of R-clan calls as recorded in 1964, 1973, and recently from R and W pods are shown in Figure 36. All calls recorded during 1981-83 from these pods are present in the 1964 sample, except the uncommon call N51. However, call N49, which comprised 8.06% of the 422 R-clan calls analysed from the 1964 tapes, was not represented in either 1973 or 1981-83 samples. It is possible that the call has been lost from the repertoires of R and W pods, or that the call was specific to some R-clan pod not present in the area today.

Figure 36. Frequency distributions of R-clan calls.



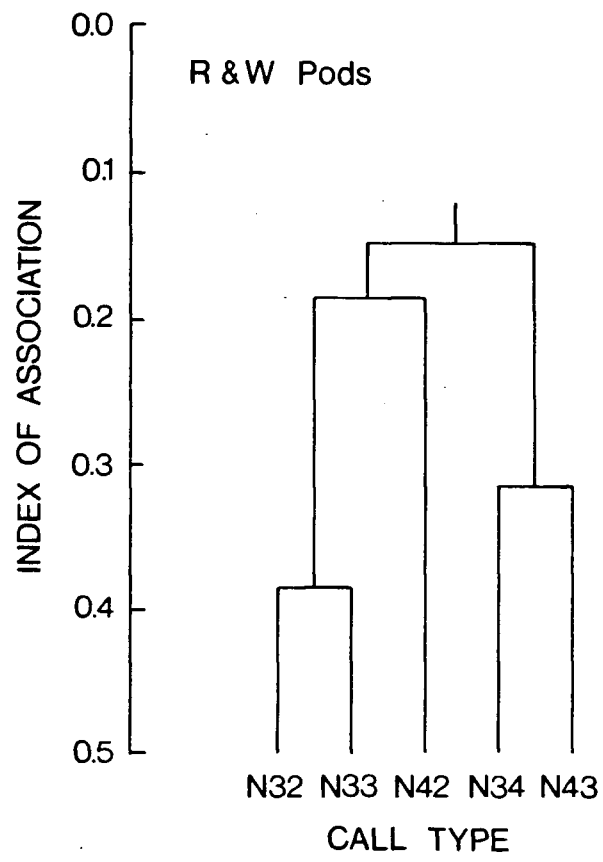
Comparing the frequency of occurrence of the remaining calls, no significant differences are apparent in the use of calls N32, N33, N34, N35, or N43 between 1964 and recent recordings of R or W. Call N42, however, is significantly less frequent in W's calling than in R's (0.7% vs 13.5%, $p < 0.001$). The uncommon calls N50 and N51 were not tested, but they comprised similar small proportions in both early and recent samples. These signals appear to be associated with low-arousal contexts, as are certain calls in the repertoires of A- and G-clan pods described above.

Analyses of transition frequencies of the common calls of R and W pods combined show significant associations between call types ($G = 180.2$, $df = 16$, $p < 0.001$). As in other clan repertoires, calls tend to occur together in bouts, thus transitions between the same call type have significantly greater-than-expected occurrences. Indices of association of different call types (Fig. 37) show that the abundant calls N32 and N33 tend to occur together, and there is a strong association between calls N34 and N43.

III) Summary of acoustic associations: R-clan

The two pods making up the R-clan are very closely related in call use. The only major difference appears to be in subtype N32ii, which is made by R but not W pod. The index of repertoire similarity between these two pods equals 0.947, which is among the highest levels observed in resident pods.

Figure 37. Cluster diagram of call associations in the repertoires of R and W pods combined.



3. Dialects of Southern Community Resident Pods.

The southern community is comprised of three pods, J, K and L, which belong to a single acoustic association referred to as the J-clan. A total of 40 pod encounters was made with J-clan pods between 1978 and 1983; pod J was encountered 18 times, K pod 10 times, and L pod on 12 occasions (Appendix I). K pod was encountered alone on only two occasions. Repertoire description is based on these as well as three K-pod recordings made by R. Osborne (Moclips Cetological Society) during 1979-80.

A. J-Clan

Pods J, K and L are comprised of 19, 10 and 50 individuals, respectively (Table VIII). L pod is the largest resident pod occurring in the study area. A total of 26 call types, listed in Table XII, was described from recordings of J-clan pods. Four of these call types have two or three discrete subtypes. J pod has a total repertoire of 17 call types, K pod has 10 calls, and L pod has 15 calls. Four calls, S6, S8, S10 and S42, are shared by all three pods, 9 are given by two pods, and 13 are exclusive to single pods.

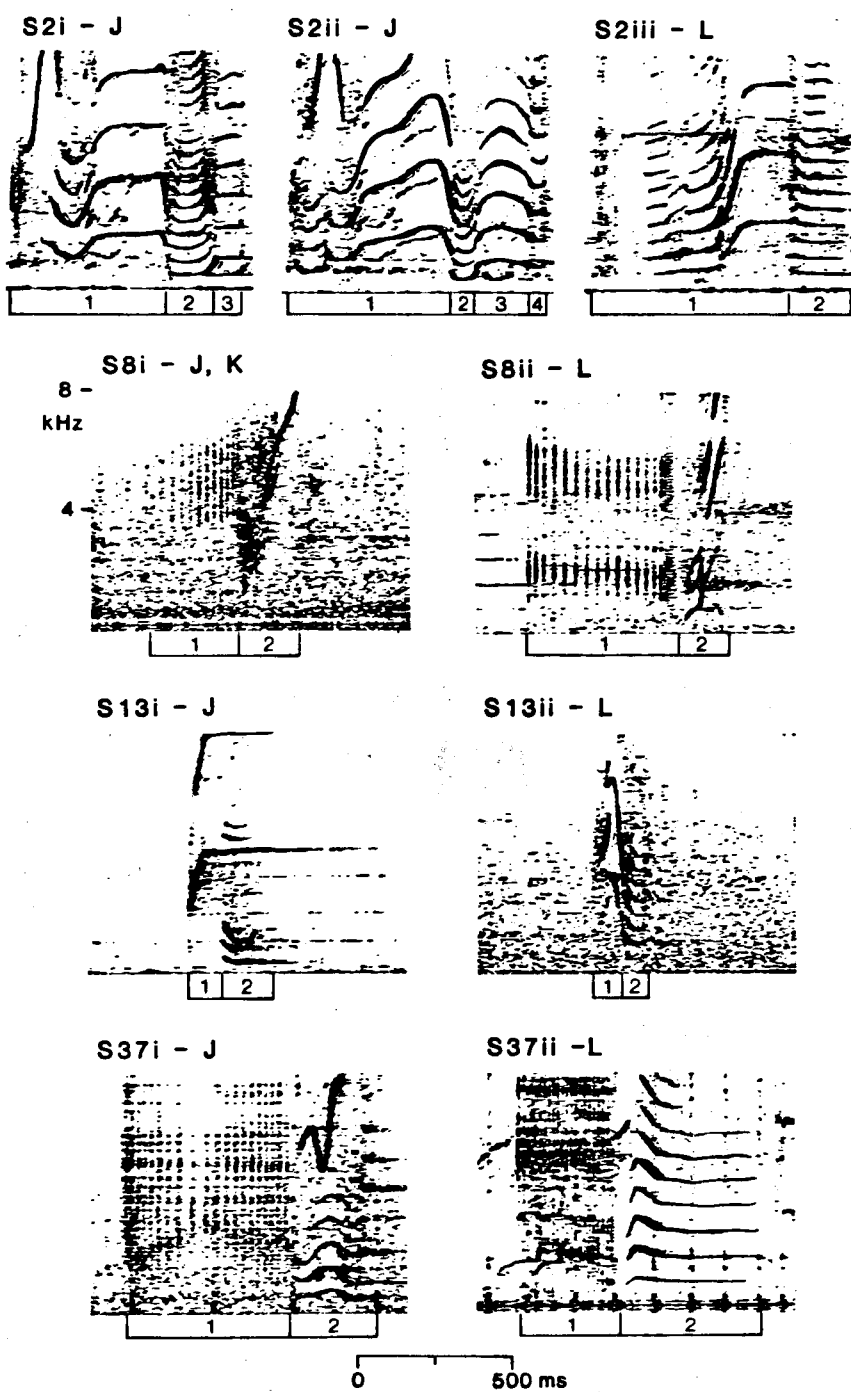
1) Call characteristics

Of the 13 call types shared by two or all three J-clan pods, 4 have discrete subtypes. There are three subtypes of call S2 (Fig. 38). Subtypes S2i and S2ii, both given by J pod, can be distinguished by the presence of a downsweep at the end of part 3 in S2ii. S2iii, used exclusively by L pod, lacks part

Table XII. Call types and subtypes produced by pods of the J clan in the southern resident community.

Pods				Pods			
Calls	J	K	L	Calls	J	K	L
S1	X	X		S16		X	X
S2 — i ii iii	X			S17		X	X
	X			S18			X
			X	S19			X
S3	X			S22			X
S4	X	X		S31			X
S5	X	X		S33			X
S6	X	X	X	S36			X
S7	X	X		S37 — i ii	X		
S8 — i ii	X	X					X
			X	S40			X
S9	X			S41	X		
S10	X	X	X	S42	X	X	X
S12	X			S44	X		
S13 — i ii	X						
			X				
S14	X			Total	18	10	15

Figure 38. Spectrograms of J-clan call types S2, S8, S13 and
S37.



3 entirely. No form of S2 call was recorded from K pod. The characteristic sharp upsweep in the brief call S8 begins at a higher SBI in S8i, produced by J and K pods, than in S8ii given by L pod (> 1500 Hz in S8i, < 1000 Hz in S8ii; Fig. 38). Another short duration two-part call, S13 (Fig. 38) also occurs in two forms, one made exclusively by J pod (S13i) and the other by L pod (S13ii). The two subtypes differ primarily in the pitch of part 1. In J-pod's versions, this component consistently reach SBI's of > 3500 Hz, while in L-pod samples, the SBI's were all < 3400 Hz. Finally, call S37 is given in two forms; S37i is used by J pod only, and S37ii by L pod. The subtypes differ in the pitch contour of the second of their two-parts (Fig. 38). The nine remaining J-clan calls which are used by more than one pod are illustrated in Figure 39.

Calls produced only by J pod are shown in Figure 40, and those given by L pod alone are shown in Figure 41. S18, a common call in L-pod's repertoire, has an interesting composite structure. The main component of the call is a 250-600 ms pulsed tone, which is usually preceded by 3 or 4 (range = 0-9) 50-100 ms long upsweeps, or 'chirps', spaced about 200-250 ms apart. Occasionally, the chirps are heard without the pulsed tone, and vice versa. Although unrelated to the call types discussed here, another noteworthy feature of J-clan sound production is the tendency for whistles to occur in long, repetitive series of pulses, especially during socializing activities. Each whistle pulse is 100-400 ms in duration, and has a constant pitch within a bandwidth of about 4000 to 8000

Figure 39. Spectrograms of J-clan call types S1, S4, S5, S6, S7, S10, S16, S17, and S42.

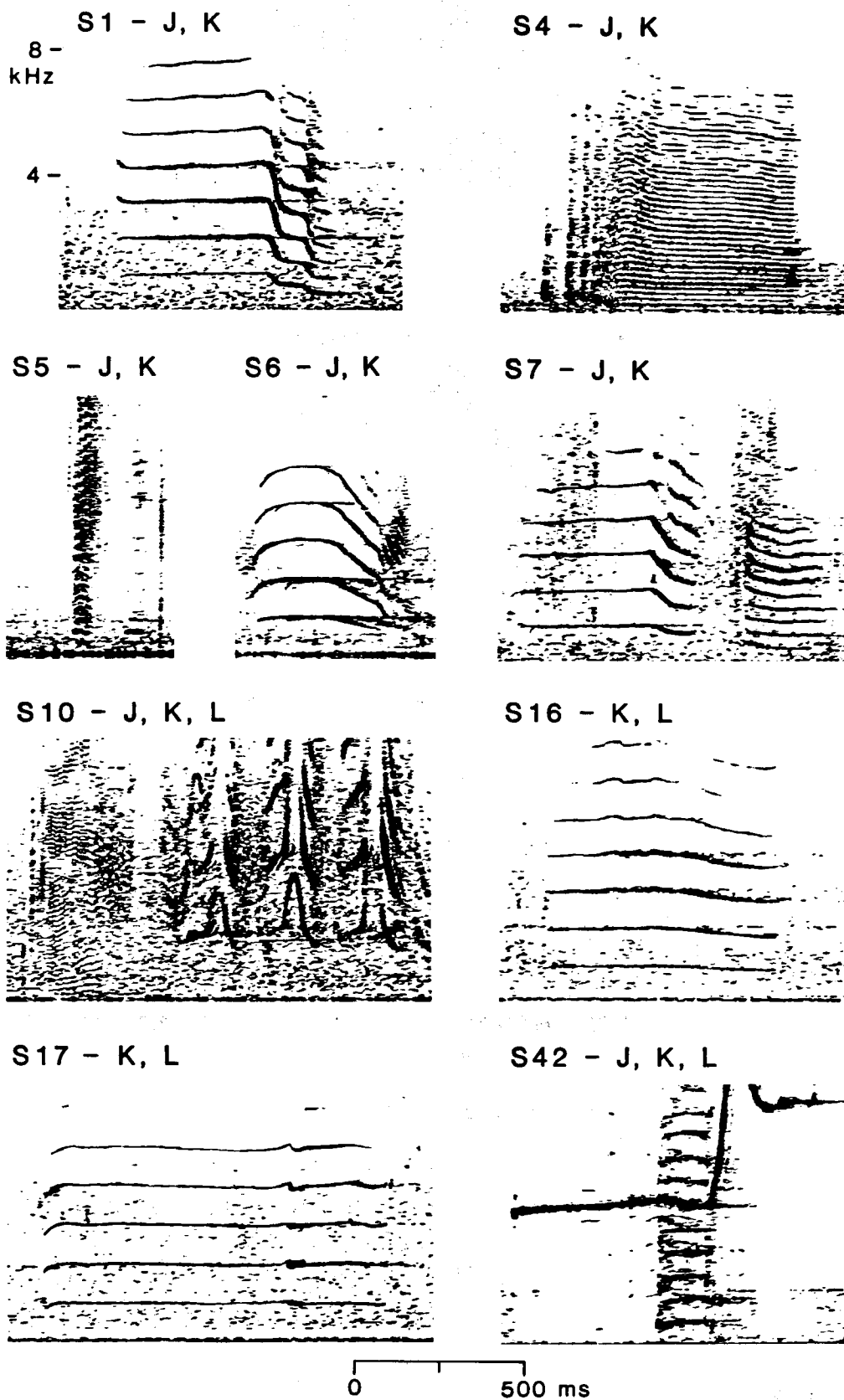
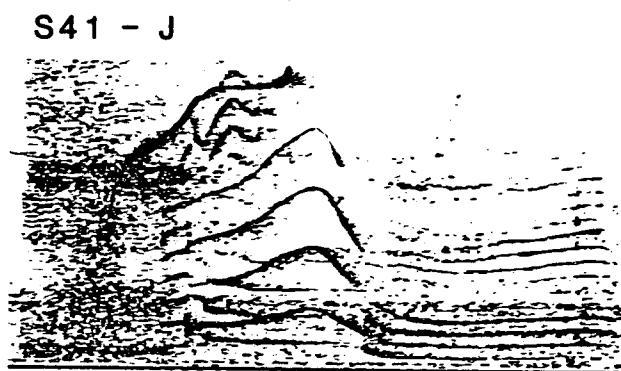
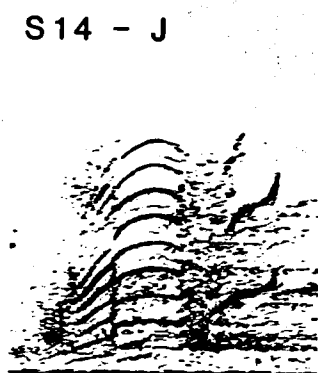
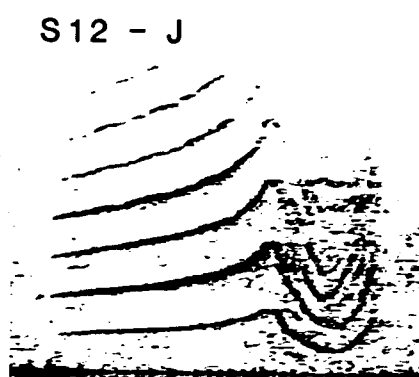
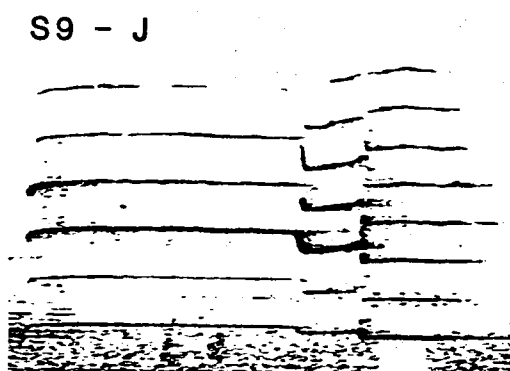
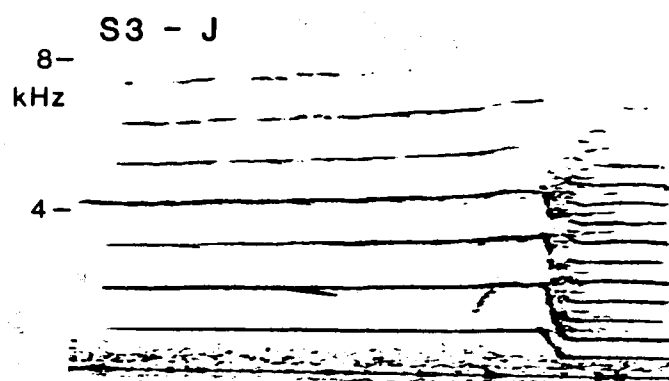
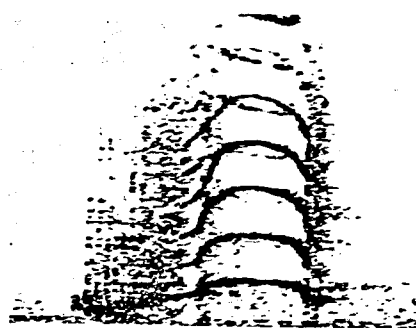


Figure 40. Spectrograms of call types S3, S9, S12, S14, S41, S44, given only by J pod.

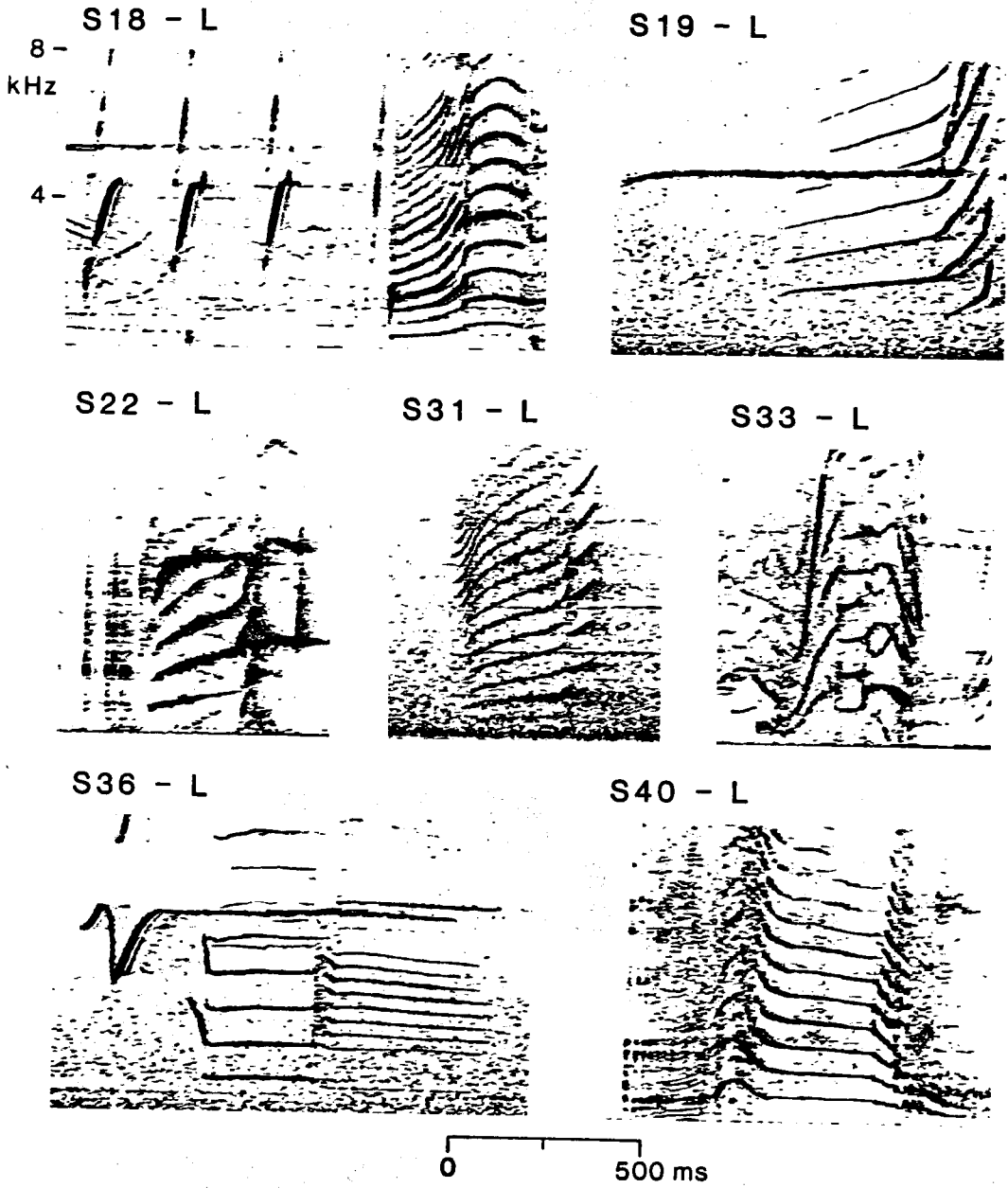


S44 - J



0 500 ms

Figure 41. Spectrograms of call types S18, S19, S22, S31, S33, S36, S40, given only by L pod.



Hz. These pulses are repeated at rates of about 1-8/s for periods of 3 to > 30 s. Often, whistle pulses within a series are given at alternating frequencies up to 3000 Hz apart. Series of pulsed whistles were not recorded from any other clan.

II) Call use

The frequency of occurrence of call types produced by J pod during foraging and travelling in 1979-83 are illustrated in Figure 42. As described in Part I, there are many significant differences in call use between these activities in this pod. Calls S1, S4 and S7 tend to predominate in foraging contexts, while S2, S44, S42, and S1 are, in that order, the most important calls during travelling. Six calls recorded during foraging episodes were not heard during travelling. Calls S14 and S41 were exclusive to travelling contexts. Analyses of transition frequencies among common calls indicate that call occurrence is non-random in foraging ($G = 1990.9$, $df = 49$, $p < 0.001$) and travelling ($G = 341.2$, $df = 49$, $p < 0.001$). Much of this variation results from the tendency for calls to occur in repetitive series, as in northern resident pods. Cluster diagrams of call associations based on transition frequencies (Fig. 43) indicate that no J-pod calls are strongly linked.

I examined three historical field recordings made apparently in the presence of J pod. The earliest was made on February 19, 1958, in Saanich Inlet, Vancouver Island, in the presence of an estimated 18 whales. J pod is the only resident group which has been seen at this location since 1973 (M. Bigg,

Figure 42. Frequency distributions of J. pod calls recorded in foraging and travelling contexts, 1979-83.

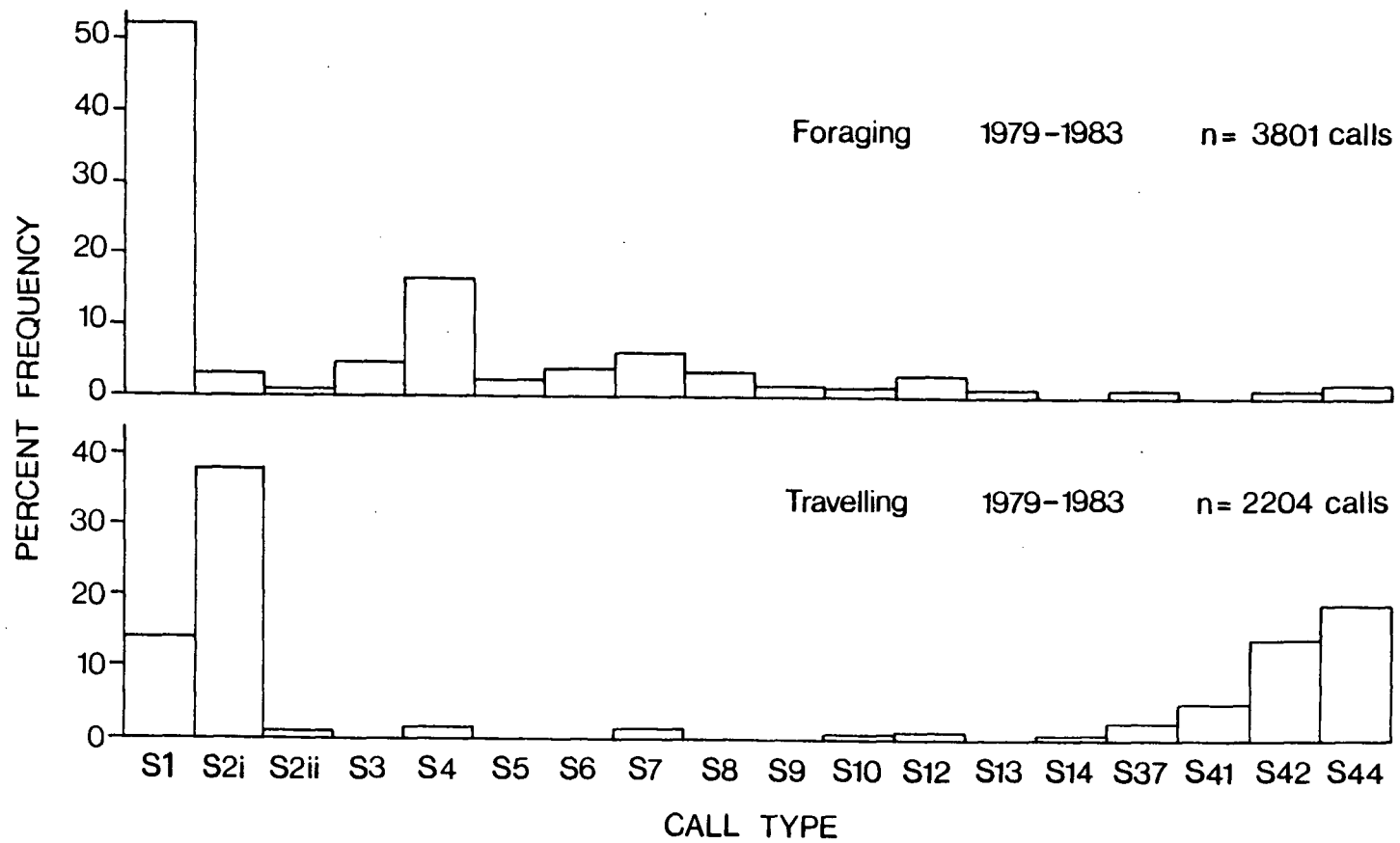
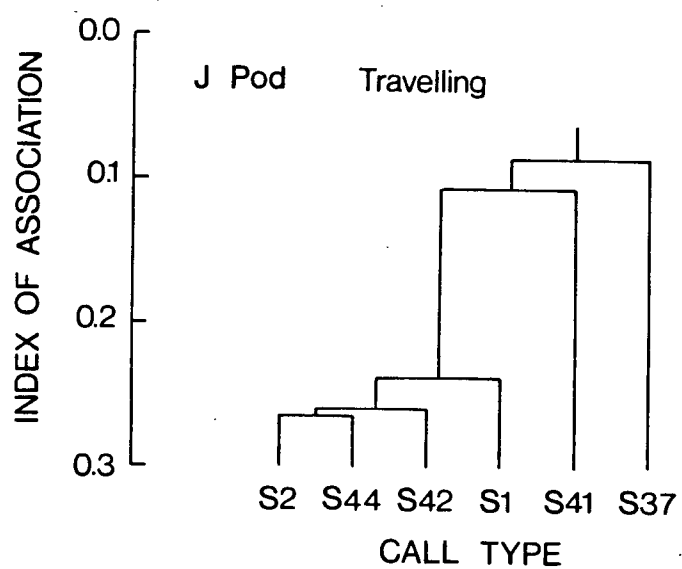
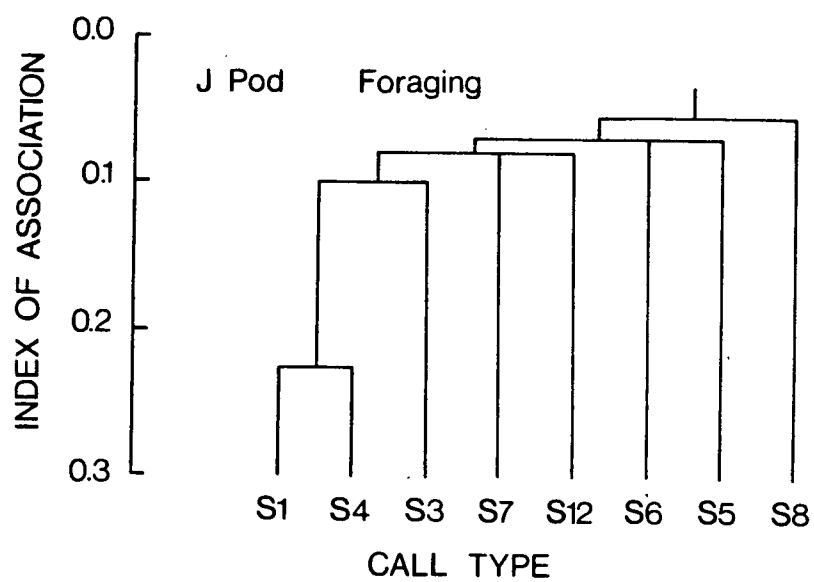


Figure 43. Cluster diagram of call associations in the repertoire of J pod. See Figure 24 caption for details.

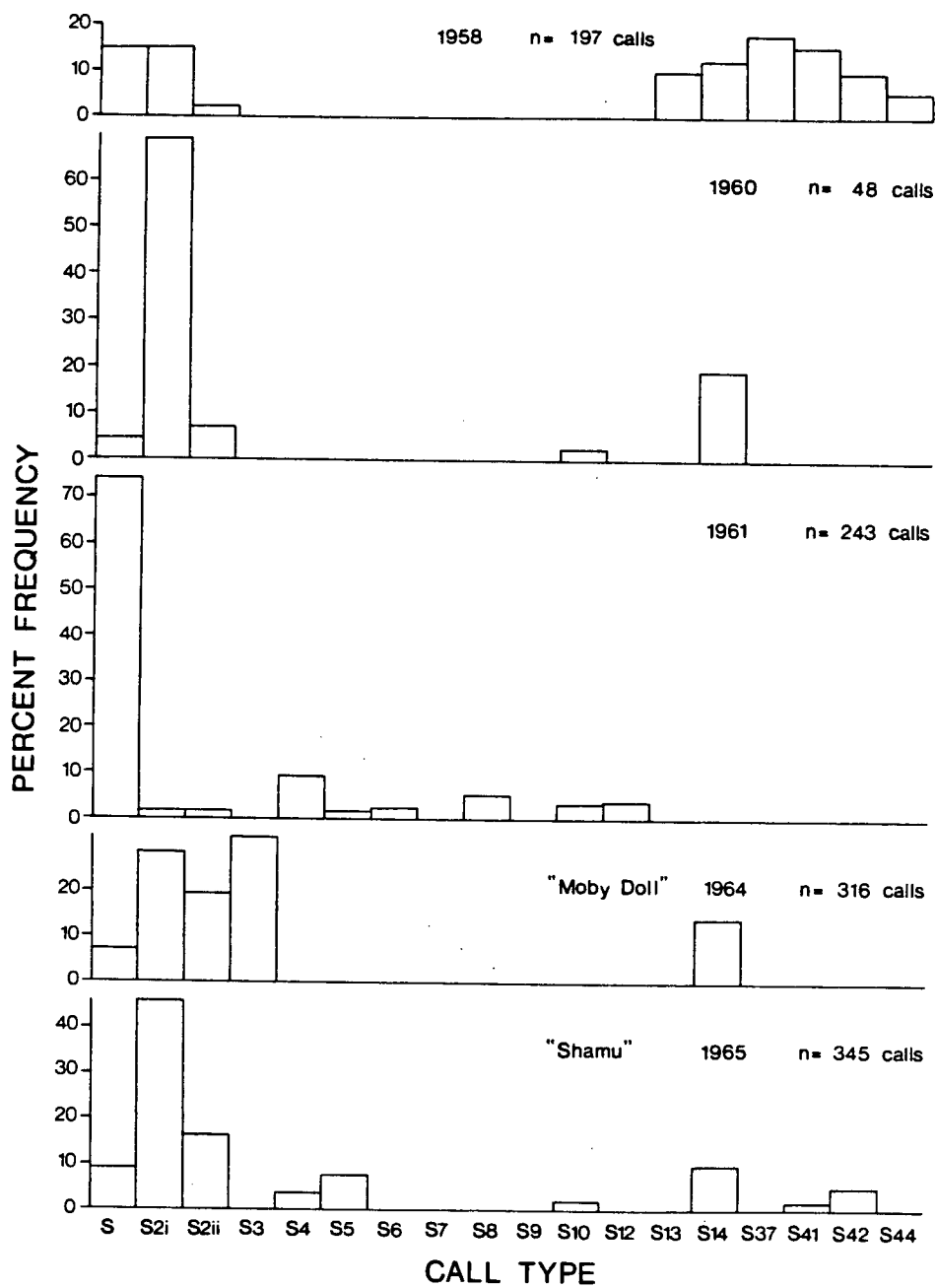


pers. comm.). This tape contains a total of 9 call types. All are from the 17-call repertoire used by J pod in 1979-83. The frequency distribution of calls most closely resembles that of J-pod's call production while travelling, although there are differences in emphases. The second recording is from October 20, 1960, in Dabob Bay, Puget Sound. This short sample primarily contains calls S2, S14 and S1. The third tape, dated 'spring 1961', was again recorded in Saanich Inlet. It also contains 9 J-pod call types, but their identity and frequency of use is more typical of recent call production during foraging contexts. Combining these recordings, it is evident that at least 14 of the present 17 J-pod call types existed in 1961 or earlier.

Although the samples are too small to draw firm conclusions, call S14 appears to have been more important in J-pod's repertoire in the early 1960's than in 1979-83. This call comprised 12.2% and 18.3% of the total recorded in 1958 and 1960, respectively, although it did not occur in the 1961 sample. Two whales captured in the southern community area in 1964 and 1965, apparently from J pod, also used S14 frequently. The call accounted for 13.9% of those produced in 1964 by "Moby Doll", a young bull, and 9.8% for the female "Shamu" in 1965 (Fig. 44). Call S14 was not recorded from J pod while foraging in 1978-83, and comprised only 0.4% of travelling-context call production in the same period.

Too few encounters were made with K pod alone to confidently describe the frequency distribution of calls in this

Figure 44. Frequency distributions of J-pod call types recorded during 1958-61, and from the captive whales "Moby Doll" and "Shamu". There is no photographic evidence that J pod was involved in these early field encounters, or that the two captive whales were taken from J pod.



group. However, S16, S17, S1 and S4 appeared to be the calls most commonly used. Call production by L pod is illustrated in Figure 45. As in J pod, there is a significant shift in call emphasis in foraging versus travelling contexts. Call transition frequencies indicate that call S16 is frequently followed within 2-4 s by an S17, and S18 is often followed by an S22. The association of calls S16 and S17 also occurs in K-pod's calling. Call intensity patterns suggested that both calls in each pair were given by the same individual. These and other call associations are shown in Figure 46.

The earliest record of L-pod calls is from a tape made in the presence of four animals taken in two captures and held together at Pedder Bay, near Victoria, B.C., in 1973. Of these 4 whales, 2 were from K pod, and the other 2 were from an undetermined group (Bigg et al., 1976; Bigg, pers. comm.). The sample recording from these animals contains calls which closely match those produced by L pod while foraging in 1980-83 (Fig. 45).

III) Summary of acoustic associations: J-clan

Indices of similarity in J-clan call repertoires are rather low in comparison to those of northern community clans. This is largely a result of the numerous calls exclusive to either J or L pods. Pods J and K are most similar acoustically with an index of 0.545. Next is K and L with an index of 0.387, and finally J and L at 0.333. K pod apparently produces no unique calls. Of the 10 call types given by K pod, 4 are shared with J

Figure 45. Frequency distributions of calls produced by L pod while foraging and travelling during 1980-83, and from captive whales in 1973.

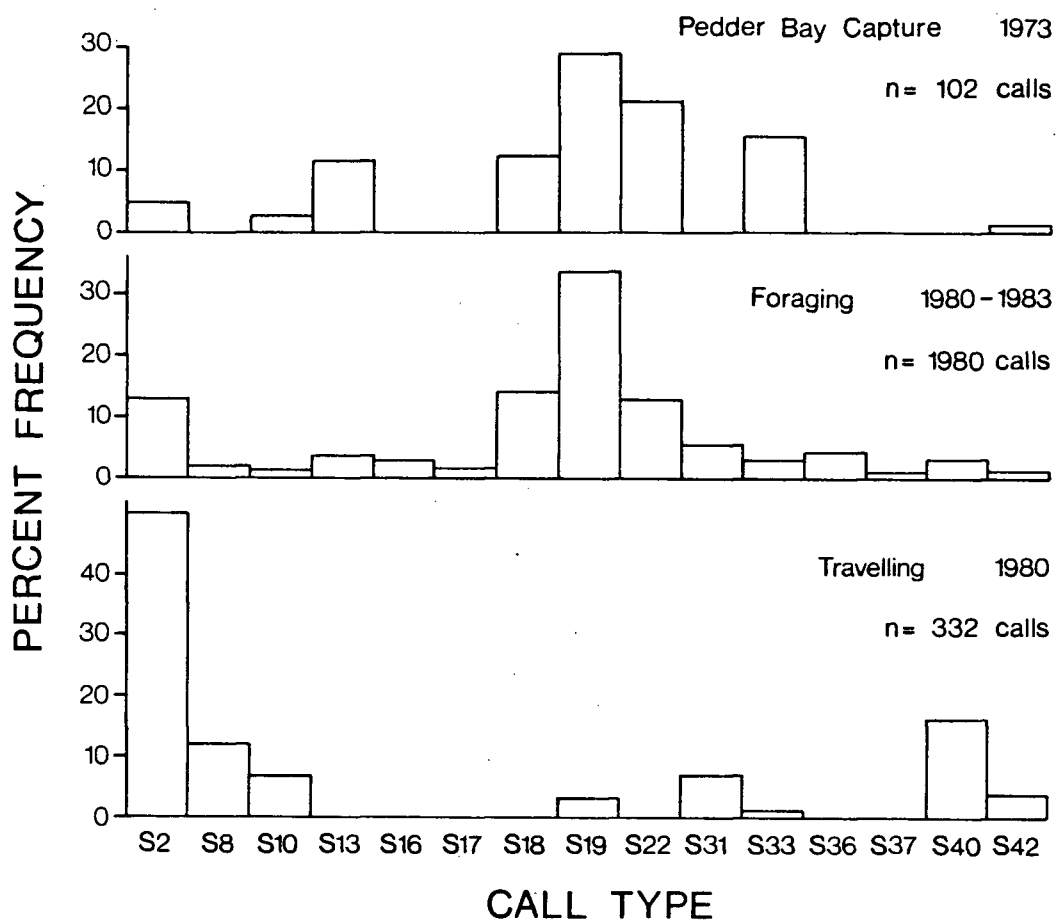
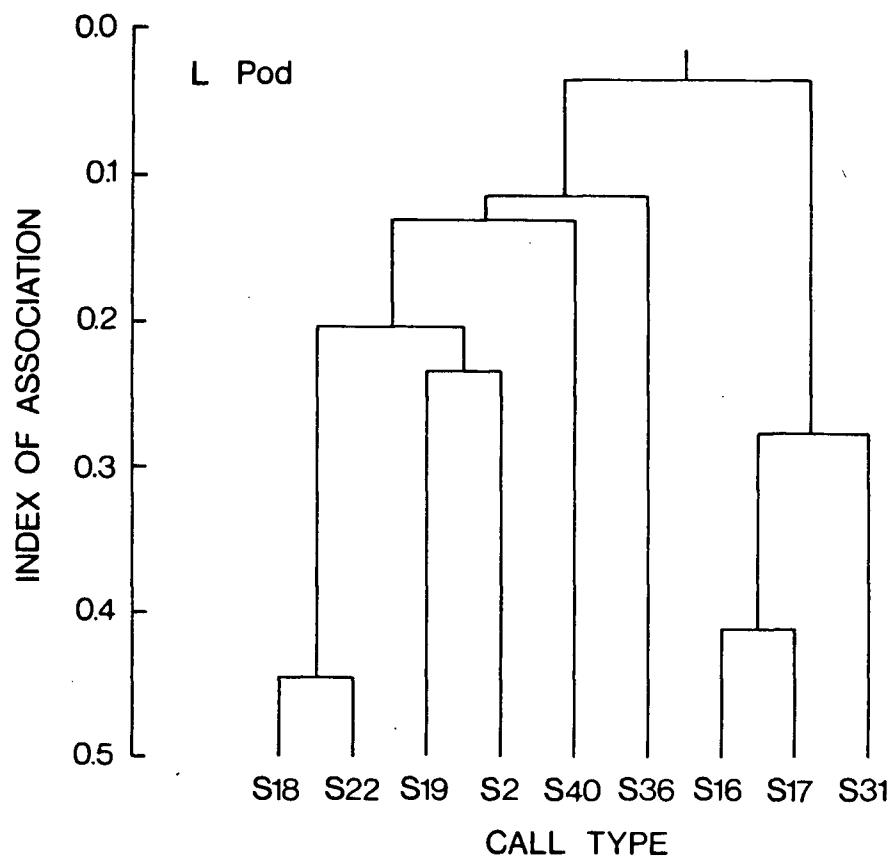


Figure 46. Cluster diagram of call associations in the repertoire of L pod. See Figure 24 caption for details.



pod only, 2 with L, and 4 with both J and L.

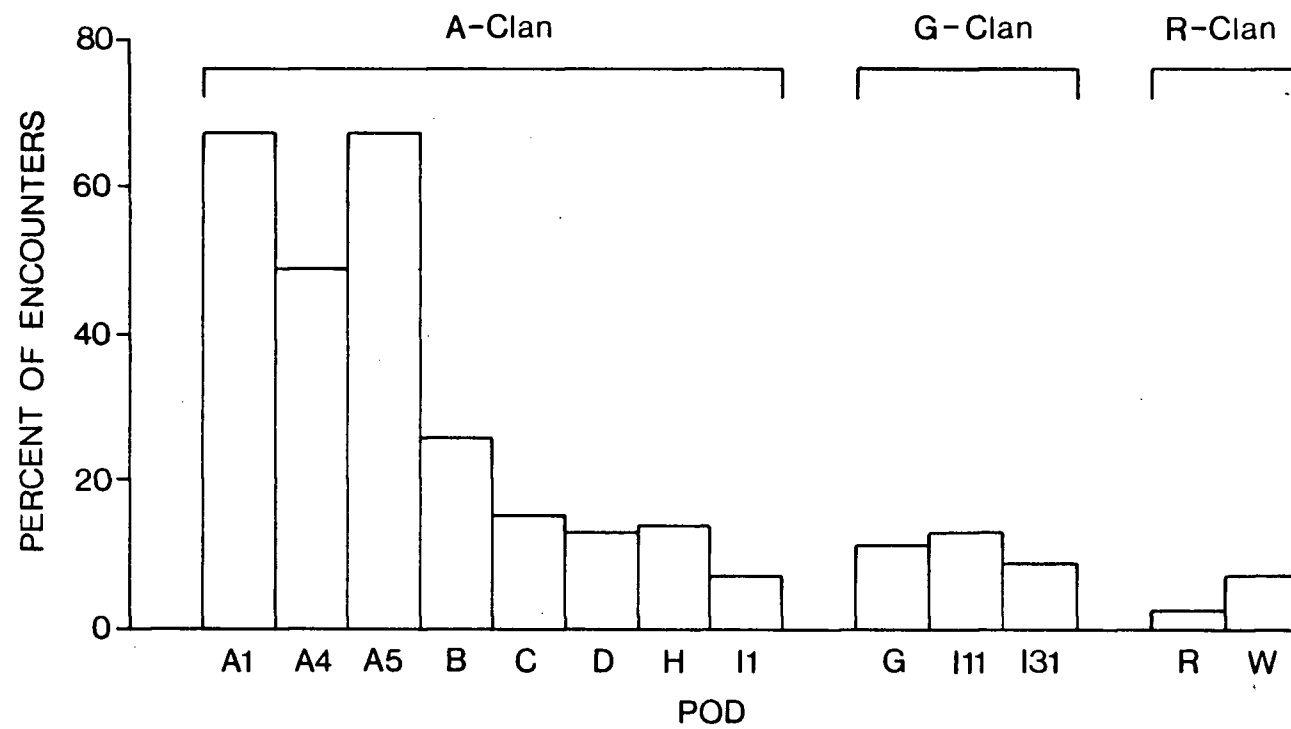
4. Comparison of Dialect Similarity and Pod Distributions.

Of the four resident clans, only J-clan, which comprises the entire southern resident community, appears to have an exclusive range. The distributions of the three northern resident clans overlap widely. The frequency of occurrence of northern resident pods off northeastern Vancouver Island during 1978-83 is shown in Figure 47. Although all pods in the community do occur in the area, pod distribution is clearly non-random. Pods A1, A4 and A5 were by far the most common (each present on > 48% of encounter days), followed by B pod, which was seen on 25.8% of the total days whales were encountered. The remaining A-clan pods were each seen on < 16% of the days. All three G-clan pods were relatively uncommon in the area. Of the three, I11 was the most often observed, being present on 13.3% of encounter days. The two R-clan pods, R and W, were the rarest in the area. R pod was seen on only 3 days (2.3%) and W on only 9 days (7.0%).

Pod occurrence also varied from year to year. The three A-pods were the most consistently seen, although A1 pod apparently left the study area for most of the 1980 field season (July-October). Many of the less common pods appeared sporadically. Some were observed several times in certain years, but not at all in others (Appendix I).

These patterns of occurrence suggest that pods have preferred areas within the overall range of the northern

Figure 47. Frequency of occurrence of northern resident pods off northeastern Vancouver Island, 1978-83. Percentages shown are the proportion of days that each pod was present in the total 128 days that whales were observed in the area.
N = 386 pod encounters



community. The waters off northeastern Vancouver Island, especially Johnstone Strait, appear to be the 'core area' of pods A1, A4 and A5. All three of these pods were absent on only 18 of the 128 days (14.1%) that whales were observed in the area during 1978-83. The remaining A-clan pods, as well as G- and R-clans, spend more time outside the study area, probably to the north and west. Unfortunately, too few encounters have been made in such regions to identify potential core areas for these pods. There is some indication that R-clan may reside predominately in the northern portions of the community range. On four of the eight occasions R pod was encountered between 1975 and 1983, the pod was north of Bella Bella, some 200 km north of the Johnstone Strait area. W pod has been sighted at Prince Rupert, near the northern-most known limit of the range of the northern community. Pods B (A-clan), I11 and I31 (G-clan) have also been sighted in the northern part of the community range and, along with W, off the central west coast of Vancouver Island. The three A-pods have not been seen in either of these areas.

In summary, the southern resident community is comprised of a unique acoustic group - the J-clan - with an exclusive geographic range. In the northern community, the three acoustically-distinct clans overlap geographically, although each may have separate core areas within the community range. In the case of the A-clan, pods A1, A4 and A5, which form an acoustic subgroup (Fig. 29), appear to have a different core area from the remainder of the clan. It should be noted that

the majority of northern resident encounters were made in the months of June-October. Pod distributions at other times of the year are mostly unknown.

5. Comparison of Dialect Similarity and Pod Associations.

To examine the relationship between repertoire similarity and the degree of social association of pods, an index of association (Dice's index, described in Morgan et al. (1976)) was calculated from the total number of days each pair combination of pods was sighted together. To provide as large a sample as possible, all encounters carried out or documented by M. Bigg (pers. comm.) prior to and during this study, were included in the analysis.

The association matrix for the northern resident community (Table XIII) represents a total of 773 pod encounters made on 353 days between 1973 and 1983, for an average of 2.19 pods/day. As is evident from the descending diagonal of the matrix, there is considerable variation in the number of occasions each pod was encountered while travelling alone. To arrive at an accurate measure of inter-pod association unaffected by each pod's degree of sociability, these 'lone' encounters were removed from the total for each pod before calculation of the association index.

Since the distribution of northern resident pods is non-random, and most sampling was carried out in a small portion of the community range, the association indices must be interpreted with care. As mentioned previously, the main study area of

Table XIII. Social associations of northern resident community pods. Based on 773 pod encounters made on 353 days between 1973 and 1983. Values along descending diagonal (e.g., A1 with A1) are number of occasions pod was seen alone, and, in parentheses, the proportion of total encounters. All other values are the number of encounters different pods were observed in association, and an index of association in parentheses. This index is explained in detail in the text.

		POD												
		A1	A4	A5	B	C	D	G	H	I1	I11	I31	R	W
POD	A1	28 (.169)												
	A4	79 (.678)	6 (.059)											
	A5	102 (.734)	76 (.647)	39 (.218)										
	B	28 (.303)	17 (.239)	30 (.321)	33 (.413)									
	C	23 (.267)	17 (.264)	20 (.230)	6 (.148)	3 (.081)								
	D	11 (.131)	11 (.176)	24 (.283)	6 (.156)	11 (.343)	2 (.063)							
	G	15 (.182)	10 (.164)	14 (.168)	10 (.270)	4 (.131)	3 (.105)	19 (.413)						
	H	16 (.190)	9 (.144)	15 (.176)	9 (.234)	6 (.188)	4 (.133)	5 (.175)	1 (.032)					
	I1	5 (.067)	4 (.075)	4 (.053)	3 (.102)	1 (.043)	2 (.095)	1 (.051)	7 (.333)	10 (.454)				
	I11	13 (.153)	8 (.126)	14 (.163)	8 (.203)	6 (.182)	2 (.065)	14 (.475)	6 (.194)	3 (.136)	3 (.086)			
	I31	9 (.115)	8 (.140)	12 (.151)	3 (.091)	3 (.113)	1 (.041)	6 (.261)	6 (.245)	4 (.258)	16 (.627)	1 (.050)		
	R	3 (.042)	3 (.061)	3 (.042)	1 (.039)	2 (.105)	0 -----	3 (.194)	3 (.176)	1 (.125)	2 (.111)	2 (.174)	4 (.500)	
	W	9 (.118)	8 (.145)	6 (.077)	2 (.065)	6 (.245)	0 -----	7 (.333)	3 (.133)	2 (.148)	12 (.511)	7 (.412)	2 (.210)	1 (.063)
TOTAL:		166	101	179	80	37	32	46	31	22	35	20	8	16

northern Johnstone Strait appears to be the core area for pods A1, A4 and A5. Other pods entered this area irregularly and usually joined with the A-pods for the duration of their visit. Thus, the high index values between the three A-pods and many other northern community pods are very likely over-representations of the actual long-term relationships of these pods outside of Johnstone Strait.

Almost all northern resident pods have been observed to associate with each other. The only exception is D pod, which was not seen with R or W pods. Within the A-clan, there is a clear correlation between the close associations of pods A1, A4 and A5, and their similar call repertoires (Fig. 29). Among the B-group of pods, C and D have the most similar dialects in the northern community with an index of similarity of 0.963. Each of these two pods associated more with the other than any other northern community pod, although the association index of 0.343 is not particularly high. The second strongest association value for C pod is with W pod of the R-clan (0.245). Pods B, H and I1 form a relatively distinct acoustic subgroup within the clan, and in some cases this is reflected in their social relationships. Pods H and I1 have an association index of 0.333, the highest value for both pods. Pod B, however, has a higher association index with G pod (0.270) than any northern resident except the A-pods. B's association with H is higher than other A-clan pods, again excluding the A-pods, but it has a weak association with I1 (0.102).

Of the three G-clan pods, I11 and I31 are closely related

in both dialect (similarity index = 0.909) and occurrence (association index = 0.627). G pod's highest association index was with I11 (0.475), but its association with I31 was lower (0.261) than with W pod (0.333). Within the R-clan, there was little indication from occurrence patterns of the close acoustic relationship between R and W pods. Although the highest association index for R pod is with W, higher values occur between W and pods C, G, I11 and I31.

Inter-pod associations in the southern resident community are confined to the three J-clan pods (Table XIV). The strongest association is between K and L (association index = 0.461). J pod associates to a similar degree with both K (0.353) and L (0.337). J pod appears to spend most time within Georgia Strait and Puget Sound, while K and L pods travel regularly through Juan de Fuca Strait to areas off the west coast of Vancouver Island.

Acoustic relationships within the J-clan do not coincide closely with these associations. Pods J and K have the highest dialect similarity index of 0.545, followed by K and L (0.387) and J and L (0.333). It is possible that social relationships have changed recently as a result of significant cropping of whales from 1967 to 1973. During this period, an estimated 27% of the total southern resident population was captured and removed for display in oceanaria (Bigg 1982). Changes in group composition may have altered the pattern of pod associations during the present study, and thus it is unclear whether the lack of correlation between dialect similarity and pod

Table XIV. Social associations of southern resident community pods. See caption of Table XIII for explanation of values.

		POD		
		J	K	L
POD	J	105 (.761)		
	K	30 (.353)	8 (.133)	
	L	28 (.337)	47 (.461)	30 (.375)
TOTAL:		138	60	80

interaction is representative of the natural state.

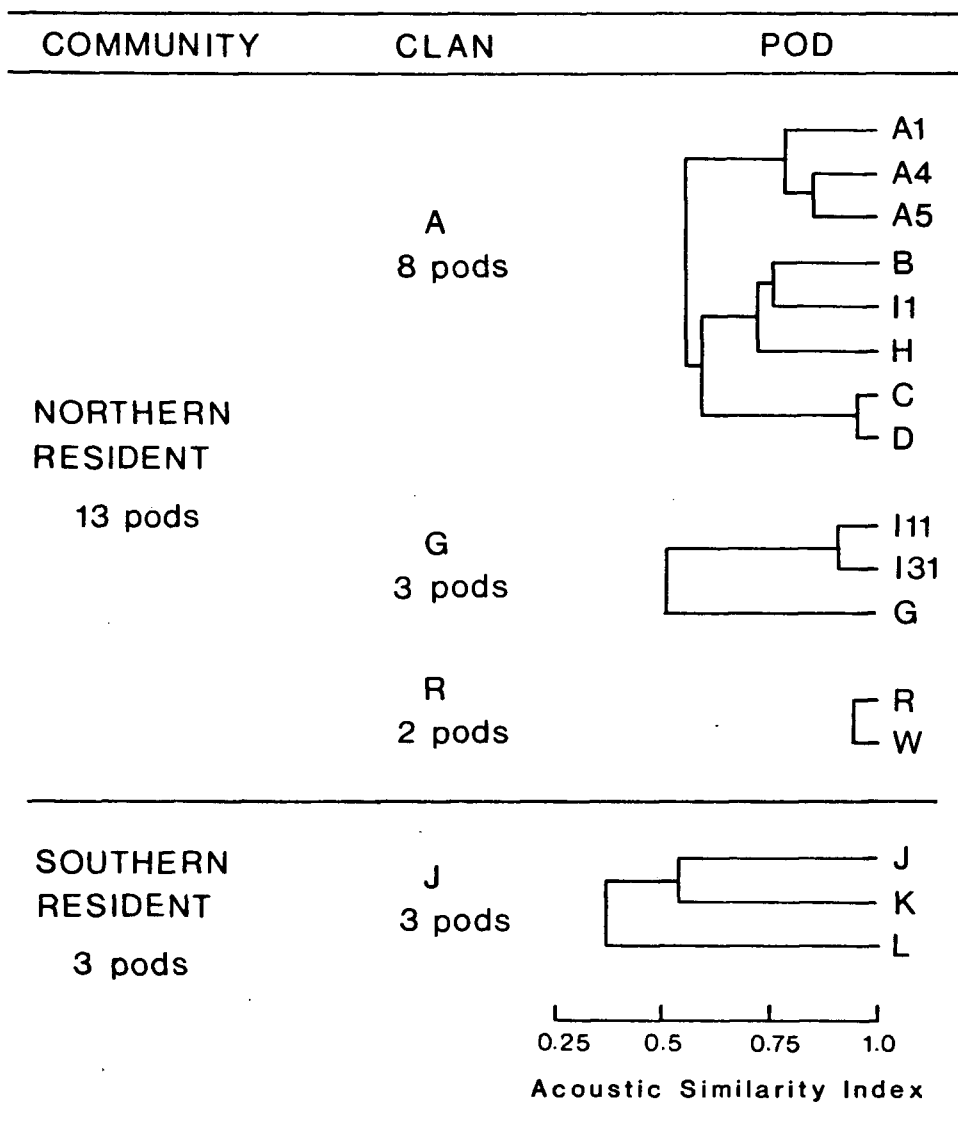
In summary, the major vocal differences between the northern and southern resident communities correlate well with their geographic and social segregation. Within each community, however, the picture is less clear. The three acoustically-distinct clans of the northern community interact socially, but the patterns of pod associations observed are, in many cases, inconsistent with dialect relationships. This may be a result of the non-random distribution of pods and a sampling emphasis in one portion of the community range. Social relationships in the southern community may have been altered by recent cropping.

DISCUSSION

The patterns of vocal variation in resident killer whales of B.C. may be summarized as follows. Each pod has a set of 7 to 17 discrete call types that dominates vocalization in most contexts. All pod members appear to use the entire call repertoire (Part I). Each pod shares several call types with other pods, but may also produce unique calls. Shared calls often differ in form among pods. The 16 resident pods can be arranged into four acoustically-distinct groups, or clans. Pods within each clan share call types, but no sharing occurs between clans. The geographic distributions of 3 of the 4 clans overlap extensively, and pods from different clans commonly associate. Vocal variation thus exists at two levels in the resident population, (1) between pods within a clan, involving modification of call structure and use, and frequent occurrence of call types unique to a portion of the clan, and (2) between clans, involving complete independence of call repertoires. A summary of acoustic relationships in the resident population is illustrated in Figure 48.

The forms of vocal variation described here appear to be unique to killer whales for several reasons. With the exception of humans, no other mammalian species has populations that differ acoustically at a local level. All previously documented cases of vocal variation involve geographically-isolated groups (Connor 1982; Ford and Fisher 1983). Different acoustic groups of killer whales can not only exist in the same area, but may also associate regularly. In birds, dialects occur among

Figure 48. Summary of acoustic relationships of resident pods in British Columbia. The two resident communities have exclusive ranges, while clans have exclusive call traditions. The three northern community clans associate with each other. All pods within a clan share calls, yet each may also have unique calls. The degree of acoustic similarity in the clan is expressed as an index value, described in the text, and displayed by cluster analysis.



neighbouring populations, but are nearly always tied to specific geographic localities (Krebs and Kroodsma 1980). Flock-specific variation occurs in a few bird species (e.g., Feekes 1982; Nowicki 1983), but such groups are territorial. Dialects in birds usually involve relatively minor modifications of a general song format that is common to the species (e.g., Trainer 1983). In species with large song repertoires, birds from neighbouring populations typically share some song types yet have others that are different (Krebs and Kroodsma 1980). In killer whales, pods occurring in the same area can have entirely different repertoires of calls.

Interpretation of the origin and possible adaptive significance of vocal variation in killer whales requires consideration of the function of discrete call repertoires and how individuals acquire these calls. As discussed in Part I, discrete calls in general probably serve to maintain contact among pod members during periods of dispersion. There is a poor correlation of most call types with behavioural context. The fine structure of discrete calls and the incidence of variable and aberrant vocalizations are better indicators of the state of arousal of the whales than are particular call types. Whether different calls have different meanings to the animals is unknown, and why they have such large repertoires remains unclear. As will be discussed below, the fact that calls vary among social groups may provide clues as to their function.

It is probable that killer-whale call repertoires are learned rather than inherited by individuals. This is in

contrast to vocal development in most other mammals, which is considered to be under complete genetic control (Nottebohm 1972, 1975; Ehret 1980; but see Newman and Symmes 1983). The family Delphinidae, which includes the killer whale, is the only non-human mammalian group known to have the ability to mimic and learn new vocal patterns (Tayler and Saayman 1973; Caldwell and Caldwell 1972; Herman 1980) (a single exception to this involved certain calls that developed artificially in three troops of Japanese monkeys (Green 1975b)). Whether learning plays a significant role in the normal development of adult vocal behaviour in delphinids has yet to be determined, although it is generally assumed to be important (e.g., Caldwell and Caldwell 1979).

Killer whales share the capacity for vocal learning with other delphinids. Occasionally, individuals in the wild will imitate call types belonging to different pods, even those from other clans (Part I). In captivity, a juvenile male northern resident from A5 pod housed together with a southern community female from K pod acquired several calls of the female and for a time used these in preference to his natal calls (Ford, unpubl.). Another case involves the bull "Namu", taken from the northern resident C pod (A-clan) in 1965. As described earlier, the numerous calls present in several recordings of this animal made shortly after capture are typical of those produced by the pod in recent years (Figs. 26, 27 and 28). However, for a period of 3 min in one recording, Namu apparently switched from his typical repertoire and emitted several examples of calls N2,

N4, N7i, and N8i, all unique to pods A1, A4 and A5, and calls N33 and N34, unique to R and W pods.

It therefore seems most probable that learning is involved in the acquisition of an individual's call repertoire and thus in the development of group-specific dialects in killer whales. It is noteworthy that development of local dialects in birds is dependent on song imitation and learning (see reviews by Nottebohm 1972; Krebs and Kroodsma 1980; Mundinger 1980).

Origins of Vocal Variation

Before discussing the potential function of killer whale vocal variation, I will consider the proximate factors responsible for its development. Vocal variations occur at two levels among resident whales, (1) within clans, and (2) between clans. Pods within a clan all share calls, many of which vary in structure from pod to pod. In studies of bird song, systems of related dialects are referred to as "local song traditions" (Payne et al. 1981) or "cultural institutions" (Mundinger 1980). Mundinger (1980) defines a cultural institution as a "single lineage of ancestral descendant populations of models (= acquired behavioural traits) that maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate." "Boundaries" between institutions are generally maintained by geographical or social isolation.

By this definition, each clan of resident pods corresponds to a distinct cultural institution or 'call tradition', made up

of an exclusive set of related call dialects. As Mundinger (1980) pointed out with respect to house finch (Carpodacus mexicanus) song, each institution is comparable in organizational terms to a different human language. Languages consist of exclusive (or nearly so) vocabularies which often have substructures of evolutionarily-related speech dialects.

How did these completely different call traditions of the four resident clans come to occur on the British Columbia coast? It seems reasonable to conclude that pods within a clan are related since there are clear similarities in their call repertoires. However, I could identify no homologous calls in the traditions of different clans, and thus it is unlikely that clans have originated from a common ancestral group, at least in the recent past. A more reasonable hypothesis is that each of the four call traditions developed independently over long periods in geographic isolation. Their occurrence on the B.C. coast may be the result of unrelated founding events. The founding pod of each local clan may have dispersed from a distant core area and colonized an unoccupied region along the coast. Alternatively, colonization may have involved a transition from a nomadic way of life, such as that of transient whales (Part III), to a more sedentary existence typical of resident pods. Historical founder effects are considered important in the origin and spread of human languages and dialects (Friedlaender et al. 1971; Spielman et al. 1974; Trudgill 1983) and song traditions in birds (Mundinger 1975, 1980; Payne 1981; Trainer 1983).

Of the four resident killer whale clans in B.C., only the J-clan occupies an exclusive range. Its distinct call tradition may thus be maintained through geographic isolation from other clans. The A-, G- and R-clans of the northern resident community overlap in distribution yet each maintains a unique call tradition. Social or behavioural isolating mechanisms are probably important in preserving the integrity of these traditions.

Assuming pods in a clan are descended from a common founding group, dialects within the clan's call tradition probably developed locally as the lineage evolved. Formation of new pods most likely involves the gradual splitting of old pods (Bigg 1982). Dialects in a call tradition could thus be viewed as behavioural reflections of the common heritage of the clan's pods and the divergence that has occurred within the lineage.

Several mechanisms of vocal change leading to dialect formation have been identified in birds and man (Lemon 1975; Slater and Ince 1979; Slater et al. 1980; Mundinger 1980; Payne 1981; Trudgill 1983). Those that could potentially have a role in the formation of killer whale dialects include (1) cultural drift, (2) innovation and (3) cultural diffusion.

Cultural drift involves the appearance of random errors in vocal copying and the transmission of these changes across generations. Errors might accumulate as pods grow and split, resulting in the complex group-specific modifications in call structure evident within clans. Drift might result only in changes to established call types in the clan. The creation of

new calls in a pod's repertoire would require vocal innovation and subsequent imitation. Both of these forms of variation exist in dialects within clans, and thus both drift and innovation may be involved.

The manner in which killer whales learn calls has important implications for the development of dialects. If young whales selectively learn only the calls of their mother, call divergence could begin among matrilineal lines before a pod splits. If an individual's repertoire is established early in life and is thereafter resistant to change, pod-specific call patterns would be slow to evolve. If calls change slightly with each generation, old whales in the pod would have more archaic forms of calls than juveniles. These old versions would eventually disappear as animals die. Newly innovated vocal patterns might spread quickly among younger animals in a pod but never be adopted by older whales. This was observed with certain calls in Japanese monkeys (Green 1975b). Unfortunately, we cannot tell which of these learning mechanisms is correct without intensive studies of the vocal patterns of individual whales.

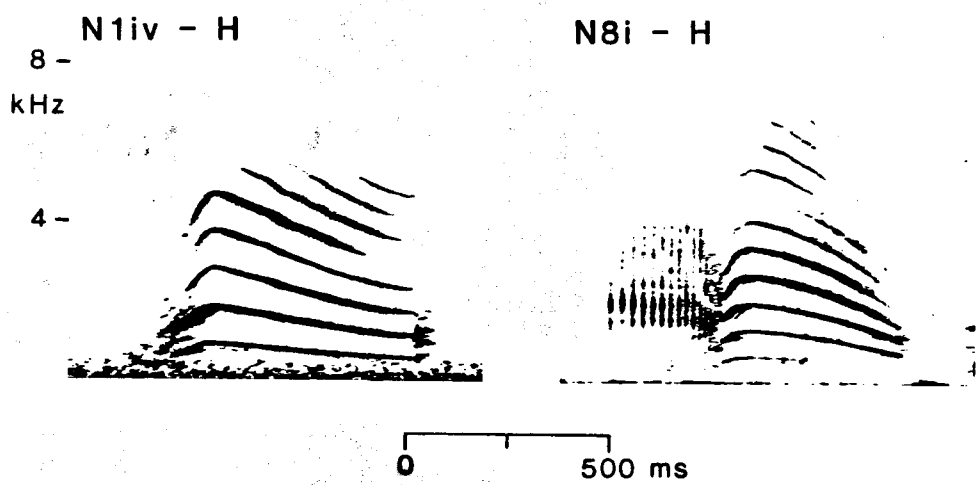
Certain calls within a clan's tradition appear more susceptible to change than others, which would not be expected if random drift is the primary mechanism involved. For example, the resting call N3 is produced in essentially the same manner by all 8 pods of the A-clan, yet most other shared calls differ markedly. There are several other indications that some call variations do not result from chance learning errors. As an example, A5-pod's versions of 5 of the 11 calls shared by the

three A-pods have strongly emphasized terminal components, both in duration and frequency shifts. In A1 and A4 pods, however, these calls all have weakly developed or non-existent terminal parts. Another example is in the convergence of structure in versions of calls N1 and N8 emitted by H pod (Fig. 49). These two calls show no structural similarity in other A-clan repertoires, yet in H pod they have both acquired the same very distinctive sound quality. In some cases, the two calls could only be distinguished by the consistent association of call N7 and N8.

These observations suggest that development of dialects within call traditions may be influenced by unique behavioural trends within each group. Thus, vocal divergence in the three closely-related A-pods, for example, may have been directed by a generalized predisposition towards strong call endings in A5 pod (or an ancestral group), or towards reduced call endings in A1 and A4 pods. Perhaps these tendencies can be attributed to the behavioural idiosyncracies of a socially-dominant member in each pod or lineage, possibly a founding matriarch.

Cultural diffusion can be an important source of vocal variation in birds and humans. New sounds are introduced into a vocal tradition by immigrants and these sounds spread into the recipient population's repertoire (Mundinger 1980; Slater et al. 1980; Payne 1981). Diffusion may also result from temporary contact of different vocal traditions, especially in human populations (Spielman et al. 1974; Trudgill 1983). There is, however, no indication that diffusion is involved in the

Figure 49. Examples of call types N1 and N8 given by H pod. These two call types appear to have become structurally modified in a similar manner in this pod's repertoire.



formation of call dialects in killer whales.

No dispersal from or immigration into pods has been observed since monitoring of the B.C. killer whale population began in 1973 (Bigg 1982; pers. comm.). If transfer of individuals occurred between pods, it would be expected that the dialect systems within clans, as well as the acoustic integrity of the clan itself, might be broken down through cultural diffusion. Migrants would presumably introduce their own natal repertoire into the pod they join, which would then have a blend of dialects. It is possible, however, that a transferring animal could switch its call repertoire to that of its new group. This seems unlikely, however, because there is a pod with a composite call repertoire which may be a result of immigration. This single case involves I1 pod of the A-clan, which usually produces call subtypes that are either unique to the group or shared with B pod. However, a small proportion of calls recorded from the pod is consistently comprised of subtypes typical of H pod (Table IX). This suggests that an animal from H pod may have transferred to I1 and retained its natal repertoire. If so, it is probably a rare occurrence.

The innovation of new call types or structural differentiation of shared calls seems to occur without the use of any 'raw material' from other call traditions to which a pod is exposed. It is clear that the animals can reproduce calls of other traditions since they do so on rare occasions (Part I). However, no call transfer has occurred among the four call traditions in the resident population. It is apparent that

there is a strong conservatism in the process of vocal divergence which prevents diffusion from unrelated dialects and serves to preserve the distinctiveness of each tradition.

Finally, vocal variation in killer whales also results from the loss of calls from group-specific repertoires. An example of a gradual loss of a call type can be seen in J-pod's use of S14. This signal was very common in the early 1960's, both in the calling of captive whales and in field recordings. In recent years, however, the call has been heard very rarely. Similarly, call N49 comprised 8.1% of the signals recorded from an R-clan pod in 1964, but did not occur in R-clan samples from 1973 or 1981-83. There are numerous cases of calls apparently being lost from the repertoires of certain pods in a clan. Pod A5, for example, is the only one of the eight A-clan pods that does not have some version of call N1. Call N5 has apparently been lost from the repertoires of pods C and D, while it remains a common component in the repertoires of the rest of the clan.

Killer Whale Dialects: Byproducts or Adaptations?

Perhaps the most important questions to be considered concern the potential ultimate factors responsible for the development of dialects in killer whales. Do call variations within a clan represent byproducts of the processes of vocal learning and population evolution, and thus have no adaptive significance? Or, can dialects be viewed as active modifications and, if so, what might be their selective value? Current evidence is insufficient to confidently answer such

questions, but it is possible to offer some speculations.

The simplest interpretation of group-specific dialects is that they represent non-functional cultural drift. Changes in call traditions may result from transcription errors during vocal learning or from behavioural idiosyncracies of individual whales, which are transmitted to other animals in the pod. These changes may be neither advantageous or disadvantageous and have simply accumulated over generations. Group-specific modifications are maintained in the pod as a result of strong social bonding and the lack of dispersal.

An alternative hypothesis is that dialects function as indicators of kinship, and thus could be considered active modifications. There are several potential advantages to such a system. First, discrete calls most likely serve as contact signals during periods of dispersion of a pod. The calls probably convey information on the vocalizer's identity, location, and state of arousal (Part I). With the addition of group-identity information, the calls would have an enhanced usefulness in maintaining group cohesion at times when several pods are together in the same vicinity (Ford and Fisher 1983). Interestingly, a similar function was proposed in 1962 by Andrew to account for vocal mimicry in dolphins. In developing his argument, Andrew (1962) suggested that mimicry as seen in dolphins may have allowed the development of group-specific patterns of vocalization in early man. These patterns would have been important in maintaining the integrity of the group, especially in a hunting society where group members were often

subdivided when foraging. In addition, the capacity for vocal learning may also have led to large repertoires of sounds to provide a better "match" against external sounds.

A second potential function of a kin-recognition system in killer whales may be inbreeding avoidance. Whales in the study area may be especially susceptible to inbreeding because of the apparent lack of dispersal of individuals from the natal group. As Moore and Ali (1984) point out, behavioural inbreeding avoidance may evolve where dispersal patterns result in a high risk of incest. It is unknown whether breeding occurs within or between pods since matings have not been observed. For one pod in the northern community, I11, breeding is clearly exogamous since the group has no mature males, yet females in the pod give birth regularly. Resident pods might interbreed with any other pods with which they associate. If individuals can assess their relatedness by dialect, they may be able to choose mating partners who are optimally related, thus avoiding both excessive inbreeding and outbreeding. Depending on community demography, whales may breed outside the pod but within the clan, or outside the clan.

Treisman (1978) has proposed that dialect variations in bird song may function in a similar way as a mechanism for kin recognition. A song dialect would serve as a "family badge" (Krebs and Kroodsma 1980) which reflects the degree of relatedness of kin in a more versatile and flexible manner than would be possible with a genetic marker. Repertoires of several varying songs would allow the encoding of more detailed

genealogical information than a single song type. Kin-recognition systems appear to be common in vertebrates (Moore and Ali 1984; Beecher 1982). Wild vervet monkeys (Cercopithecus aethiops), for example, can recognize individuals within their own group and in neighbouring groups on the basis of distinctive features in each animal's calls (Cheney and Seyfarth 1982). There is evidence that, within groups, vervets can classify individuals according to the maternal subgroups to which they belong. Whether they are able to assess relatedness across groups by this means is unknown.

Vocal Variation and Population Structure

Examination of the acoustic associations among resident killer whale pods can provide useful information on the structure of the population. If each clan, as defined by its distinctive call tradition, represents an independent lineage, it is probable that each has become genetically differentiated to some degree. It may also be that each pod is genetically distinct from others in its clan, and that vocal dialects within the tradition reflect this differentiation.

In social primates, new groups often form by division of formerly cohesive larger groups along lines of maternal relatedness (Nash 1976; Chepko-Sade and Sade 1979; Olivier et al. 1981). This is probably also the manner of pod formation in killer whales (Bigg 1982). Because matrilineal groups in primates are genetically distinct, such non-random splitting can, under certain demographic conditions, result in large variations in

gene frequencies between daughter groups (Buettner-Janusch et al. 1983; Cheney and Seyfarth 1983; Melnick and Kidd 1983; Melnick et al. 1984). Similar genetic divergence, or 'lineal effects', occur among villages of American Indian tribes that form by matrilineal division (Neel and Ward 1970).

Perhaps the best documented lineal effects exist among the Yananamo Indians of South America (Neel 1978). The Yananamo tribe is genetically and culturally distinct from other South American tribes, and villages within the tribe show marked genetic divergence from each other. Of significance in the context of the present study is that the villages have also become differentiated linguistically into a number of dialect groups. Patterns of linguistic divergence correspond closely to those of genetic microdifferentiation. Those villages with similar dialects tend also to be the most closely related genetically (Spielman et al. 1974).

The degree of genetic differentiation that might exist between pods depends on the extent of lineal effects resulting from pod fission and whether mating is endogamous within the pod, clan, or community. It does seem reasonable, however, that call traditions and dialects reflect the phylogenetic history of the resident population in B.C. It is therefore interesting that the patterns of social association and distribution observed among resident pods has, in most cases, given little indication of this underlying demographic structure within the population.

Time Depth of Vocal Differentiation

Although call traditions and dialects may provide an outline of the evolutionary history of resident killer whales in B.C., assigning a time scale to the process of population change and vocal differentiation is difficult. Examination of historical killer whale recordings revealed few differences in resident dialects between as early as 1958 and 1983. Without an accurate measure of the rate of vocal change, it is not possible to apply techniques used in estimating the time depth of linguistic divergence (e.g., Spielman et al. 1974; Payne et al. 1981). However, it is possible to make some rough estimates. The complete lack of homologous calls among the four resident clans suggests that each call tradition developed independently over long periods in isolation and came together subsequently on the B.C. coast. This period of development could involve hundreds of years. Each clan may have become established on the coast at widely spaced intervals. The A-clan has differentiated into eight pods with divergent dialect patterns, and therefore, might have had a long period of local occupancy. The R-clan, however, consists of only two acoustically-similar groups and hence may be relatively recent colonizers. Unfortunately, several potential factors, such as differential reproductive success of clans and founding-group sizes, complicate these speculations.

Because of the extremely slow growth rate of resident pods and the longevity of individuals, it may be decades before a pod begins to split, a gradual process which itself may take many

years to complete. As an example, when first identified in 1973, pods A1, A4 and A5 were closely associated but clearly discrete social units. After 10 years, they still spend most of their time travelling together. The call repertoires of the three pods have diverged to only a minor extent compared to the large differences apparent in other A-clan dialects.

It is possible to draw comparisons between killer whale dialects and those of other animal groups. However, these must be interpreted with caution because of the diversity of social structure, function of acoustic signals, and adaptive significance of the dialects. Long-term studies of song dialects in several bird species have documented the persistence of local song types across several generations. Payne et al. (1981) observed some song types in a population of indigo buntings (Passerina cyanea) to have survived in recognizable form over 15 years. Dialects of white-crowned sparrows (Zonotrichia leucophrys) at one location were found by Trainer (1983) to have retained the same basic structure over 18 years.

There may be a better analogy between the rates of dialect divergence in certain human societies and killer whales because of the similar longevity of individuals. Spielman et al. (1974) estimate from shared cognates that the Yananamo language group has evolved in isolation from other related South American Indian languages for 1500-3000 years. Within the Yananamo tribe, the maximum duration of separation between distantly related villages is estimated to be 600-1200 years, and the minimum for closely related villages is 75-200 years.

While it is doubtful that the retention rate of killer whale calls is the same for words within human languages, this comparison does serve to emphasize that cultural traditions may persist for extremely long periods in mammals. Continued sampling of resident killer whale vocalization in future years will hopefully result in a precise measure of the rate of dialect divergence. With this it will be possible to reconstruct the details and timing of growth and social evolution in the population with better accuracy.

PART III

VOCAL BEHAVIOUR AND DIALECTS IN TRANSIENT KILLER WHALES

INTRODUCTION

A ten-year study of killer whales (Orcinus orca) in British Columbia based on a photographic technique for identifying individual whales has documented the abundance, distribution and natural history of the species in the region (Bigg et al. 1976; Bigg 1982). Killer whales were found to live in stable social groups, or pods, which probably consist of kin-related animals. Two types of pods inhabit B.C. coastal waters (Bigg 1982). 'Resident' pods occur in relatively predictable locations during the summer months and probably remain in the area year round. The resident population is divided into two geographically-segregated communities. Pods within each community mix and travel together, but the two communities do not interact. 'Transient' pods are uncommon, and occur sporadically in unpredictable locations. They range throughout both resident communities, but do not associate with residents. Transient and resident whales differ in morphology, social structure, diet, and behaviour.

Bigg's photo-identification technique was also used in an examination of the underwater vocal behaviour of known killer-whale pods in the same area. Resident pods were found to have repertoires of structurally-discrete calls which vary from pod to pod (Ford and Fisher 1982, 1983). The 16 resident pods in B.C. can be divided into four 'clans' based on dialects. Each clan constitutes a distinct call tradition made up of a set of pods which share a portion of their call repertoire. Three of the four resident clans occur in one community and pods from

these clans mix on a regular basis (Part II).

This chapter examines the underwater sounds of transient killer whales. Transient's vocal behaviour is compared to that of resident whales and possible functions are discussed. Dialects of transient pods are interpreted in terms of social associations and geographical distribution.

MATERIALS AND METHODS

1. Field Observations and Recording

Transient killer whales were encountered on 15 occasions during 1979-83 in the waters surrounding Vancouver Island, B.C. Observations and recordings were obtained in the manner described in Parts I and II. Pod identities were determined from photographs taken of the dorsal fin and saddle patch of each individual observed. This technique is described in detail in Part II and Bigg (1982). Photo-identifications were made by M. Bigg. Underwater recordings were made using equipment and procedures detailed in Part II. Additional tapes of transient whale vocalizations were obtained from several other individuals (Table XVI). These were made on a variety of recording systems.

2. Sound Analysis

Recorded vocalizations were analyzed as described in Part II. As with resident killer whales, the underwater signals of transient whales consist primarily of repetitious calls which can be organized into discrete structural categories. Call types were determined initially by ear, and then confirmed with examination of spectrograms made on a Kay Elemetrics 7029A spectrum analyzer. Each call type is identified with the letter 'T', indicating that it was given by a transient pod, and a number.

RESULTS

1. Characteristics of Transient Whales

Most of the following information on the population dynamics and social organization of transient whales results from the work of Bigg (1982, pers. comm.). Seventeen transient pods containing 55 individuals have been identified on the coast of British Columbia. These differ from resident pods in many respects. The size and composition of transient pods are listed in Table XV. Pod sizes range from 1-8, with an average of 3.24 individuals per pod. In contrast, resident pods average 13.4 members (range 4 - 50).

Unlike resident pods, transients do not appear to have any well-defined range or foraging routine. They are seen infrequently at irregular times of the year, and in unpredictable locations. While foraging, members of transient pods tend to stay together and travel close to shore. Residents, on the other hand, scatter over wide areas while foraging. Transients usually swim deeply into bays, blind channels, and through dense kelp beds. They change direction frequently, and tend to dive for long periods. In a sequence of 18 dives by a foraging transient pod, dive times averaged 5.8 min (SD = 1.72 min) within a range of 2.25 - 9.0 min. Dives of resident whales are rarely over 3 min in duration during foraging. Transients may spend several hours at a single feeding location, and they may be seen within the same area of 10-20 km of coastline for several days. However, one transient

Table XV. Size and composition of transient pods identified off Vancouver Island. Pod sizes considered exact, except those marked by *, which are probably accurate to within one individual. Data from M. Bigg (1982 and pers. comm.).

Pod	Size	No. of bulls	No. of cows	No. of juveniles	No. of of calves
E	5*	1+	?	?	?
F	1	1	0	0	0
M	3	1	1	1	0
N	1	1	0	0	0
O2	3	0	3	3	0
O4	2	1	1	0	0
P	2	1	1	0	0
Q	5	0	3	2	0
S1	4	0	?	?	0
S8	1	0	1	0	0
T	4*	2	?	?	?
U	4	0	1+	?	1
V1	2	1	?	?	0
V10	8	?	?	?	?
X	5	0	1+	?	1
Y	3	1	1	1	0
Z	2	1	?	?	0

pod was observed to travel a minimum straight-line distance of about 600 km over 6 days (Bigg et al. 1976).

Evidence from stomach contents of stranded animals and field observations indicate that marine mammals are a major component of the diet of transient killer whales. Species taken by transients in local waters are mainly harbour seals (Phoca vitulina), Steller sea lions (Eumetopias jubatus), harbour porpoise (Phocoena phocoena) and elephant seals (Mirounga angustirostris). Resident whales, in contrast, appear to feed predominantly on salmon (Oncorhynchus spp.) and other fish species in the study area (Part II).

The 17 transient pods form a community similar to but distinct from the two resident communities. Transient pods frequently join and travel with other transients in the community, as do pods within each of the two resident communities (Part II). Transients travel throughout both the northern- and southern-resident community ranges, but do not associate with resident pods. Transient pods were twice observed to meet residents. On both occasions, the two types of whales continued on without mixing or showing any observable reaction. The range of local transient pods is unknown, but it includes at least the northern and southern resident communities. One group, V10, has been sighted off northeastern Vancouver Island and in Fredrick Sound, Southeast Alaska, about 900 km to the north (G. Ellis and D. McSweeney, pers. comm.).

Transient whales also differ from residents in morphology. A high proportion of transient cows have dorsal fins which taper

to a sharp point, unlike the rounded tips on most resident cows. The shape of the leading edge of the fin also differs slightly, and the dorsal saddle patch tends to be larger and extends further anteriorly in transients.

2. Acoustic Behaviour

Transient whales are very quiet compared to residents. A total of 13 transient pods was encountered on 15 occasions in the waters around Vancouver Island. The animals were observed and monitored acoustically over a total of 45.4 h, for a mean of 3.03 h per encounter. Sounds were heard during only 5 of these 15 encounters, and usually for only a few minutes on each occasion.

Transients tend to be completely silent while foraging, which is their most common activity. This includes echolocation-type clicks, which, in contrast, are heard throughout foraging episodes in resident pods. Occasionally, foraging transient whales emit a low-level call, T1, which appears to be a characteristic signal throughout the community. Several examples of call T1 as rendered by different pods are shown in Figure 50. This signal was the only one recorded during a meeting between two transient pods, Y and Q. The meeting was associated with much apparent excitement, including a variety of aerobatics and speed swimming, yet the rate of calling and call diversity were much lower than in similar contexts in resident pods.

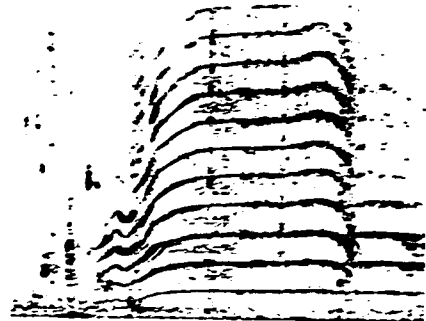
Loud, discrete calls typical of resident killer whales have

Figure 50. Sample spectrograms of call type T1. Examples shown for pods M, X and Y, recorded in B.C., and SEA pod recorded in southeast Alaska.

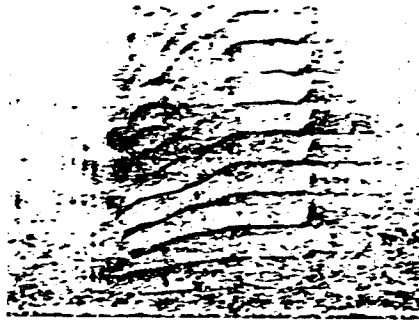
8- T1 - M
kHz



T1 - X



T1 - Y



T1 - SEA



0 500 ms

been recorded on only a few occasions. The best sample of calls was obtained from pod X, a group of five whales, as the animals milled slowly at the surface for approximately 2 h. They were nearly continuously vocal throughout this period, emitting a total of 6 discrete call types. Sample spectrograms of these signals are illustrated in Figure 51, and their frequency of occurrence in Figure 52. On another occasion, Y pod, consisting of a bull, cow, and juvenile, was observed for a period of 4 h while foraging. The animals were consistently silent, except for an interval of 1.5 min as the pod separated and approached a reef where harbour seals were hauled out. A total of 6 calls, belonging to 3 call types, were emitted by the juvenile during this vocal period. Several other observations of pods splitting temporarily and approaching seal haul-outs were not accompanied by vocalization.

Although transients generally forage in silence, they seem to become vocal while in the process of capturing prey. This was observed on all three occasions that transient pods were monitored acoustically while making a kill or feeding (G. Ellis, D. McSweeney, R. Osborne, pers. comms.).

Group-resting behaviour similar to that of residents was seen only once in transients. Two pods, Y and Q, were observed to group-rest together in a small bay for 1.5 h. The pods stayed 100-200 m apart and each dived independently for 5-7 min at a time. The animals remained silent throughout the resting period.

3. Dialects

Call types produced by transient pods recorded in British Columbia, California, and southeast Alaska waters are listed in Table XVI. These call types are unlike those given by any resident pod (Part II). A total of 8 identified pods and 2 unidentified groups were involved in these encounters. The recording of O4 pod was obtained while the group was held temporarily in a captive pen in Budd Inlet, Puget Sound, Washington, in 1976. This pod was encountered in 1982 off southern Vancouver Island, but no sounds were recorded.

The California tape was made in the presence of 3 whales, a bull, cow and juvenile, who approached the recording vessel following underwater playback of recorded transient vocalizations (X pod, recorded in B.C.). Photographs of these animals indicate that they are a different pod than any previously identified in B.C. waters. The two encounters in southeast Alaska involved a pod of 5 whales, tentatively identified as 'SEA', which has not been observed in B.C. waters. On one of the two encounters, V10 pod, a group which was previously identified off northern Vancouver Island, was travelling with SEA pod.

All transient pods recorded share at least one call type, T1. As described above, it is a rather quiet call that is given in occasional bouts during foraging episodes. T1 was the only call recorded during 3 of the 10 encounters. Seven other calls, T2 to T8, were identified on other encounters. Four of these, T2, T3, T5 and T6, were produced only by X pod (Figure 51).

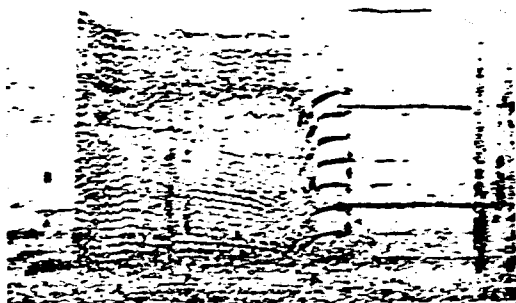
Table XVI. Discrete call types recorded from transient pods.

Pod	Location	Date	Source *	Call							
				T1	T2	T3	T4	T5	T6	T7	T8
O4	Puget Sound, WA	10 Mar 1976	R.O.	X						X	X
M	S. Vancouver Is.	15 Oct 1979	G.E.	X							
?	S. Vancouver Is.	28 Sep 1979	R.O.	X						X	X
S8, X	N. Vancouver Is.	09 Aug 1980	J.F.	X							
X	N. Vancouver Is.	13 Aug 1980	J.F.	X	X	X	X	X	X		
Y	S. Vancouver Is.	09 Sep 1980	J.F.	X						X	X
Q, Y	S. Vancouver Is.	13 Sep 1980	J.F.	X							
?	Soberanes Pt., CA	16 Jan 1983	C.M.	X			X			X	X
SEA, V10	S.E. Alaska	13 Aug 1983	D.McS.	X						X	X
SEA	S.E. Alaska	31 Aug 1983	D.McS.	X					X		X

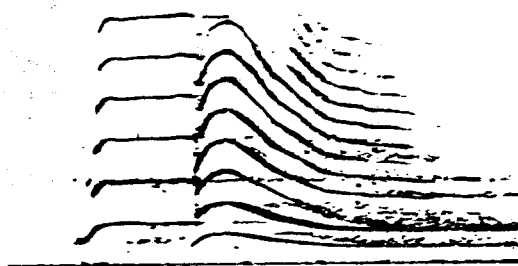
* Sources: G. E. = G. Ellis; West Coast Whale Research Foundation
J. F. = J. Ford
C. M. = C. Malme; Bolt, Beranek and Newman, Inc.
D. McS. = D. McSweeney; independent researcher
R. O. = R. Osborne; Moclips Cetological Society

Figure 51. Spectrograms of X-pod calls T2, T3, T4, T5, and
T6.

T2 - X



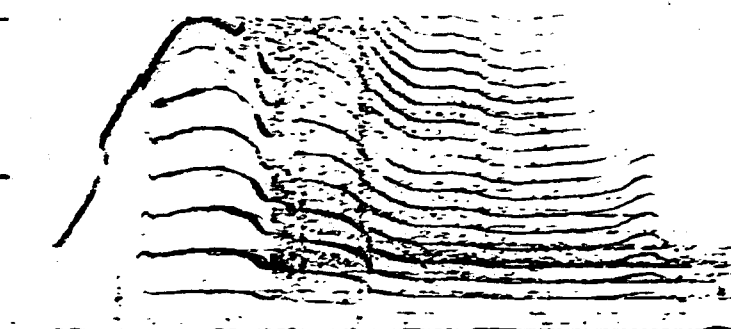
T3 - X



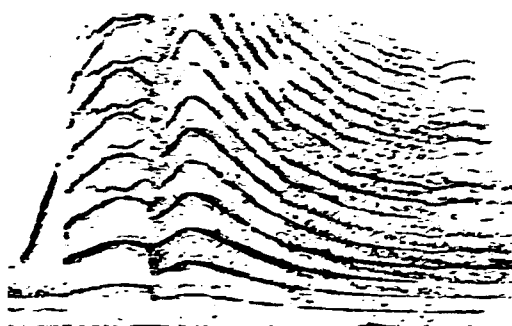
T4 - X

8 -
kHz

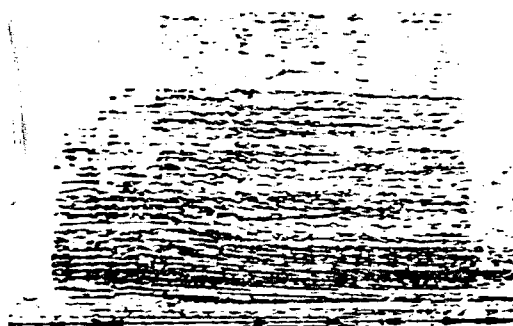
4 -



T5 - X

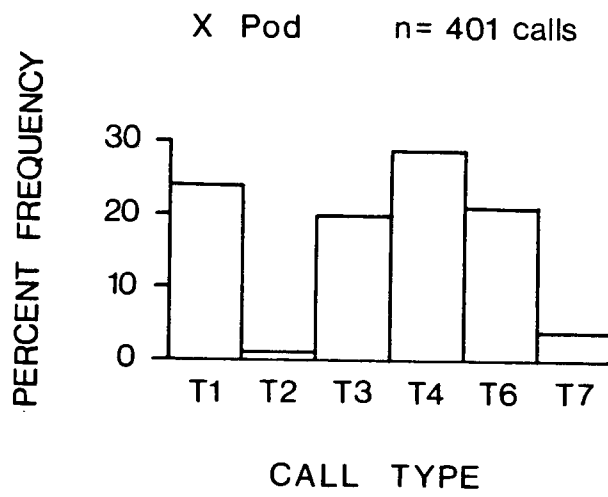


T6 - X



0 500 ms

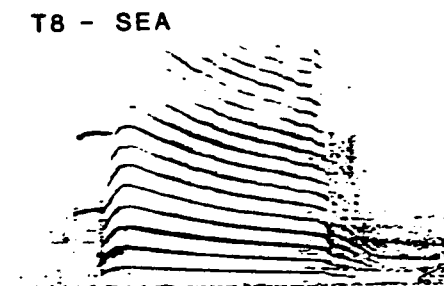
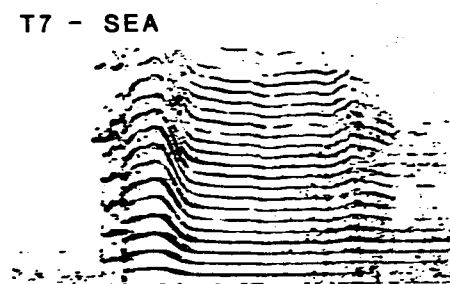
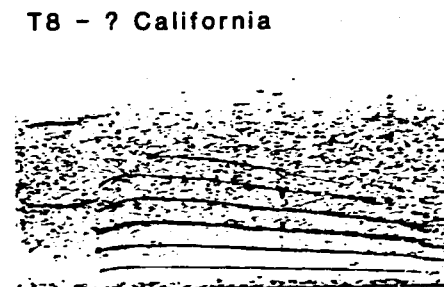
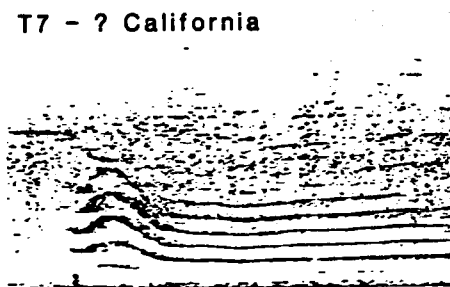
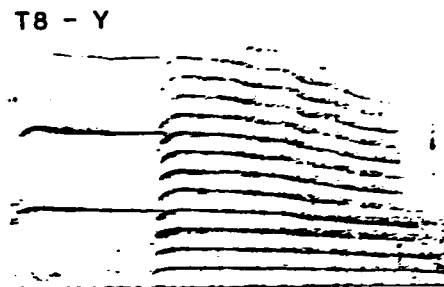
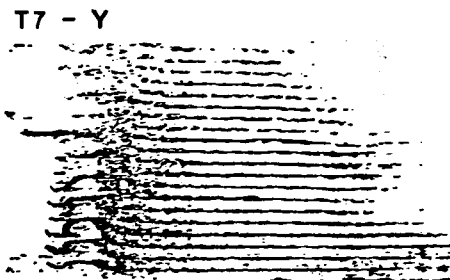
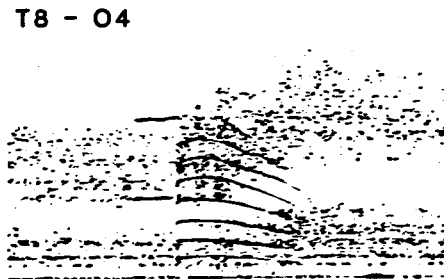
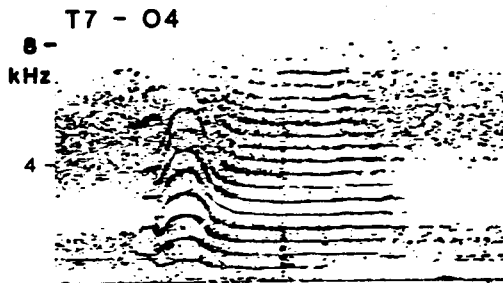
Figure 52. Frequency distribution of calls produced by X
 pod.



Calls T7 and T8 were both recorded on 5 occasions involving at least 4 different pods located in California, B.C., and southeast Alaska. The minimum distance between the California and Alaska locations is about 3700 km. Examples of the two call types recorded from these groups are shown in Figure 53. Some differences in fine structure can be seen, but unfortunately there are inadequate samples to determine whether these represent group-specific variations.

The community of transient pods on the west coast of North America therefore may be a single acoustic association equivalent to the clans within resident communities (Part II). As in resident clans, there is some call sharing among all member pods, yet certain pods or sets of pods appear to produce calls which are not used by all in the clan.

Figure 53. Spectrograms of transient pod calls T7 and T8.
Note diagnostic narrowband component between 5 and 6 kHz
at the start of T7 calls.



0 500 ms

DISCUSSION

Transient killer whales differ from residents in numerous ways. Their significantly smaller pod sizes suggest that transients have a different social system than residents. Transients range more widely than residents, and have no well-defined or predictable distribution at any time of the year. Transients form a community of associating pods which is sympatric with resident communities, but the two types of whales appear not to interact socially when they meet. Transients hunt in small groups for marine mammal prey, while larger resident pods feed primarily on fish.

Transient and resident killer whales also differ strikingly in acoustic behaviour. Residents tend to vocalize frequently while foraging, using an array of discrete social signals as well as echolocation clicks. Transients, on the other hand, generally forage in silence, apparently without echolocation.

Many aspects of the foraging behaviour of transients suggest that they hunt opportunistically, relying on stealth to surprise and capture prey. They tend to dive for long periods and surface in unpredictable places, especially when around reefs and islets where seals are hauled out. A surprise strategy would seemingly be most effective if the whales hunted in silence, since seals and other marine mammals have good underwater hearing and may learn to avoid approaching whales. The lack of echolocation signals indicates that the whales may locate their prey visually or through passive listening. This strategy may only be effective when hunting in small groups,

since larger pods would require the exchange of calls to coordinate movements. Presumably, large group size and high rates of vocalization do not negatively affect and may even enhance the foraging success of resident pods when feeding on fish.

All transient pods recorded to date are related acoustically and, using the definitions in Part II, may tentatively be regarded as a single 'clan' with a distinct call tradition. Within the tradition are call dialects exclusive to subsets of pods. The range of the transient clan is large, spanning at least 3700 km of coastline, and overlaps geographically with the four resident clans studied here.

The processes of pod formation and dialect development in transients may be similar to those proposed for residents (Part II). The transient clan may represent a single phylogenetic lineage composed of related pods which have originated from a common ancestral group. Their shared call tradition is a reflection of this unique evolutionary history and probable genetic differentiation from other lineages. The social isolation of transients and residents and morphological differences between the two also suggest that transients comprise a genetically distinct population. Transients have apparently become adapted to a marine-mammal hunting existence which involves small group sizes, a nomadic distribution and silent foraging. Residents, on the other hand, feed primarily on salmon, and their social structure, distribution and behaviour may be adaptations to a life style dependent upon this

resource.

Intraspecific variation in social structure and foraging has been reported in other mammals (see review by Lott 1984). Such variations may be consistent for several generations, but given a change in prey abundance or territory availability, animals can switch from one strategy to another. Whether transients are able to switch to a resident-type of living, or vice versa, is unknown. However, the acoustic, behavioural, and morphological differences between the two types of whales suggest a long period of segregation and divergence.

GENERAL SUMMARY AND CONCLUSIONS

This study examines the patterns of underwater vocal communication of killer whales in British Columbia coastal waters. The primary objective of the study was to gain a better understanding of this important aspect of the animals' behaviour and its role in the maintenance of social structure. The following summarizes the principal findings described in this thesis.

The underwater sounds of 16 'resident' and 6 'transient' killer whale pods were recorded in the waters surrounding Vancouver Island during 1978-83. Historical field recordings made in the same area during 1958-76, and several recordings of captive whales taken from local waters were also examined.

Three general categories of social signals were identified: (1) repetitious, pulsed calls which can be organized into discrete categories, (2) variable pulsed sounds which are not repeated and thus cannot be classified into call types, and (3) narrowband whistles. In resident pods, the first sound category, discrete calls, dominates vocal exchanges in most contexts. However, the frequency of use of discrete calls, variable calls and whistles, as well as aberrant versions of discrete calls, varies with activity. Discrete calls comprise more than 90% of calling during foraging and travelling. However, during socializing and beach-rubbing, behaviours associated with close interindividual spacing and physical interaction, the occurrence of variable sounds, aberrant pulsed calls, and whistles increases significantly.

Discrete calls probably serve to keep pod members in touch while dispersed and out of sight of each other. Modifications in call structure appear to reflect arousal level. Variable sounds and whistles may convey more subtle information about arousal and social affiliations during close interactions.

Repeated encounters with pods demonstrate that each group produces a limited repertoire of discrete call types. In most pods, all call types are used in all 'active' contexts, although their frequency distribution varies. Few call types could be correlated with any specific behaviour. Recordings of captive whales of known pod origin indicate that most or all of the calls in the repertoire are produced by both sexes, and that repertoires can be stable for periods of at least 15 years. Historical recordings made in local waters provide evidence of repertoire persistence over 25 years. Killer whales and other dolphins can mimic and learn new vocal patterns, a capability otherwise exclusive to humans among the mammals. It is therefore likely that call repertoires are passed across generations by cultural transmission.

A previous study (Bigg 1982) discovered that two types of killer whales occur in B.C. waters. A population of 'resident' pods is divided into two communities with exclusive ranges. A third community of 'transient' pods travels throughout the two resident community ranges. Pods within each community associate with one another, but the three communities do not mix.

The 16 resident pods in the study area can be divided into four acoustic groups, or 'clans'. Pods within a clan share call

types, but no call sharing occurs between clans. Therefore, each clan represents a distinct call tradition. Calls shared within clans often have consistent structural variations unique to pods or sets of pods. These, as well as calls produced exclusively by certain pods, form a system of dialects within each tradition.

Three of the four resident clans belong to the 'northern' resident community, and pods from each associate frequently. Observed patterns of pod association are in many cases unrelated to acoustic relationships. The 'southern' resident community is comprised of a single clan, and the same appears to be the case for the transient community.

The origin and adaptive significance of call traditions and dialects within the killer whale population are unknown. It is probable that a clan represents a single lineage of related pods which has descended from a common ancestor. New pods appear to form by the gradual splitting of formerly large pods along lines of maternal relatedness. This process is accompanied by dialect divergence and, possibly, genetic differentiation among 'daughter' groups. It is likely that each clan has a separate evolutionary history and developed its unique call tradition over long periods in geographic isolation. Their occurrence on the B.C. coast may be the result of independent founding events at different times in the past.

Dialects may represent byproducts of pod evolution and cultural drift with no functional significance, or adaptations with some selective value. Vocal divergence among related pods

could result from random copy errors in call learning. However, there is evidence that repertoire variation may not occur randomly. Dialects may serve as indicators of kinship or pod identity. As such, dialects could function to enhance the usefulness of discrete calls in maintaining pod cohesion and integrity, or to act as a behavioural means for avoiding inbreeding. An active process of acoustic divergence would better explain the apparent innovation of new call types in pod repertoires.

The call traditions and dialects of killer whales described here appear to be unique among not only cetaceans, but all mammals. This study has provided an initial description of this unusual acoustic system and has speculated on its evolution and function. Further research is required to test these ideas. In-depth analyses of the vocal exchanges within pods must be undertaken to document in detail the specific behavioural contexts in which call types occur. Additional information on the distribution and social associations of pods throughout the year is required for a more complete comparison with call traditions and dialects. Knowledge of the mating system of killer whales must be obtained, since this may have important consequences for hypotheses concerning dialect function. Finally, annual monitoring of social dynamics and vocalizations in a resident community should be continued for as long as is required to document the process of pod formation and dialect differentiation. With this it should be possible to construct a model of the evolutionary history of the killer whale population

in B.C. based on acoustic relationships.

Many broad questions remain to be considered. Do similar group-specific dialects exist in other cetaceans, or are they a peculiarity of killer whales, perhaps related to the species' unusually closed social system? Are killer whale dialects a byproduct of the delphinid's ability of vocal learning, or is vocal learning a byproduct of the evolution of dialects? Why should a dialect system have evolved in a cetacean and not in any non-human terrestrial mammals? Hopefully, as the trend toward studies of the life history, ecology and behaviour of wild cetaceans continues to grow, answers to these questions will be forthcoming.

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APPENDIX I

SUMMARY OF RESIDENT POD ENCOUNTERS 1978 TO 1983

Northern Resident Community Encounters:

Date	Pod(s)
<u>1978</u>	
Jul 19	A1, A4, A5
Jul 20	A1, A4, A5, H
Jul 21	A1
Jul 23	A1, H, I11, I31
Jul 24	A1, I11
Jul 26	A1, A4, A5, D
Jul 29	A1, A5, D
Jul 30	H, I11
Aug 01	A1, A4, A5, D
Aug 02AM	A1, A4, A5, C, D, H, I11, I31
Aug 02PM	B
Aug 05	A1, A4, A5, B, C
Aug 07	A1, A4, A5, C
Aug 12	A5, C, I11
Aug 17	A1
Aug 18	A1, (B)
Aug 20	A1
<u>1979</u>	
Jul 11	A1
Jul 12	A1, A5
Jul 13	A1, H
Jul 14	A1
Jul 15	A1, A4, A5, H
Jul 22	A1, A4, A5
Jul 23	A1, A4, A5
Jul 24	A1, (A4), A5
Jul 26	A5
Jul 29	A1, A4, A5
Jul 30	A1, A4, A5
Aug 01	A1, A5
Aug 02	A1
Aug 03	A4, B
Aug 04	A1, A4, A5
Aug 05	A1, A5
Aug 07	A1, A5, (B)
Aug 13	A1, A4, A5, I1
Aug 14	I1

Date	Pod(s)
<u>1980</u>	
Jul 07	A4, A5, C, D, (H, G)
Jul 09	A5, (C)
Jul 10	A4, A5, C, D
Jul 11	B
Jul 12	B
Jul 14	A5, (B)
Jul 15	A5, C, D
Jul 16	A5, (C), D
Jul 18	A5, D
Jul 19	A5, D
Jul 20	A4, A5, D
Jul 21	A5, D
Jul 22	A5, D
Jul 23	A4, A5
Jul 24	A5
Jul 25	A4, A5, D
Jul 28	A5
Aug 01	B
Aug 02	A4, A5, B, D, G, I11
Aug 06	B, G, I11
Aug 07	B
Aug 08	B, G, I11
Aug 14	I1
Aug 15	I1
Sep 09	A4, A5
Oct 01	A1, A5
<u>1981</u>	
Jul 05	A5, B
Jul 06	A1
Jul 08	B, A5
Jul 09	A5
Jul 10AM	A5, (B)
Jul 10AM	A1, A4, A5, B, C, G, H, R
Jul 11	A1, A5
Jul 12	A5
Jul 13	A4
Jul 14	A1, A4, A5
Jul 15	A1, A4, (A5)
Jul 16	A5
Jul 17	A1, A4
Jul 18	A1, A4, (A5)

Date	Pod(s)
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1981 - cont'd...

Jul 21	A1, A4, A5, G, I11, I31, R, W
Jul 23	A1, A4, A5
Jul 24	A1, A4, A5, I11, I31, W
Jul 27	A1, A4, A5
Jul 29	A1, A4, A5
Jul 30	A1, A4, A5
Jul 31	A1, A4, A5
Aug 01	A1, A4, A5
Aug 02	A1, A4, A5
Aug 03	A1, A4, A5
Aug 04	A1, A4, A5
Aug 05	A1, A4, A5
Aug 06	A1, A4, A5
Aug 07	A1, A4, A5
Aug 08	A1, A4, A5
Aug 09	A1, A4, A5
Aug 26	B
Aug 27	B
Aug 28	B, H, I1, I11, I31
Aug 29	B, (A1, A4, A5)
Aug 30	A1, A4, A5, H, I31

1982

Jul 09	H
Jul 10	A1, H
Jul 11	B
Jul 11	B, D, H, I1
Jul 12	A4
Jul 14	A1, C, H
Jul 16	A5, (A1, C), G, H, I1, I11, I31, W
Jul 17	A1
Jul 18	A1, A5, B, D, H, I1
Jul 20	A1, A5, G
Jul 21	B
Jul 22	A1, A4
Jul 23	A1, A4
Jul 24	A1, A4, A5, B, G
Jul 25	A1, A4, (A5, B)
Jul 26	A1, A4, A5, B, C, G, I11, I31, W
Jul 27	C, I11, W
Jul 28	A1, A4
Jul 29	B
Aug 02	A1, B, H
Aug 03	A1, A4, A5, B
Aug 04	B

Date	Pod(s)
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1982 - cont'd...

Aug 06	A1, A4, (A5, I11, I31), C, W
Aug 07	A1, A4, A5, C, G, H, I11, I31, R, W
Aug 08	A1, A5, B, G
Aug 09	A1, A4, A5
Aug 11	A1, A5

1983

Aug 05	A1
Aug 07	A1, C
Aug 09	A1, A4, C, I1
Aug 11	A1, C
Aug 12	A1, A4, C, G, I11, W
Aug 13	A1, G, I11, W
Aug 14	I31
Aug 15	A1
Sep 16	A5
Sep 17	A1, A5
Sep 18	A1, A5

Southern Resident Community Encounters:

Date	Pod(s)
------	--------

1978

Sep 27	J, K, L
Oct 02	J, K, L

1979

May 03	J
May 18	J
Jun 07	J
Jul 16	J, K, L
Aug 22	J
Aug 26	J
Sep 25	J, K, L

Date	Pod(s)
<u>1980</u>	
Jun 02	J
Jun 22	K
Jun 26	J
Aug 05	J, K, L
Aug 30	L
<u>1981</u>	
Feb 20	J
May 22	J
May 29	J
Sep 15	J, K, L
Sep 16	L
Oct 13	K, L
<u>1982</u>	
Feb 03	K, L
Jun 04	J
Aug 27	L
<u>1983</u>	
Aug 12	J, K, L

APPENDIX II

SUMMARY OF HISTORICAL FIELD RECORDINGS EXAMINED IN THIS STUDY

Appendix II: Historical Field Recordings Examined

Date	Location	Pods Present	Source
<u>Northern Community:</u>			
Aug 29 1964	Johnstone Strait	A1, C, R	HDF
Aug 31 1964	Johnstone Strait	A1, C, R	HDF
Aug 08 1970	Blackfish Sound	A1, H	PS
Aug 19 1971	Blackfish Sound	A1	PS
Aug 22 1971	Blackfish Sound	B	PS
Aug 05 1973	Johnstone Strait	A's	EH
Aug 09 1973	Johnstone Strait	A's	EH
Aug 10 1973	Blackfish Sound	A1, A4, A5, C/D, I11, (I31?)	PS
Aug 11 1973	Johnstone Strait	A1, C/D	EH
Aug 12 1973	Blackfish Sound	A1, C/D	PS
Aug 18 1973	Johnstone Strait	A1, A5, C/D	EH
Aug 20 1973	Johnstone Strait	A1, A5	EH
Aug 24 1973	Johnstone Strait	A1, A5, B	EH
Aug 26 1973	Blackfish Sound	A1	PS
Aug 27 1973	Blackfish Sound	D	PS
Aug 30 1973	Blackfish Sound	A1, A5	PS
Aug 31 1973	Blackfish Sound	A1, A5, C/D, R	PS
Sep 07 1973	Blackfish Sound	C/D	PS
Jul 27 1974	Johnstone Strait	A1, A5	EH
Jul 30 1974	Johnstone Strait	A1, A5, H	EH
Aug 11 1974	Johnstone Strait	A1, A4	EH
<u>Southern Community:</u>			
Feb 19 1958	Saanich Inlet	J	DREP
Oct 20 1960	Puget Sound	J	USN
Spring 1961	Saanich Inlet	J	DREP
Mid-1960's	unknown	J, K, L	TP

Sources: HDF = H.D. Fisher, U of B.C.
PS = Paul Spong, OrcaLab
EH = E. Hoyt
DREP = Defence Research Establishment Pacific
USN = United States Navy
TP = T. Poulter Collection

* Identifications of pods based on vocalizations.

APPENDIX III

DESCRIPTIVE STATISTICS AND ANOVA COMPARISONS OF CALL VARIABLES

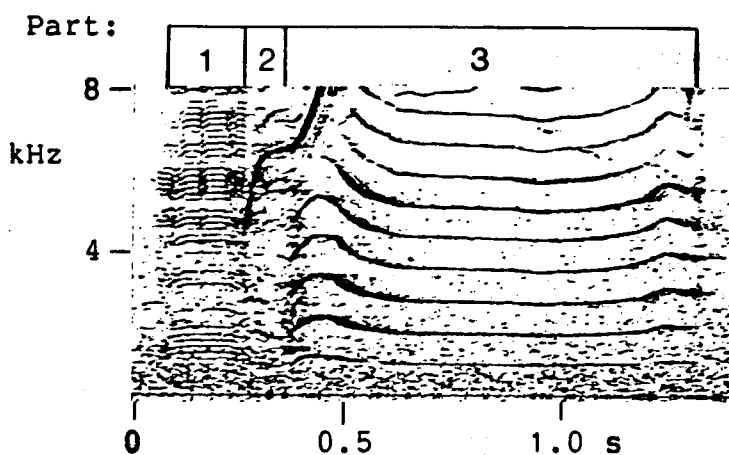
Call types are described according to measurements of structural subdivisions, or "parts", which are identified numerically in the following tables. In simple parts, only single duration and sideband, or harmonic interval measurements were made. In complex parts, several measurements were made, usually of sideband interval's at various points in the part. Simultaneous narrowband components, or "tones", were measured when present. No attempt was made to describe components at frequencies of > 8 kHz. Statistical comparisons are ANOVA's with Scheffe's multiple comparisons testing a null hypothesis that variable measurements were equal.

Abbreviations used in the tables are as follows:

C.V.	=	coefficient of variation
Dur	=	duration
SBI	=	sideband (or harmonic) interval
ms	=	milliseconds
Hz	=	Hertz
f	=	frequency
Δf	=	change in frequency
SB2	=	second sideband or harmonic
IPI	=	interpulse interval
PRL	=	pulse rate leveling (or, point at which pitch stops increasing or decreasing)
p	=	probability level from Scheffe's test
MD	=	captive whale "Moby Doll"
Sh	=	captive whale "Shamu"
Na	=	captive whale "Namu"
64	=	1964
73	=	1973

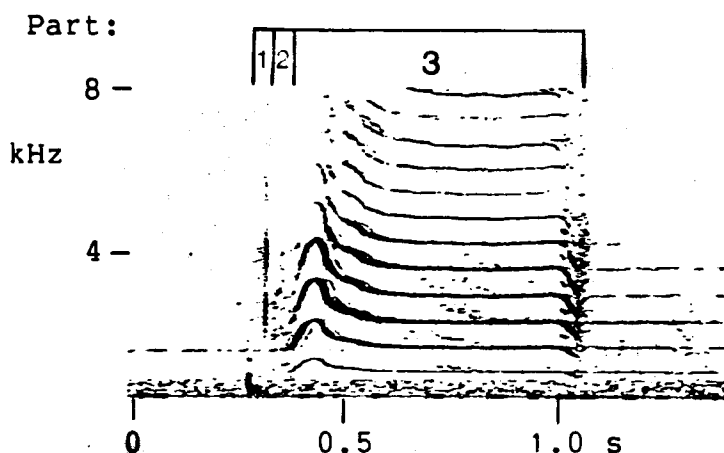
 NORTHERN COMMUNITY CALLS:

CALL N1i



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	A1	1339	13.6	931	1772	26
<u>Part 1:</u>						
Dur (ms)	A1	212	14.1	130	274	26
SBI (Hz)	A1	161	13.2	120	203	18
<u>Part 2:</u>						
Dur (ms)	A1	117	20.5	78	160	26
<u>Part 3:</u>						
Dur (ms)	A1	1011	17.6	626	1373	26
SBI, start (Hz)	A1	870	17.7	515	1135	26
SBI, peak (Hz)	A1	1010	5.5	921	1119	26
SBI, mid (Hz)	A1	784	5.1	715	858	26
SBI, end (Hz)	A1	975	11.5	813	1263	26
<u>Tone:</u> f, start (Hz)	A1	4407	10.6	3305	5375	24

CALL Niii



Measurement	Pod	Mean	C.V.	Min	Max	n	p
Duration (ms)	B	997	12.2	811	1346	28	ns
	I1	1051	10.3	839	1270	26	
<u>Part 1:</u>							
Dur (ms)	B	119	29.0	54	220	28	<0.001
	I1	180	45.6	92	397	29	
SBI (Hz)	B	80	22.7	52	133	20	<0.001
	I1	55	33.4	24	83	15	
<u>Part 2:</u>							
Dur (ms)	B	36	47.4	4	66	27	<0.01
	I1	53	45.2	9	90	28	
<u>Part 3:</u>							
Dur (ms)	B	798	16.3	607	1156	28	ns
	I1	762	16.3	556	1071	29	
SBI, start (Hz)	B	815	24.8	399	1165	28	ns
	I1	859	13.9	579	1067	26	
SBI, peak (Hz)	B	1029	8.8	860	1297	28	ns
	I1	979	19.0	100	1115	28	
SBI, mid (Hz)	B	708	7.0	610	808	28	<0.001
	I1	788	7.2	694	887	24	

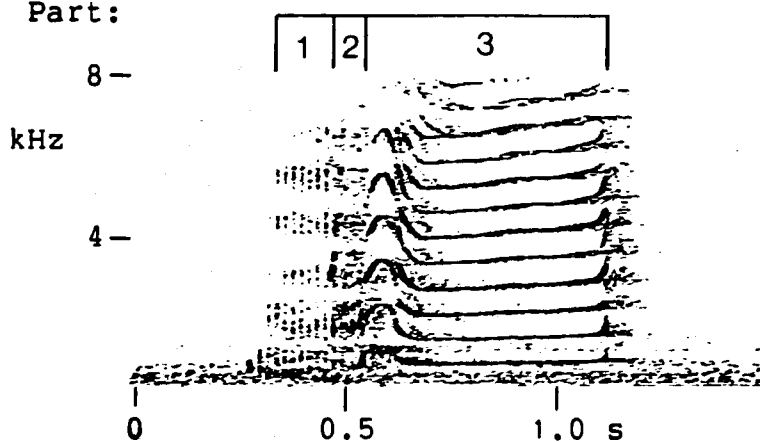
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CALL N1ii - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n	p
SBI, end (Hz)	B	663	7.0	590	767	28	ns
	I1	697	19.7	100	829	28	
<u>Tone:</u>							
f, start (Hz)	B	3368	23.4	2575	5633	25	<0.001
	I1	2520	20.3	1970	3898	25	

CALL N1iii

Part:



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	C	835	10.6	643	948	31
	D	846	14.8	569	1016	24
	Na	901	14.4	687	1171	17

Part 1:

Dur (ms)	C	152	30.6	64	278	31
	D	173	31.1	90	320	26
	Na	171	31.1	89	292	17

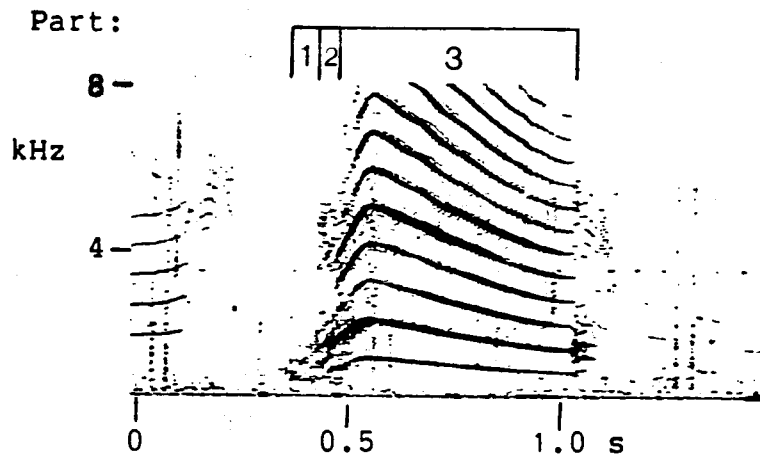
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 CALL N1iii - continued...

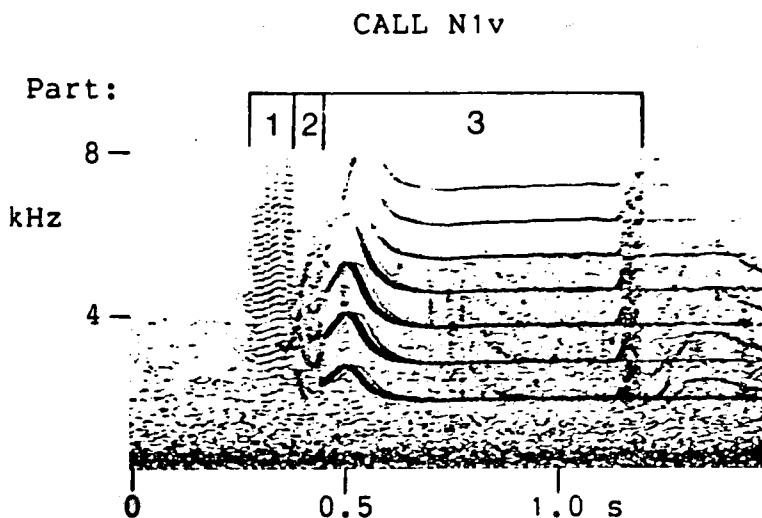
Measurement	Pod	Mean	C.V.	Min	Max	n
<u>Part 2:</u>						
SBI (Hz)	C	49	18.6	32	77	28
	D	49	11.7	37	59	20
	Na	40	11.5	32	53	17
Dur (ms)	C	40	34.6	8	73	31
	D	45	37.1	2	68	26
	Na	36	41.0	17	59	17
<u>Part 3:</u>						
Dur (ms)	C	594	13.0	442	730	31
	D	580	15.1	366	693	26
	Na	648	18.9	419	833	17
SBI, start (Hz)	C	828	16.2	544	1080	29
	D	940	16.7	507	1190	26
	Na	707	20.4	500	976	17
SBI, peak (Hz)	C	1035	11.1	588	1183	31
	D	1117	7.9	961	1441	26
	Na	1097	5.8	1000	1222	17
SBI, mid (Hz)	C	674	7.4	571	775	29
	D	666	6.9	574	767	26
	Na	621	7.0	560	707	17
SBI, end (Hz)	C	657	8.9	504	757	29
	D	685	6.1	599	746	26
	Na	657	5.7	598	736	17
<u>Tone: f, start (Hz)</u>	C	3884	15.9	3032	5065	13
	D	3784	13.9	2866	4735	18
	Na	3174	19.1	2614	5422	17

CALL N1iii - Measurement Comparisons			
Measurement	C vs D	C vs Na	D vs Na
Duration (ms)	ns	ns	ns
<u>Part 1:</u>			
Dur (ms)	ns	ns	ns
SBI (Hz)	ns	<0.001	<0.001
<u>Part 2:</u>			
Dur (ms)	ns	ns	ns
<u>Part 3:</u>			
Dur (ms)	ns	ns	ns
SBI, start (Hz)	<0.05	<0.05	<0.001
SBI, peak (Hz)	<0.05	ns	ns
SBI, mid (Hz)	ns	<0.01	<0.05
SBI, end (Hz)	ns	ns	ns
<u>Tone: f, start (Hz)</u>	ns	<0.01	<0.05

CALL N1iv

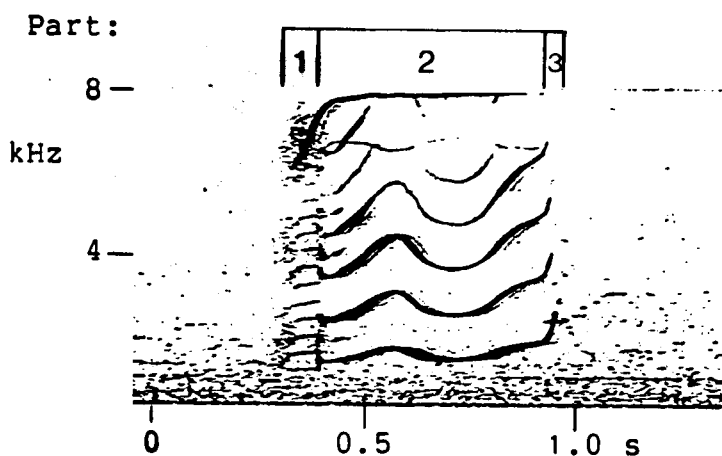


Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	H	768	12.6	642	1026	25
<u>Part 1:</u>						
Dur (ms)	H	82	37.0	33	160	25
SBI (Hz)	H	82	20.3	40	113	20
<u>Part 2:</u>						
Dur (ms)	H	51	40.0	14	111	25
<u>Part 3:</u>						
Dur (ms)	H	632	11.3	517	805	25
SBI, start (Hz)	H	787	11.2	531	916	25
SBI, peak (Hz)	H	958	4.3	875	1028	25
SBI, mid (Hz)	H	575	10.6	467	704	25
<u>Tone: f, start (Hz)</u>	H	2825	14.2	2330	3498	12



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	A4	827	18.3	594	1099	20
<u>Part 1:</u>						
Dur (ms)	A4	105	21.7	60	164	20
SBI (Hz)	A4	173	15.6	130	218	17
<u>Part 2:</u>						
Dur (ms)	A4	30	42.2	2	55	20
<u>Part 3:</u>						
Dur (ms)	A4	648	20.4	434	897	20
SBI, start (Hz)	A4	870	15.4	656	1213	20
SBI, peak (Hz)	A4	1428	5.7	1292	1568	20
SBI, mid (Hz)	A4	1000	6.9	953	1150	20
SBI, end (Hz)	A4	1012	7.2	899	1135	20
<u>Tone: f, start (Hz)</u>	A4	4192	15.5	3109	5310	18

CALL N2



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	A1	664	21.00	511	1066	31
	A4	654	19.39	468	942	25
	A5	715	17.26	504	1030	30
<u>Part 1:</u>						
Dur (ms)	A1	71	86.99	30	395	31
	A4	75	89.83	23	289	25
	A5	55	41.04	16	103	30
SBI (Hz)	A1	479	14.58	291	611	30
	A4	493	11.81	373	580	18
	A5	473	12.28	362	574	23
<u>Part 2:</u>						
Dur (ms)	A1	593	20.68	460	1001	31
	A4	578	18.96	415	775	25
	A5	659	18.07	438	929	30
SBI, start (Hz)	A1	1046	8.21	830	1191	31
	A4	1185	9.12	1022	1419	25
	A5	1081	9.11	832	1295	30

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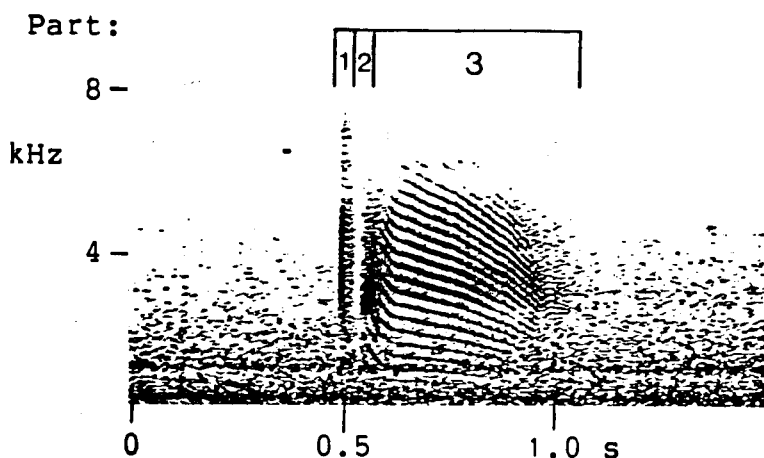
 CALL N2 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
SBI, 1st peak (Hz)	A1	1455	5.62	1320	1608	31
	A4	1569	12.15	1206	2098	25
	A5	1679	11.45	1179	2049	30
SBI, end (Hz)	A1	1604	10.35	1418	2062	31
	A4	1928	11.20	1648	2459	24
	A5	1954	17.57	1515	2766	30
Time to 1st peak (Hz)	A1	179	24.29	98	265	31
	A4	94	25.50	56	168	25
	A5	133	19.85	83	208	30
<u>Part 3:</u>						
Dur (ms)	A1	61	47.56	27	109	7
	A4	60	36.28	32	127	24
	A5	66	26.97	33	104	29
f, SB2, end (Hz)	A1	5114	27.33	3829	7913	8
	A4	6384	12.98	4906	7935	25
	A5	6660	11.86	5352	7943	29
<u>Tone:</u>						
f, start (Hz)	A1	6396	8.21	5229	7544	31
	A4	6331	7.90	5590	7114	25
	A5	6435	9.19	4825	7253	26
f, midpoint (Hz)	A1	7631	10.66	3326	7982	31
	A4	7311	22.04	2418	8020	17
	A5	7869	1.70	7559	8081	17

 CALL N2 - Measurement Comparisons

Measurements	A1 vs A4	A1 vs A5	A4 vs A5
Duration (ms)	ns	ns	ns
<u>Part 1:</u>			
Dur (ms)	ns	ns	ns
SBI (Hz)	ns	ns	ns
<u>Part 2:</u>			
Dur (ms)	ns	ns	ns
SBI, start (Hz)	<0.001	ns	<0.001
SBI, 1st peak (Hz)	--	--	--
SBI, end (Hz)	<0.001	<0.001	ns
Time to 1st peak (Hz)	<0.001	<0.001	<0.001
<u>Part 3:</u>			
Dur (ms)	ns	ns	ns
f, SB2, end (Hz)	<0.01	<0.001	ns
<u>Tone:</u> f, start (Hz)	ns	ns	ns
f, midpoint (Hz)	ns	ns	ns

CALL N3



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	A1	474	34.8	239	819	28
	A4	531	18.3	405	634	5
	A5	439	22.4	268	574	11
	B	731	35.3	509	1102	4
	C	628	27.4	438	903	7

Part 1:

Dur (ms)	A1	27	80.0	8	77	17
	A4	22	100.0	11	55	4
	A5	18	56.5	7	42	9
	B	16	12.5	14	18	3
	C	15	----	--	--	1

Part 2:

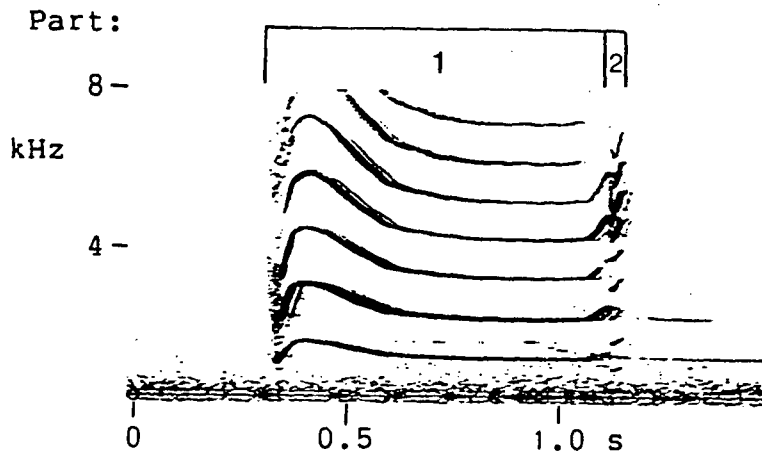
Dur (ms)	A1	51	58.8	8	111	28
	A4	49	45.2	17	78	5
	A5	69	44.3	21	121	11
	B	68	19.8	52	85	4
	C	91	30.8	45	127	7

continued...

CALL N3 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
SBI, start (Hz)	A1	301	28.2	193	518	17
	A4	343	13.9	276	383	4
	A5	363	16.5	271	473	9
	B	272	17.5	222	317	3
	C	323	----	---	---	1
SBI, peak (Hz)	A1	413	33.6	250	658	17
	A4	471	11.7	422	549	4
	A5	447	19.4	307	592	9
	B	370	24.2	274	457	4
	C	568	24.8	429	752	7
SBI, end (Hz)	A1	286	24.2	170	463	28
	A4	277	26.7	237	409	5
	A5	281	25.2	156	413	11
	B	284	17.0	236	334	4
	C	335	10.1	288	387	7
<u>Part 3:</u>						
Dur (ms)	A1	440	34.1	239	779	28
	A4	489	18.3	405	592	5
	A5	393	22.7	240	538	11
	B	690	39.2	469	1083	4
	C	599	30.0	393	887	7
SBI, end (Hz)	A1	123	23.1	71	182	28
	A4	118	21.4	77	143	5
	A5	131	16.7	97	167	11
	B	143	15.9	117	165	4
	C	180	20.3	126	223	7

CALL N4



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	A1	735	29.3	197	1028	39
	A4	772	31.3	211	1171	35
	A5	781	35.3	226	1177	42
<u>Part 1:</u>						
Dur (ms)	A1	723	30.3	197	1028	39
	A4	719	34.5	211	1125	36
	A5	719	36.5	222	1115	42
SBI, start (Hz)	A1	884	22.3	526	1355	39
	A4	877	18.0	572	1257	36
	A5	906	17.4	530	1269	42
SBI, peak (Hz)	A1	1429	5.5	1230	1576	39
	A4	1464	5.2	1246	1710	36
	A5	1380	6.7	1170	1627	42
SBI, end (Hz)	A1	1178	6.1	1062	1270	7
	A4	1205	8.8	995	1464	30
	A5	1160	10.2	672	1322	25
^f, upswEEP at end (Hz)	A1	252	84.3	13	673	7
	A4	416	38.7	150	880	30
	A5	214	42.4	39	439	25

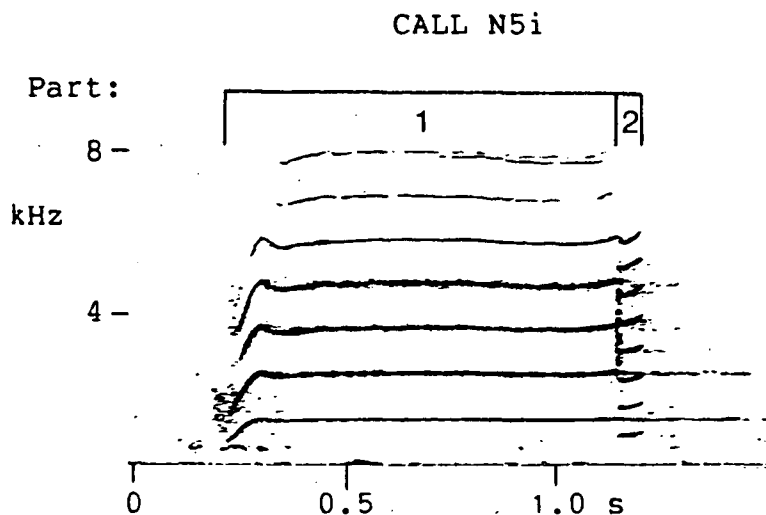
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 CALL N4 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
<u>Part 2:</u>						
Dur (ms)	A1	35	28.7	18	49	13
	A4	41	26.0	24	73	33
	A5	65	27.1	6	100	40
SBI (Hz)	A1	709	30.0	395	1056	13
	A4	712	14.4	492	949	33
	A5	703	9.5	444	791	40

 CALL N4 - Measurement Comparisons

Measurement	A1 vs A4	A1 vs A5	A4 vs A5
Duration (ms)	ns	ns	ns
<u>Part 1:</u>			
Dur (ms)	ns	ns	ns
SBI, start (Hz)	ns	ns	ns
SBI, peak (Hz)	ns	<0.05	<0.001
SBI, end (Hz)	ns	ns	ns
\hat{f} , upswing at end (Hz)	<0.05	ns	<0.001
<u>Part 2:</u>			
Dur (ms)	ns	<0.001	<0.001
SBI (Hz)	ns	ns	ns



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	A1	989	11.0	703	1224	33
	A4	956	17.9	504	1168	13
	A5	992	24.6	405	1281	24
	B	842	26.6	505	1272	28
	H	749	18.3	595	1044	20
	I1	663	16.6	545	916	13

Part 1:

Dur (ms)	A1	953	11.7	666	1224	33
	A4	901	20.2	427	1121	13
	A5	924	25.8	330	1190	24
	B	785	28.2	477	1199	28
	H	601	20.5	459	915	20
	I1	608	15.7	474	785	13
SBI, start (Hz)	A1	1035	13.7	743	1339	33
	A4	998	20.6	687	1345	13
	A5	960	17.5	570	1213	24
	B	1021	8.5	734	1179	28
	H	1121	15.6	683	1396	19
	I1	1058	10.3	891	1318	13

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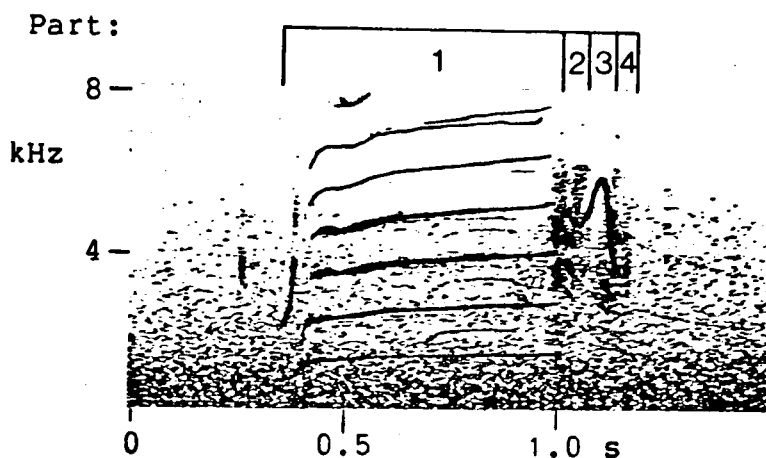
CALL N5i - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
SBI, mid (Hz)	A1	1197	12.2	1009	1578	33
	A4	1230	13.6	1055	1566	13
	A5	1171	8.7	1005	1504	24
	B	1211	6.3	1076	1375	28
	H	1281	4.2	1155	1359	19
	I1	1211	5.1	1130	1346	13
SBI, end (Hz)	A1	1276	16.2	1034	1842	33
	A4	1372	18.3	916	1751	13
	A5	1277	12.3	1071	1682	24
	B	1264	10.0	1045	1636	28
	H	1291	6.5	1173	1485	19
	I1	1261	5.3	1159	1419	13
^f, SB3, 1st peak	A1	378	67.2	58	970	26
	A4	287	43.0	223	507	5
	A5	324	37.4	151	562	11
	B	---	---	---	---	---
	H	366	28.9	150	511	15
	I1	---	---	---	---	---
<u>Part 2:</u>						
Dur (ms)	A1	29	22.4	17	45	29
	A4	35	27.3	24	62	13
	A5	48	23.0	29	69	24
	B	26	37.0	14	51	28
	H	92	32.6	27	140	20
	I1	33	71.1	16	108	13
SBI (Hz)	A1	714	18.2	467	1044	29
	A4	719	18.2	565	968	13
	A5	771	14.0	525	1061	24
	B	491	28.2	300	779	28
	H	724	12.2	487	935	19
	I1	512	31.8	284	840	13
<u>Tone:</u>						
f, start (Hz)	A1	5766	25.6	2585	7916	32
	A4	6637	9.9	5132	7844	13
	A5	6314	17.0	2678	7795	23
	B	2588	26.1	1402	4224	28
	H	2936	16.0	2095	3732	17
	I1	2165	17.0	1805	3092	12

CALL N5i - MEASUREMENT COMPARISONS

Comparison	Duration	Part 1			Part 2		Tone
		Dur	SBI start	SBI end	Dur	SBI	f, start
A1 vs A4	ns	ns	ns	ns	ns	ns	ns
A1 vs A5	ns	ns	ns	ns	<0.05	ns	ns
A1 vs B	ns	<0.05	ns	ns	ns	<0.001	<0.001
A1 vs H	<0.001	<0.001	ns	ns	<0.001	ns	<0.001
A1 vs I1	<0.001	<0.001	ns	ns	ns	<0.001	<0.001
A4 vs A5	ns	ns	ns	ns	<0.01	ns	ns
A4 vs B	ns	ns	ns	ns	ns	<0.001	<0.001
A4 vs H	ns	<0.001	ns	ns	<0.001	ns	<0.001
A4 vs I1	<0.01	<0.01	ns	ns	ns	<0.01	<0.001
A5 vs B	ns	ns	ns	ns	<0.001	<0.001	<0.001
A5 vs H	<0.01	<0.001	<0.05	ns	<0.001	ns	<0.001
A5 vs I1	<0.001	<0.001	ns	ns	ns	<0.001	<0.001
B vs H	ns	<0.05	ns	ns	<0.001	<0.001	ns
B vs I1	ns	ns	ns	ns	ns	ns	ns
H vs I1	ns	ns	ns	ns	<0.001	<0.01	ns

CALL N5ii



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	B	657	9.6	573	759	9
	H	736	11.4	640	960	15
	I1	921	10.0	751	1029	9
<u>Part 1:</u>						
Dur (ms)	B	618	8.4	539	717	9
	H	553	19.2	461	787	15
	I1	731	10.3	604	806	9
SBI, start (Hz)	B	1124	7.6	997	1246	9
	H	1026	16.9	746	1218	15
	I1	1113	8.6	957	1285	9
SBI, mid (Hz)	B	1257	2.8	1215	1331	9
	H	1279	4.4	1211	1410	15
	I1	1299	4.0	1211	1374	9
SBI, end (Hz)	B	1283	8.6	1047	1366	9
	H	1296	5.3	1175	1399	15
	I1	1331	6.0	1193	1445	9
\hat{f} , SB3, 1st part (Hz)	B	---	---	---	---	--
	H	311	36.3	91	592	15
	I1	---	---	---	---	--

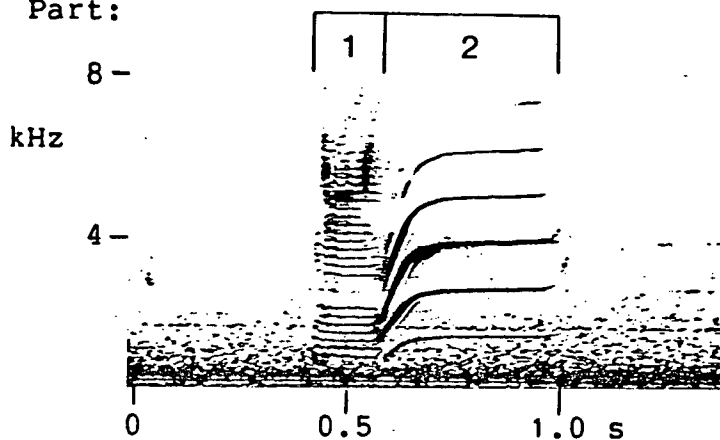
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 CALL N5ii - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
<u>Part 2:</u>						
Dur (ms)	B	22	23.8	14	30	9
	H	92	16.5	66	119	15
	I1	33	30.4	17	48	9
SBI (Hz)	B	564	37.4	260	866	9
	H	711	6.2	649	798	15
	I1	508	23.5	362	723	9
<u>Parts 3 and 4:</u>						
Dur (ms)	B	117	9.9	96	133	9
	H	90	24.1	62	156	15
	I1	132	26.3	84	193	9
<u>Part 3:</u>						
f, peak (Hz)	B	6099	6.1	5354	6612	9
	H	4172	-----	---	---	1
	I1	7012	11.5	5877	7989	6
<u>Part 4:</u>						
SBI (Hz)	B	752	13.3	631	938	9
	H	796	11.1	678	1010	15
	I1	891	17.6	569	1082	9
<u>Tone:</u>						
f, start (Hz)	B	2811	30.0	2163	4976	9
	H	3231	19.1	2452	4916	15
	I1	2517	16.3	2146	3352	8

CALL N7i

Part:

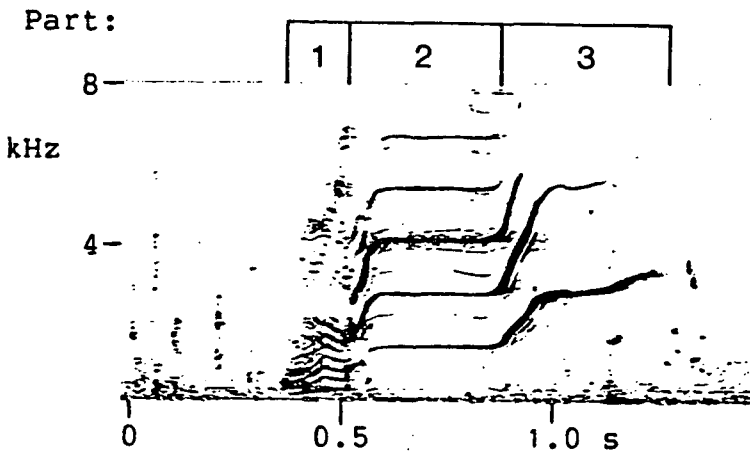


Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	A1	570	24.1	418	929	27
	A4	702	11.5	577	868	19
	A5	692	19.1	496	949	25
<u>Part 1:</u>						
Dur (ms)	A1	198	23.3	136	345	27
	A4	166	14.4	116	215	19
	A5	172	21.6	98	255	25
SBI (Hz)	A1	147	13.0	120	180	27
	A4	172	17.6	144	226	13
	A5	164	15.1	128	216	22
<u>Part 2:</u>						
Dur (ms)	A1	371	33.2	243	653	27
	A4	535	13.2	405	679	19
	A5	519	21.7	339	729	25
Time to PRL (ms)	A1	84	20.0	57	132	27
	A4	75	24.6	50	113	19
	A5	96	18.6	65	141	25
SBI (Hz)	A1	1271	9.0	1092	1477	27
	A4	1349	4.5	1223	1466	19
	A5	1379	4.6	1281	1506	25

 CALL N7i - Measurement Comparisons

Measurement	A1 vs A4	A1 vs A5	A4 vs A5
Duration (ms)	<0.01	<0.01	ns
<u>Part 1:</u>			
Dur (ms)	<0.05	<0.05	ns
SBI (Hz)	ns	ns	ns
<u>Part 2:</u>			
Dur (ms)	<0.001	<0.001	ns
Time to PRL (ms)	ns	<0.05	<0.001
SBI (Hz)	ns	<0.001	ns

CALL N7ii



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	A1	722	16.2	516	863	8
	A4	720	17.6	528	872	9
	A5	775	17.3	568	915	9
	H	886	19.1	495	1223	38
	I1	831	15.1	596	989	10

Part 1:

Dur (ms)	A1	174	20.1	125	240	8
	A4	173	25.4	86	223	9
	A5	153	17.6	122	187	9
	H	160	27.6	105	303	38
	I1	152	21.9	99	200	10

SBI (Hz)	A1	160	10.1	128	179	8
	A4	168	17.6	121	203	8
	A5	135	6.8	120	147	9
	H	225	17.7	166	309	24
	I1	210	17.5	160	247	6

Part 2:

Dur (ms)	A1	461	26.4	279	597	8
	A4	458	16.4	366	546	9
	A5	541	18.5	347	625	9
	H	462	11.5	344	603	38
	I1	442	22.0	263	613	10

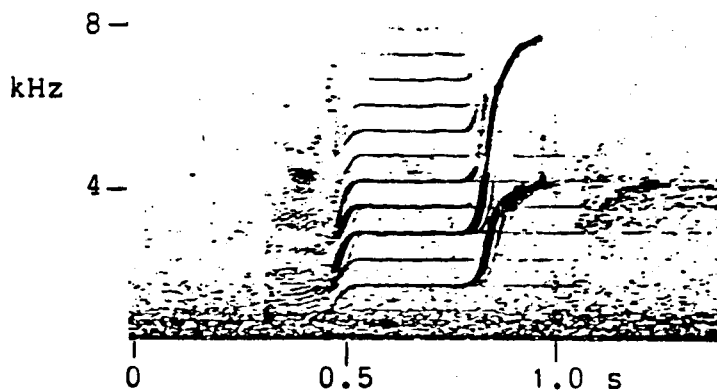
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CALL N7ii - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
Time to PRL (ms)	A1	83	15.3	67	105	8
	A4	70	20.4	47	92	9
	A5	95	33.3	61	152	9
	H	77	47.8	46	256	38
	I1	59	19.6	40	77	10
SBI (Hz)	A1	1330	7.5	1172	1434	8
	A4	1313	5.6	1188	1405	9
	A5	1399	5.7	1257	1483	9
	H	1359	3.3	1194	1458	38
	I1	1394	6.6	1264	1581	10
<u>Part 3:</u>						
Dur (ms)	A1	85	40.8	42	146	8
	A4	88	47.9	40	165	9
	A5	81	47.4	38	152	9
	H	333	17.4	171	411	30
	I1	263	11.5	221	309	9
SBI, start (Hz)	A1	1346	7.9	1166	1444	8
	A4	1309	5.4	1196	1381	9
	A5	1407	4.9	1278	1471	9
	H	1341	5.1	1158	1588	36
	I1	1412	10.5	1157	1602	10
f, SB2, end (Hz)	A1	3986	29.3	2469	5972	8
	A4	3855	14.0	3194	4568	9
	A5	3963	14.4	3227	4882	9
	H	6253	13.1	3205	6921	32
	I1	7021	6.2	6391	7503	10

CALL N7iii

Part:



Measurement	Pod	Mean	C.V.	Min	Max	n	p
Duration (ms)	B	768	11.0	626	922	24	<0.05
	I1	695	10.1	555	786	10	
<u>Part 1:</u>							
Dur (ms)	B	139	21.0	93	182	24	ns
	I1	163	27.4	97	231	10	
SBI (Hz)	B	134	17.4	83	175	19	<0.05
	I1	157	7.3	137	168	10	
<u>Part 2:</u>							
Dur (ms)	B	417	15.4	325	571	24	<0.001
	I1	330	14.4	257	374	10	
Time to PRL (ms)	B	59	19.6	45	96	24	<0.001
	I1	29	57.9	9	61	10	
SBI (Hz)	B	647	5.4	566	705	24	ns
	I1	678	7.8	630	792	10	

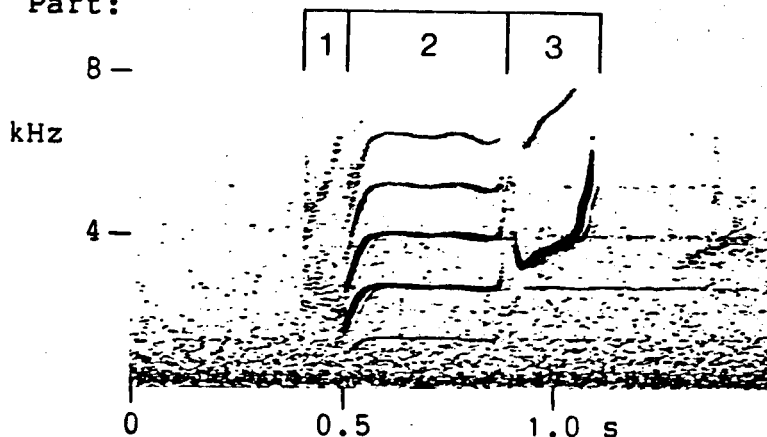
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 CALL N7iii - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n	p
<u>Part 3:</u>							
Dur (ms)	B	211	19.3	168	359	24	ns
	I1	226	20.9	156	289	10	
SBI, start (Hz)	B	1259	5.0	1149	1361	24	ns
	I1	1275	4.5	1185	1387	10	
f, SB2, end (Hz)	B	7642	2.5	7303	7953	24	<0.01
	I1	7896	3.1	7694	8401	10	

CALL N7iv

Part:



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	C	658	12.9	508	832	28
	D	605	20.0	446	851	28
	Na	654	11.3	538	800	16
<u>Part 1:</u>						
Dur (ms)	C	94	29.4	46	144	21
	D	88	42.0	45	152	23
	Na	81	26.8	45	127	16
SBI (Hz)	C	146	14.9	96	179	15
	D	143	13.2	107	168	19
	Na	111	17.5	85	145	16
<u>Part 2:</u>						
Dur (ms)	C	383	9.6	285	460	30
	D	340	15.6	254	467	28
	Na	377	12.2	307	484	16
Time to PRL (ms)	C	71	37.8	43	197	30
	D	55	32.1	33	110	28
	Na	39	18.7	27	49	16
SBI (Hz)	C	1354	2.1	1285	1401	30
	D	1362	2.6	1298	1423	28
	Na	1382	4.8	1244	1484	16

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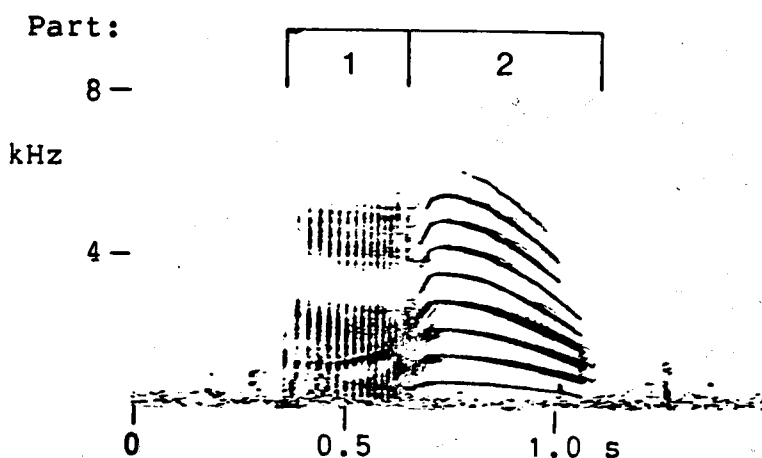
CALL N7iv - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
<u>Part 3:</u>						
Dur (ms)	C	529	9.6	405	632	28
	D	477	16.3	368	646	28
	Na	533	12.8	440	684	16
SBI, start (Hz)	C	3023	15.5	967	3711	28
	D	3388	9.9	2449	4272	24
	Na	3074	8.1	2686	3543	9
f, SB1, end (Hz)	C	6006	11.8	5069	7889	28
	D	6503	11.2	5193	7854	28
	Na	5974	9.8	4592	6807	16

CALL N7iv - Measurement Comparisons

Measurement	C vs D	C vs Na
Duration (ms)	ns	ns
<u>Part 1:</u>		
Dur (ms)	ns	ns
SBI (Hz)	ns	<0.001
<u>Part 2:</u>		
Dur (ms)	<0.001	ns
Time to PRL (ms)	<0.001	<0.001
SBI (Hz)	ns	ns
<u>Part 3:</u>		
Dur (ms)	<0.01	ns
SBI, start (Hz)	--	--
f, SB1, end (Hz)	<0.05	ns

CALL N8i



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	A1	614	17.7	369	802	15
	A4	603	9.2	491	705	22
	A5	665	9.8	583	867	29
	H	712	11.8	446	880	32
<u>Part 1:</u>						
Dur (ms)	A1	487	19.1	225	623	26
	A4	446	12.3	325	548	22
	A5	444	14.2	357	602	29
	H	312	19.7	101	402	32
IPI, start (ms)	A1	21	16.3	16	30	24
	A4	24	18.5	17	32	19
	A5	25	17.4	17	36	27
	H	29	17.9	19	47	31
<u>Part 2:</u>						
Dur (ms)	A1	171	26.7	102	280	26
	A4	157	10.9	121	194	22
	A5	221	10.1	171	265	29
	H	399	10.0	306	478	32

continued...

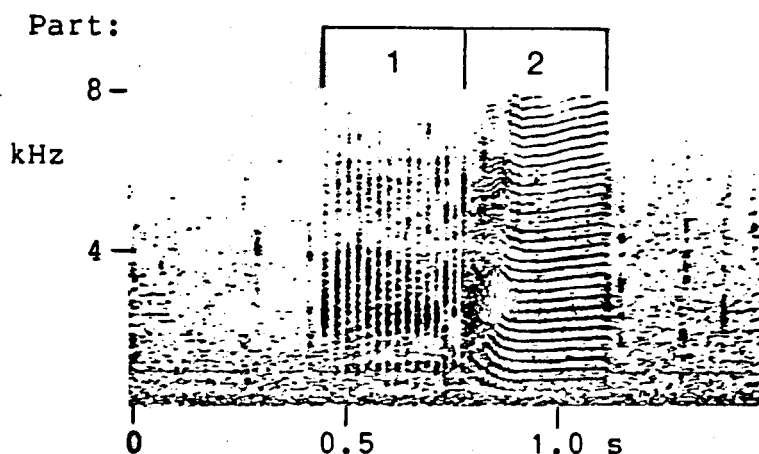
CALL N8i - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
SBI, start (Hz)	A1	255	23.4	180	381	12
	A4	355	15.0	241	469	22
	A5	312	16.5	229	404	29
	H	487	25.4	216	677	32
SBI, peak (Hz)	A1	377	11.8	323	440	11
	A4	439	9.0	364	512	22
	A5	435	7.9	365	528	29
	H	670	25.1	273	913	32
SBI, end (Hz)	A1	214	23.7	132	348	15
	A4	301	14.1	217	378	22
	A5	255	14.8	173	323	29
	H	277	27.3	114	434	32

CALL N8i - Measurement Comparisons

Measurement	A1 vs A4	A1 vs A5	A4 vs A5	A's vs H
Duration (ms)	ns	ns	<0.05	<0.01
<u>Part 1:</u>				
Dur (ms)	ns	ns	ns	<0.001
IPI, start (ms)	ns	<0.01	ns	<0.01
<u>Part 2:</u>				
Dur (ms)	ns	<0.001	<0.001	<0.001
SBI, start (Hz)	<0.001	<0.05	<0.05	<0.001
SBI, peak (Hz)	<0.001	<0.001	ns	<0.001
SBI, end (Hz)	<0.001	<0.05	<0.01	ns

CALL N8ii



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	C	557	17.7	445	801	28
	D	552	17.6	407	733	29
	Na	649	17.0	451	919	16
<u>Part 1:</u>						
Dur (ms)	C	231	15.9	147	303	28
	D	263	33.3	153	432	28
	Na	233	24.9	174	420	16
IPI, start (ms)	C	29	13.4	22	36	27
	D	30	10.4	26	37	29
	Na	31	12.1	25	38	16
<u>Part 2:</u>						
Dur (ms)	C	325	30.7	192	582	28
	D	297	22.5	228	595	29
	Na	416	22.4	277	575	16
SBI, start (Hz)	C	315	24.3	137	457	28
	D	295	17.9	146	419	28
	Na	241	17.9	156	351	16

continued...

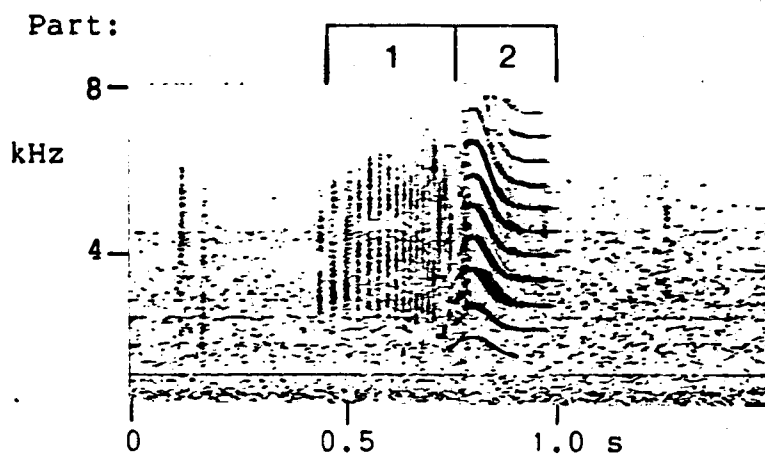
CALL N8ii - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
SBI, midpoint (Hz)	C	253	11.1	204	318	28
	D	257	8.6	192	309	29
	Na	255	10.9	214	307	16
SBI, end (Hz)	C	251	7.6	193	301	28
	D	274	8.7	205	337	29
	Na	258	6.7	230	286	16

CALL N8ii - Measurement Comparisons

Measurement	C vs D	C vs Na	D vs Na
Duration (ms)	ns	<0.01	<0.05
<u>Part 1:</u>			
Dur (ms)	--	--	--
IPI, start (ms)	ns	ns	ns
<u>Part 2:</u>			
Dur (ms)	ns	ns	<0.001
SBI, start (Hz)	ns	<0.001	<0.05
SBI, mid (Hz)	ns	ns	ns
SBI, end (Hz)	<0.001	ns	ns

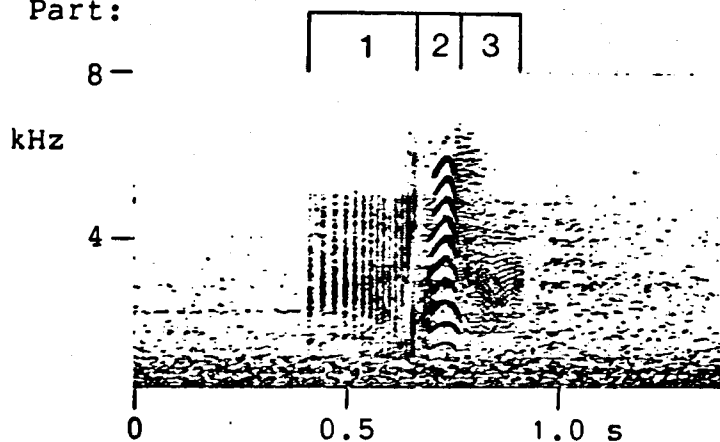
CALL N8iii



Measurement	Pod	Mean	C.V.	Min	Max	n	p
Duration (ms)	B	535	10.1	448	623	12	ns
	I1	544	8.9	509	626	6	
<u>Part 1:</u>							
Dur (ms)	B	323	19.1	240	437	12	ns
	I1	291	15.6	237	373	6	
IPI, start (ms)	B	28	11.5	24	35	11	<0.05
	I1	28	8.8	26	33	6	
<u>Part 2:</u>							
Dur (ms)	B	211	15.0	155	255	12	ns
	I1	252	10.1	226	291	6	
SBI, start (Hz)	B	752	20.8	468	962	12	ns
	I1	691	35.3	455	1009	5	
SBI, peak (Hz)	B	858	9.7	678	974	12	<0.01
	I1	979	5.4	910	1070	6	
SBI, end (Hz)	B	569	6.0	514	617	12	--
	I1	614	15.4	445	711	6	

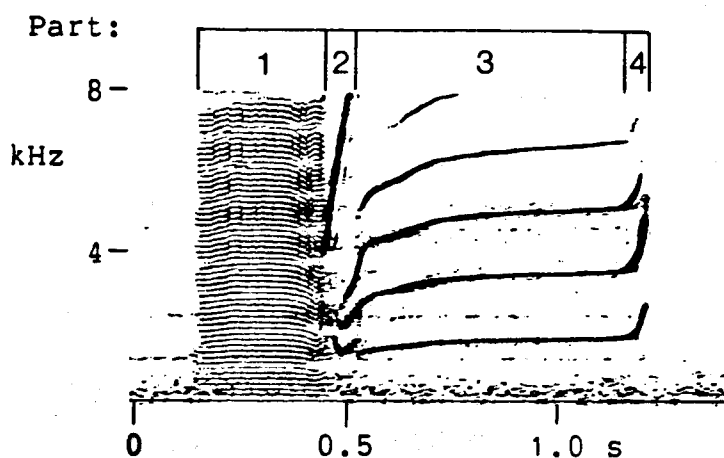
CALL N8iv

Part:



Measurement	Pod	Mean	C.V.	Min	Max	n	p
Duration (ms)	B	558	15.3	436	773	15	ns
	I1	522	7.8	478	606	10	
<u>Part 1:</u>							
Dur (ms)	B	314	22.7	242	554	15	ns
	I1	292	6.2	269	324	10	
IPI, start (ms)	B	34	16.9	27	47	15	ns
	I1	26	15.6	21	31	10	
<u>Part 2:</u>							
Dur (ms)	B	244	17.3	185	346	15	ns
	I1	229	15.1	173	282	10	
SBI, start (Hz)	B	425	20.9	249	568	15	<0.01
	I1	371	15.3	324	489	10	
SBI, peak (Hz)	B	633	12.3	505	759	14	--
	I1	656	4.0	604	698	10	
SBI, end (Hz)	B	255	43.2	180	568	15	ns
	I1	281	34.6	145	470	10	
<u>Part 3:</u>							
Dur (ms)	B	116	35.5	12	156	15	ns
	I1	112	30.1	46	148	10	

CALLS N9i (A1 pod), N9ii (A4 pod) and N9iii (A5 pod)



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	A1	1082	9.0	889	1269	27
	A4	984	14.6	675	1277	32
	A5	933	10.9	743	1135	32
<u>Part 1:</u>						
Dur (ms)	A1	333	19.4	189	490	27
	A4	288	19.9	187	428	32
	A5	334	23.3	216	511	32
SBI (Hz)	A1	144	12.4	120	181	27
	A4	197	17.0	132	260	32
	A5	148	16.3	104	192	32
<u>Part 2:</u>						
Dur (ms)	A1	71	25.4	39	104	27
	A4	85	25.3	51	131	32
	A5	71	16.7	47	101	32
SBI (Hz)	A1	656	17.7	467	931	27
	A4	652	9.5	500	785	32
	A5	617	9.7	457	728	32

continued...

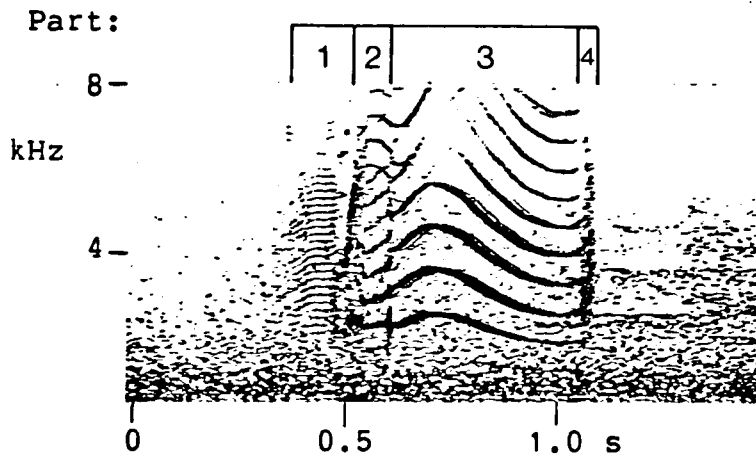
CALL N9 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
<u>Part 3:</u>						
Dur (ms)	A1	644	13.4	477	835	27
	A4	501	20.4	314	705	32
	A5	434	8.8	366	525	32
Dur, downsweep at end (ms)	A1	----	----	----	----	--
	A4	46	38.5	13	77	31
	A5	----	----	----	----	--
SBI, start (Hz)	A1	1386	9.8	1130	1611	27
	A4	1577	6.0	1287	1848	32
	A5	1410	6.7	1128	1612	32
SBI, end (Hz)	A1	1695	13.2	1410	2152	27
	A4	3058	9.7	2418	3652	32
	A5	1730	7.1	1429	2014	32
<u>Part 4:</u>						
Dur (ms)	A1	34	32.7	5	55	27
	A4	108	19.1	70	144	32
	A5	94	15.0	58	120	32
SBI (Hz)	A1	----	----	----	----	--
	A4	781	14.2	518	1043	26
	A5	866	12.5	633	1069	30
^f, SB2, upsweep (Hz)	A1	905	47.4	497	2294	24
	A4	----	----	----	----	--
	A5	----	----	----	----	--

 CALL N9 - Measurement Comparisons

Measurement	A1 vs A4	A1 vs A5	A4 vs A5
Duration (ms)	<0.01	<0.001	ns
<u>Part 1:</u>			
Dur (ms)	ns	ns	ns
SBI (Hz)	<0.001	ns	<0.001
<u>Part 2:</u>			
Dur (ms)	<0.01	ns	<0.01
SBI (Hz)	ns	ns	ns
<u>Part 3:</u>			
Dur (ms)	<0.001	<0.001	<0.01
SBI, start (Hz)	<0.001	ns	<0.001
SBI, end (Hz)	<0.001	ns	<0.001
<u>Part 4:</u>			
Dur (ms)	<0.001	<0.001	<0.01
SBI (Hz)	---	---	<0.01

CALL N10



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	A1	857	12.3	638	1022	18
	A4	829	14.5	691	1012	8
	A5	853	7.0	706	967	27
<u>Part 1:</u>						
Dur (ms)	A1	215	24.0	131	282	13
	A4	175	23.8	130	233	10
	A5	160	24.4	105	242	19
SBI (Hz)	A1	117	14.0	84	136	18
	A4	143	22.5	100	203	10
	A5	131	27.2	76	215	23
<u>Part 2:</u>						
Dur (ms)	A1	201	60.8	65	449	18
	A4	146	43.7	84	254	10
	A5	133	40.2	51	294	27
SBI (Hz)	A1	603	11.5	469	730	17
	A4	607	16.2	481	745	10
	A5	565	11.9	433	729	23

continued...

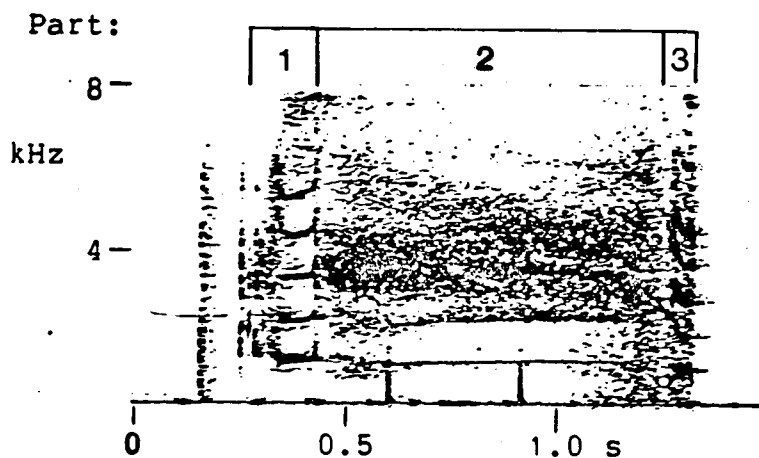
CALL N10 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
<u>Part 3:</u>						
Dur (ms)	A1	478	15.5	342	654	18
	A4	518	15.6	376	603	10
	A5	507	10.4	431	635	27
SBI, start (Hz)	A1	913	14.5	451	1050	18
	A4	1005	11.1	876	1227	10
	A5	926	16.1	541	1226	27
SBI, peak (Hz)	A1	1036	8.6	737	1139	18
	A4	1114	4.8	1013	1164	10
	A5	1135	7.8	965	1281	27
SBI, end (Hz)	A1	796	13.6	576	1053	18
	A4	826	11.1	736	974	10
	A5	891	14.9	655	1171	27
<u>Part 4:</u>						
Dur (ms)	A1	40	30.2	26	62	10
	A4	43	36.3	22	63	10
	A5	99	57.6	22	209	27
SBI (Hz)	A1	593	23.9	273	766	11
	A4	592	18.5	468	745	10
	A5	643	13.6	466	847	27
Tone: f, start (Hz)	A1	3996	17.9	2849	5503	13
	A4	3721	9.0	3228	4139	9
	A5	4051	17.2	2533	5512	19

 CALL N10 - Measurement Comparisons

Measurement	A1 vs A4	A1 vs A5	A4 vs A5
Duration (ms)	ns	ns	ns
<u>Part 1:</u>			
Dur (ms)	ns	<0.01	ns
SBI (Hz)	ns	ns	ns
<u>Part 2:</u>			
Dur (ms)	ns	<0.05	ns
SBI (Hz)	ns	ns	ns
<u>Part 3:</u>			
Dur (ms)	ns	ns	ns
SBI, start (Hz)	ns	ns	ns
SBI, peak (Hz)	ns	<0.01	ns
SBI, end (Hz)	ns	<0.05	ns
<u>Part 4:</u>			
Dur (ms)	ns	<0.01	<0.05
SBI (Hz)	ns	ns	ns
Tone: f, start (Hz)	ns	ns	ns

CALL N11i



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	A1	1389	22.7	987	1937	11
	A4	1501	26.7	948	2035	6
	A5	1428	34.4	832	2216	8

Part 1:

Dur (ms)	A1	112	21.1	81	163	11
	A4	122	26.2	84	181	6
	A5	107	16.3	89	142	8
SBI (Hz)	A1	1073	14.3	727	1315	11
	A4	925	2.3	901	963	6
	A5	1100	11.7	917	1336	8

Part 2:

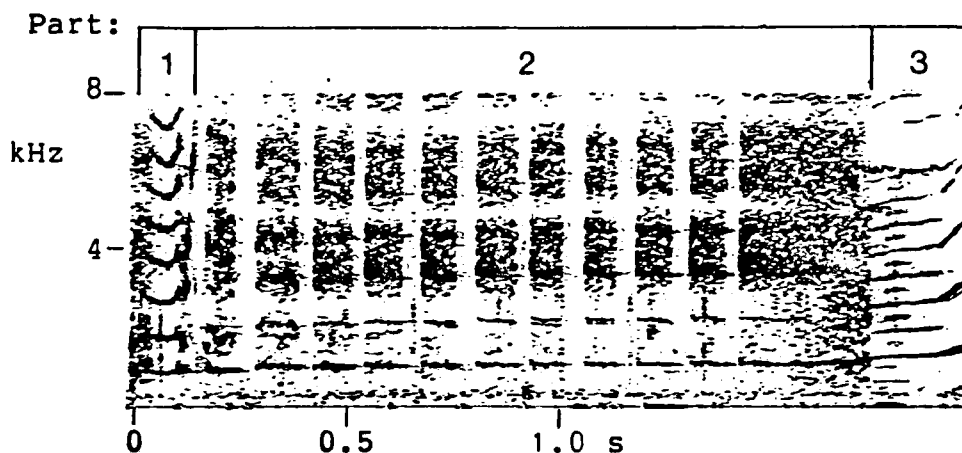
Dur (ms)	A1	1078	22.8	653	1480	11
	A4	1097	32.4	652	1549	6
	A5	1129	43.1	511	1984	8
SBI (Hz)	A1	1027	8.2	840	1195	11
	A4	1061	1.9	1036	1088	6
	A5	1046	9.4	872	1177	7

continued...

 CALL N11i - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
<u>Part 3:</u>						
Dur (ms)	A1	68	27.5	44	112	11
	A4	92	30.8	58	124	6
	A5	69	30.7	45	108	8
SBI (Hz)	A1	815	11.0	686	971	11
	A4	863	12.5	668	951	6
	A5	919	15.0	731	1095	8

CALL N11ii



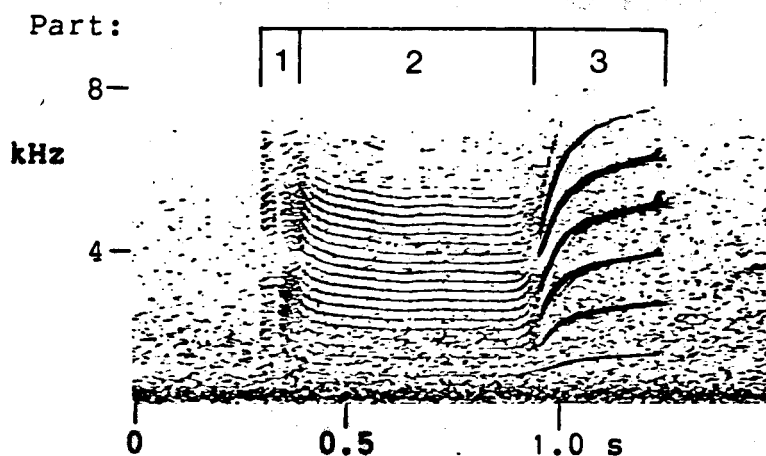
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	B	1384	----	----	----	1
	C	1582	16.5	1312	1849	4
	Na	1245	47.2	790	2091	4
<u>Part 1:</u>						
Dur (ms)	B	134	----	----	----	1
	C	189	43.6	146	313	4
	Na	125	5.8	117	134	4
SBI (Hz)	B	1129	----	----	----	1
	C	1083	13.9	865	1190	4
	Na	919	8.3	836	1019	4
<u>Part 2:</u>						
Dur (ms)	B	1187	----	----	----	1
	C	1312	16.9	1089	1600	4
	Na	996	51.8	567	1722	4
SBI (Hz)	B	1111	----	----	----	1
	C	1141	9.9	1007	1270	4
	Na	961	12.0	846	1121	4

continued...

CALL N11ii - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
Dur, pulses (ms)	B	106	9.1	92	119	5
	C	65	26.0	33	89	16
	Na	60	20.7	39	82	13
IPI (ms)	B	67	24.6	52	83	4
	C	86	14.4	65	105	20
	Na	99	37.9	42	228	17
<u>Part 3:</u>						
Dur (ms)	B	53	----	----	-----	1
	C	80	21.8	63	103	4
	Na	124	68.8	67	252	4
SBI (Hz)	B	968	----	----	-----	1
	C	929	7.2	861	1011	4
	Na	868	----	----	-----	1

CALL N12



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	A1	961	18.3	565	1369	26
	A4	847	13.9	432	1088	29
	A5	804	14.7	498	1101	27
	B	724	13.7	525	881	27
	C	757	18.0	517	1063	22
	D	744	19.0	450	1280	37
	H	683	15.5	552	1014	27
	I1	808	11.7	674	1049	16
	Na	735	8.0	615	831	15

Part 1:

Dur (ms)	A1	122	18.5	78	193	25
	A4	115	33.1	77	206	29
	A5	167	17.7	129	248	27
	B	97	19.1	49	131	27
	C	93	22.6	57	149	22
	D	85	20.3	48	123	37
	H	120	17.2	78	158	27
	I1	124	20.0	61	161	16
	Na	65	7.9	61	79	15

continued...

CALL N12 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
SBI (Hz)	A1	591	10.7	478	719	25
	A4	573	16.7	236	709	28
	A5	634	8.4	506	734	27
	B	470	14.4	350	589	27
	C	291	37.5	107	537	22
	D	287	29.4	157	467	25
	H	439	17.3	237	678	27
	I1	480	15.6	276	591	15
	Na	338	31.6	221	545	13

Part 2:

Dur (ms)	A1	790	20.2	451	1130	26
	A4	671	25.0	230	953	29
	A5	483	20.9	233	684	27
	B	545	16.0	362	683	27
	C	428	31.1	179	615	22
	D	375	43.4	69	815	37
	H	365	26.6	267	662	27
	I1	537	13.8	441	713	16
	Na	536	12.1	449	654	15

SBI (Hz)	A1	236	14.2	176	310	26
	A4	298	11.4	217	339	27
	A5	308	13.6	229	404	27
	B	230	8.4	194	276	27
	C	261	10.7	215	326	22
	D	273	9.2	204	313	37
	H	225	13.5	167	275	27
	I1	219	10.5	179	255	16
	Na	244	11.3	195	285	15

Part 3:

Dur (ms)	A1	55	52.0	33	160	25
	A4	43	35.3	22	85	27
	A5	154	21.7	115	264	27
	B	81	29.1	44	140	27
	C	235	50.1	90	491	22
	D	283	26.3	172	466	37
	H	197	14.8	149	256	27
	I1	146	21.4	106	196	16
	Na	133	40.5	94	260	15

continued...

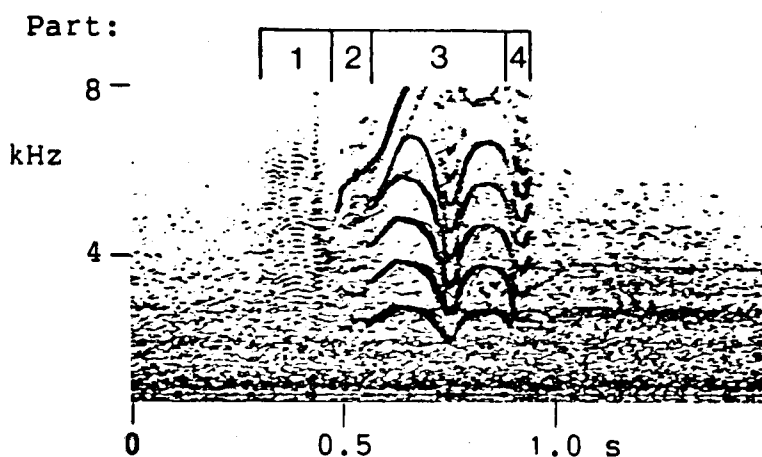
 CALL N12 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
SBI, start (Hz)	A1	207	22.9	144	340	25
	A4	271	11.4	206	325	27
	A5	284	14.6	216	392	27
	B	389	34.3	168	731	27
	C	328	39.7	164	509	22
	D	242	17.1	180	343	37
	H	208	16.7	154	286	27
	I1	184	16.9	148	259	16
	Na	874	12.1	665	1009	15
SBI, end (Hz)	A1	194	46.3	96	402	25
	A4	245	36.1	85	470	28
	A5	698	15.0	498	1011	27
	B	1320	72.7	696	3618	27
	C	1333	11.6	1008	1676	22
	D	1329	4.1	1176	1414	37
	H	1088	10.1	943	1364	27
	I1	1035	26.2	607	1364	16
	Na	1362	10.1	1113	1669	15

CALL N12 - MEASUREMENT COMPARISONS

Comparison	Duration	Part 1		Part 2		Part 3	
		Dur	SBI	Dur	SBI	SBI start	SBI end
A1 vs A4	ns	ns	ns	ns	<0.001	ns	ns
A1 vs A5	<0.01	<0.01	ns	<0.001	<0.001	ns	<0.01
A1 vs B	<0.001	ns	<0.001	<0.001	ns	<0.001	<0.001
A1 vs C	<0.001	ns	<0.001	<0.001	ns	<0.001	<0.001
A1 vs D	<0.001	<0.05	<0.001	<0.001	<0.01	ns	<0.001
A1 vs H	<0.001	ns	<0.001	<0.001	ns	ns	<0.001
A1 vs I1	ns	ns	<0.05	<0.001	ns	ns	<0.001
A4 vs A5	ns	<0.001	ns	<0.001	ns	ns	<0.05
A4 vs B	ns	ns	<0.01	ns	<0.001	<0.001	<0.001
A4 vs C	ns	ns	<0.001	<0.001	<0.05	ns	<0.001
A4 vs D	ns	ns	<0.001	<0.001	ns	ns	<0.001
A4 vs H	<0.01	ns	<0.001	<0.001	<0.001	ns	<0.001
A4 vs I1	ns	ns	ns	ns	<0.001	<0.05	<0.001
A5 vs B	ns	<0.001	<0.001	ns	<0.001	<0.001	<0.001
A5 vs C	ns	<0.001	<0.001	<0.001	<0.001	ns	<0.001
A5 vs D	ns	<0.001	<0.001	ns	<0.01	ns	<0.001
A5 vs H	ns	<0.01	<0.001	ns	<0.001	<0.05	<0.05
A5 vs I1	ns	<0.05	<0.001	ns	<0.001	<0.01	ns
B vs C	ns	ns	<0.001	ns	ns	ns	ns
B vs D	ns	ns	<0.001	<0.001	<0.001	<0.001	ns
B vs H	ns	ns	ns	<0.01	ns	<0.001	ns
B vs I1	ns	ns	ns	ns	ns	<0.001	ns
C vs D	ns	ns	ns	ns	ns	<0.01	ns
C vs H	ns	ns	<0.001	ns	<0.05	<0.001	ns
C vs I1	ns	ns	<0.001	ns	<0.05	<0.001	ns
D vs H	ns	<0.05	<0.001	ns	<0.001	ns	ns
D vs I1	ns	<0.05	<0.001	<0.05	<0.001	ns	ns
H vs I1	ns	ns	ns	<0.05	ns	ns	ns

CALL N13



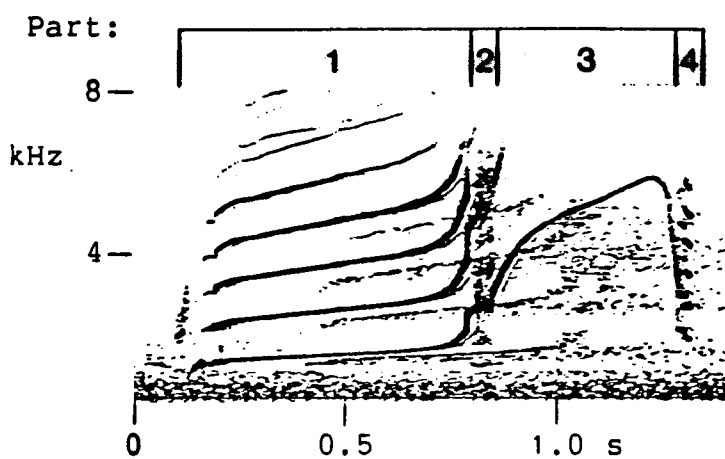
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	A4	523	17.0	426	600	3
	A5	666	7.5	562	745	20
<u>Part 1:</u>						
Dur (ms)	A4	133	1.1	132	134	2
	A5	147	34.9	55	261	17
SBI (Hz)	A4	186	31.9	144	228	2
	A5	142	16.6	96	183	16
<u>Part 2:</u>						
Dur (ms)	A4	80	52.6	41	125	3
	A5	87	32.9	48	146	20
SBI (Hz)	A4	673	9.2	629	717	2
	A5	519	22.1	312	756	18

continued...

 CALL N13 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
<u>Part 3:</u>						
Dur (ms)	A4	276	17.8	236	331	3
	A5	384	16.0	296	551	20
SBI, start (Hz)	A4	1073	35.0	665	1405	3
	A5	763	32.1	401	1289	20
SBI, 1st peak (Hz)	A4	1716	47.6	1098	2643	3
	A5	1194	9.8	1091	1637	20
SBI, dip (Hz)	A4	775	55.0	486	1265	3
	A5	742	13.2	586	927	20
SBI, 2nd peak (Hz)	A4	1001	46.9	694	1542	3
	A5	1165	6.5	1047	1304	20
SBI, end (Hz)	A4	1321	87.9	536	2655	3
	A5	926	18.7	430	1175	20
<u>Part 4:</u>						
Dur (ms)	A4	49	32.8	40	68	3
	A5	45	28.8	23	70	19
SBI (Hz)	A4	847	72.2	346	1529	3
	A5	675	16.5	456	893	19
Tone: f, start (Hz)	A4	3463	7.1	3289	3637	2
	A5	4783	14.8	3343	6234	17

CALL N16i



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	B	1301	13.3	791	1495	28

Part 1:

Dur (ms)	B	745	20.8	397	940	28
SBI, start (Hz)	B	1047	7.4	891	1166	28
SBI, end (Hz)	B	2011	13.7	1352	2386	28
Δf , SB2 (Hz)	B	2297	23.0	1385	3155	28

Part 2:

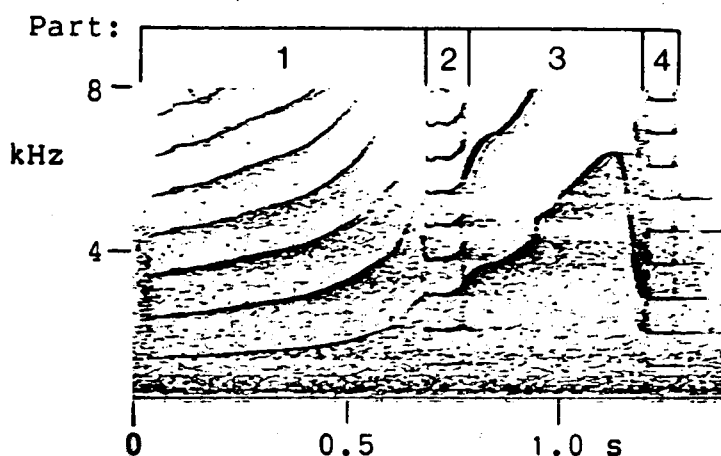
Dur (ms)	B	43	34.2	22	81	28
SBI (Hz)	B	746	21.5	505	916	10

continued...

 CALL N16i - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
<u>Part 3:</u>						
Dur (ms)	B	445	14.0	262	564	28
SBI, start (Hz)	B	2859	10.7	2174	3822	27
f, peak (Hz)	B	6176	8.9	4436	7300	27
f, end (Hz)	B	4001	11.5	3182	4788	28
<u>Part 4:</u>						
Dur (ms)	B	27	20.1	17	42	26
SBI (Hz)	B	789	11.3	601	908	26
Tone: f, start (Hz)	B	2243	12.1	1881	2966	23

CALL N16ii



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	C	1285	24.6	842	2250	50
	D	1228	27.0	564	1778	25
	Na	1114	17.3	785	1695	26
<u>Part 1:</u>						
Dur (ms)	C	708	34.1	326	1506	50
	D	661	29.3	298	977	25
	Na	557	28.3	305	983	26
SBI, start (Hz)	C	1021	10.7	789	1233	50
	D	1100	14.9	691	1470	25
	Na	1008	14.8	759	1410	26
SBI, end (Hz)	C	1977	36.5	1233	4136	50
	D	1832	27.4	1327	3049	25
	Na	1406	14.4	1186	1895	26
Δf , SB2 (Hz)	C	1770	73.9	398	5809	50
	D	1352	57.3	209	2855	25
	Na	880	52.6	277	2022	26
Dur, gap between Pts. 1 and 2 (ms)	C	79	34.3	39	136	20
	D	88	30.8	45	135	13
	Na	71	32.1	28	107	8

continued...

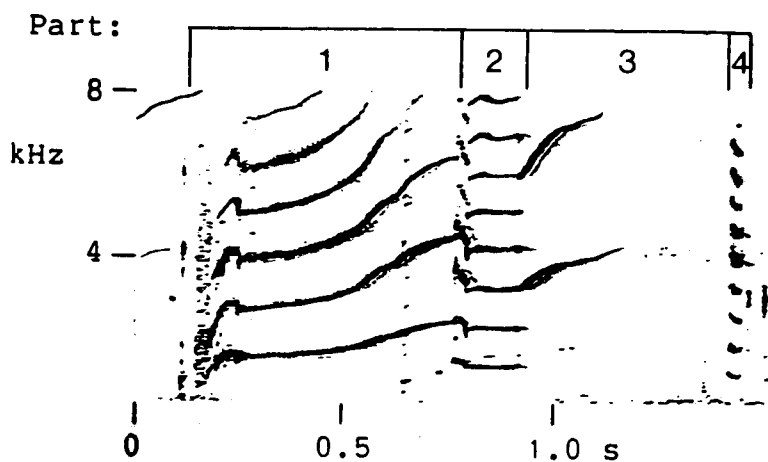
CALL N16ii - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
<u>Part 2:</u>						
Dur (ms)	C	63	22.8	39	101	50
	D	68	23.9	42	120	25
	Na	75	19.5	37	96	26
SBI (Hz)	C	809	11.3	649	966	50
	D	828	10.5	670	1029	24
	Na	743	14.0	597	949	25
<u>Part 3:</u>						
Dur (ms)	C	409	19.5	219	569	50
	D	382	26.4	152	567	25
	Na	347	16.1	258	496	26
SBI, start (Hz)	C	2757	10.0	2033	3328	50
	D	2889	11.7	2283	3535	25
	Na	2999	8.9	2422	3621	25
f, peak (Hz)	C	6735	9.7	5275	8490	50
	D	7282	9.9	5794	8821	25
	Na	6438	5.3	5590	7125	26
f, SB2, end (Hz)	C	2899	11.3	1919	3653	50
	D	3048	12.0	2427	3962	25
	Na	2799	8.5	2405	3368	26
<u>Part 4:</u>						
Dur (ms)	C	61	18.9	40	90	50
	D	65	27.6	41	113	25
	Na	96	18.8	46	136	26
SBI (Hz)	C	871	7.2	727	1038	50
	D	904	13.2	701	1191	25
	Na	767	13.1	592	993	25
Tone: f, start (Hz)	C	2723	20.1	1716	4270	36
	D	3581	17.6	2250	5066	22
	Na	3003	17.6	2035	3951	26

 CALL N16ii - Measurement Comparisons

Measurement	C vs D	C vs Na	D vs Na
Duration (ms)	ns	ns	ns
<u>Part 1:</u>			
Dur (ms)	ns	<0.05	ns
SBI, start (Hz)	ns	ns	ns
SBI, end (Hz)	ns	<0.001	<0.05
\hat{f} , SB2 (Hz)	ns	<0.01	ns
Dur, gap (ms)	ns	--	--
<u>Part 2:</u>			
Dur (ms)	ns	<0.01	ns
SBI (Hz)	ns	<0.05	<0.01
<u>Part 3:</u>			
Dur (ms)	ns	<0.01	ns
SBI, start (Hz)	ns	<0.01	ns
f, peak (Hz)	<0.01	ns	<0.001
f, SB2, end (Hz)	ns	ns	<0.05

CALL N16iii



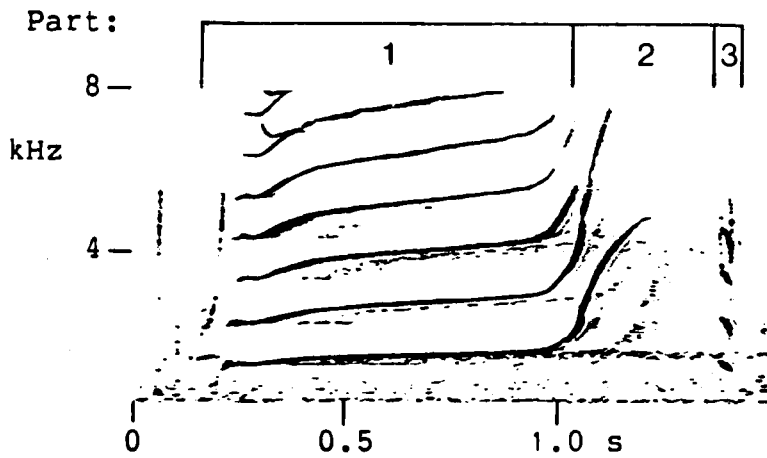
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	H	1392	10.8	963	1624	15
	I1	1302	7.5	1233	1372	2
<u>Part 1:</u>						
Dur (ms)	H	805	19.5	398	1019	15
	I1	714	3.1	699	730	2
SBI, start (Hz)	H	1108	20.7	458	1392	15
	I1	925	13.5	837	1014	2
SBI, end (Hz)	H	2068	7.2	1746	2311	15
	I1	1950	2.7	1913	1988	2
\hat{f} , SB2 (Hz)	H	2210	18.1	1569	3287	15
	I1	2199	1.7	2172	2226	2

continued...

CALL N16iii - continued...

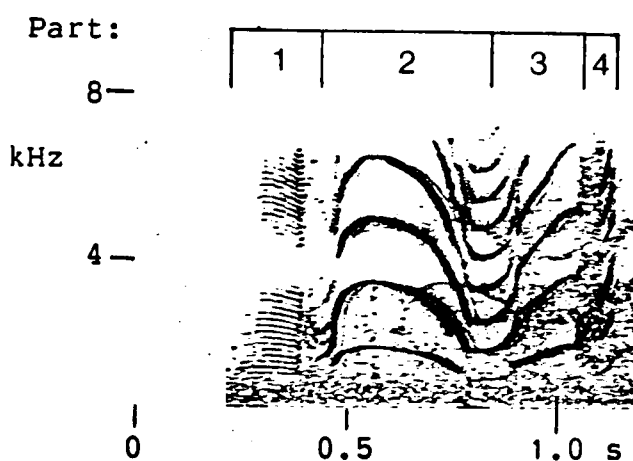
Measurement	Pod	Mean	C.V.	Min	Max	n
<u>Part 2:</u>						
Dur (ms)	H	111	11.0	93	137	15
	I1	76	39.1	55	97	2
SBI (Hz)	H	949	3.7	864	990	15
	I1	932	3.8	907	957	2
<u>Part 3:</u>						
Dur (ms)	H	430	10.0	384	521	15
	I1	459	9.7	428	491	2
SBI, start (Hz)	H	3008	6.3	2824	3419	15
	I1	2904	7.3	2754	3054	2
f, peak (Hz)	H	3943	8.6	3285	4768	15
	I1	4036	3.6	3933	4139	2
<u>Part 4:</u>						
Dur (ms)	H	22	16.8	16	30	15
	I1	24	11.8	22	26	2
SBI (Hz)	H	664	10.3	477	748	15
	I1	651	6.3	622	680	2
Tone: f, start (Hz)	H	3021	12.2	2391	3484	6
	I1	2001	----	----	----	1

CALL N16iv



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	I1	1273	10.3	1024	1534	26
<u>Part 1:</u>						
Dur (ms)	I1	749	15.0	599	1003	26
SBI, start (Hz)	I1	1009	7.0	841	1120	26
SBI, end (Hz)	I1	1600	10.2	1329	1935	26
\hat{f} , SB2 (Hz)	I1	1213	28.0	705	2122	26
<u>Part 2:</u>						
Dur (ms)	I1	493	13.8	384	631	26
SBI, start (Hz)	I1	1600	10.2	1329	1935	26
f , peak (Hz)	I1	4493	6.9	3823	4994	25
f , end (Hz)	I1	3136	13.8	2831	3441	2
<u>Part 3:</u>						
Dur (ms)	I1	30	30.2	20	54	26
SBI (Hz)	I1	795	18.7	548	1095	26
Tone: f , start (Hz)	I1	2210	14.0	1587	2990	21

CALL N17



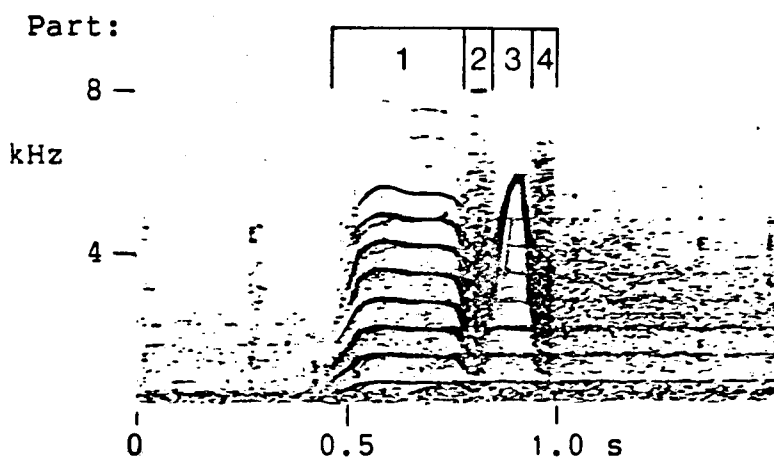
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	A5	843	8.4	700	966	19
<u>Part 1:</u>						
Dur (ms)	A5	116	64.7	15	219	18
SBI (Hz)	A5	163	14.5	108	201	11
<u>Part 2:</u>						
Dur (ms)	A5	441	15.0	297	583	19
SBI, start (Hz)	A5	619	12.5	513	750	19
SBI, peak (Hz)	A5	1516	8.0	1293	1805	19
SBI, end (Hz)	A5	841	16.3	575	1066	19
<u>Part 3:</u>						
Dur (ms)	A5	226	21.5	141	328	19
SBI, peak (Hz)	A5	2037	25.9	1354	2985	19
SBI, end (Hz)	A5	1987	19.5	1556	2678	6

continued...

CALL N17 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
<u>Part 4:</u>						
Dur (ms)	A5	60	41.7	31	81	19
SBI, end (Hz)	A5	988	18.2	668	1310	19
Tone: f, start (Hz)	A5	3869	5.9	3401	4121	10

CALL N18



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	B	678	29.2	363	1145	22
	C	765	45.2	382	1053	3
<u>Part 1:</u>						
Dur (ms)	B	400	42.2	184	826	25
	C	463	61.0	152	704	3
SBI, start (Hz)	B	495	20.2	272	713	25
	C	522	42.2	384	776	3

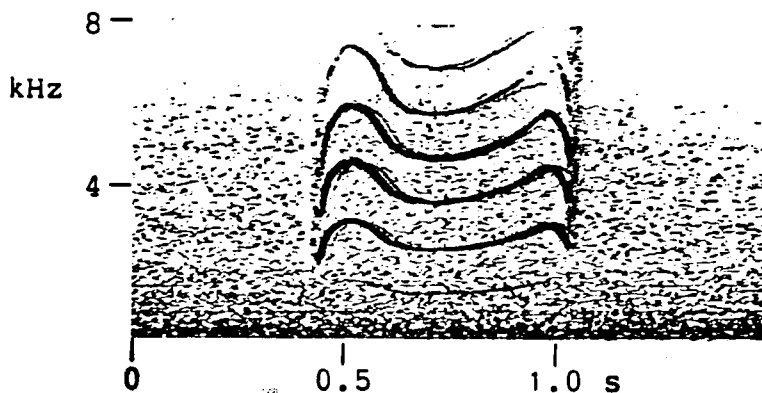
continued...

CALL N18 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
SBI, end (Hz)	B	568	19.3	372	737	25
	C	570	24.0	436	710	3
<u>Part 2:</u>						
Dur (ms)	B	38	23.8	23	54	25
	C	45	18.5	40	55	3
SBI (Hz)	B	356	16.6	290	503	18
	C	475	7.0	452	499	2
<u>Part 3:</u>						
Dur (ms)	B	177	18.5	122	249	25
	C	213	26.0	152	260	3
f, start (Hz)	B	2489	15.0	1298	2946	25
	C	2550	24.4	2142	3268	3
f, peak (Hz)	B	5597	9.1	4682	6619	25
	C	5840	10.0	5261	6427	3
f, end (Hz)	B	2801	20.2	1728	3910	25
	C	3042	9.4	2716	3250	3
<u>Part 4:</u>						
Dur (ms)	B	41	33.1	19	68	22
	C	42	14.4	37	49	3
SBI (Hz)	B	361	19.5	263	555	22
	C	642	16.5	538	750	3
Tone: f, start (Hz)	B	2288	25.7	1383	4497	20
	C	-----	-----	-----	-----	--

CALL N19

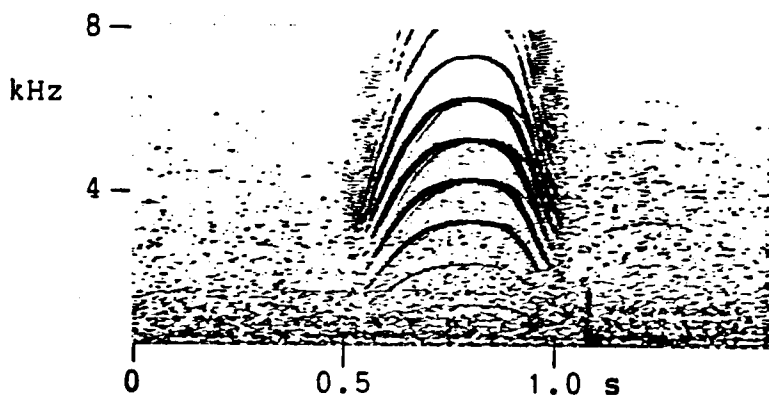
Part:



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	A4	545	14.0	409	661	23
SBI, start (Hz)	A4	1152	17.5	738	1597	23
SBI, 1st peak (Hz)	A4	1566	3.4	1411	1652	23
SBI, dip (Hz)	A4	1335	4.6	1137	1434	23
SBI, 2nd peak (Hz)	A4	1753	11.5	1540	2571	23
SBI, end (Hz)	A4	1470	13.0	1106	1814	23

CALL N20

Part:

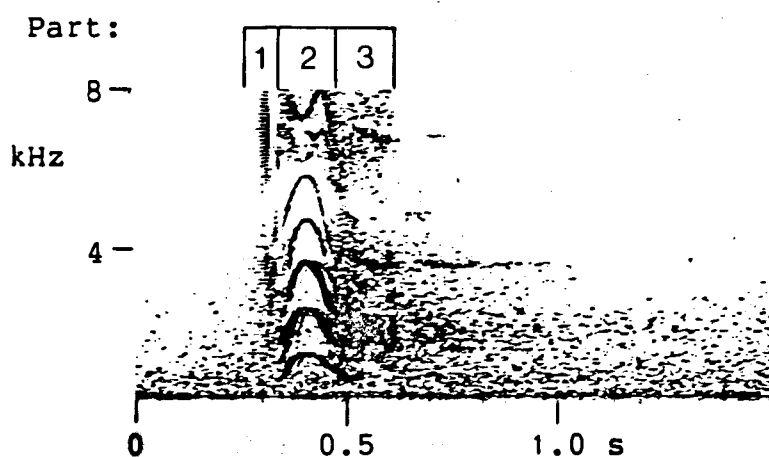


Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	B	679	19.4	371	892	30
	C	511	22.5	324	715	16
	D	535	20.6	368	757	29
	I1	649	12.4	592	706	2
Time to peak (ms)	B	451	26.2	238	709	30
	C	328	25.4	203	478	16
	D	320	27.2	206	515	29
	I1	436	9.1	408	464	2
SBI, start (Hz)	B	210	18.5	133	314	30
	C	246	27.9	164	440	16
	D	268	45.4	128	679	29
	I1	262	12.1	240	285	2
SBI, peak (Hz)	B	464	20.3	216	693	30
	C	781	35.0	404	1242	16
	D	928	25.1	409	1287	29
	I1	484	22.5	407	561	2
SBI, end (Hz)	B	217	40.4	73	367	30
	C	383	49.6	160	791	16
	D	402	36.2	172	860	29
	I1	296	18.8	257	336	2

CALL N20 - Measurement Comparisons

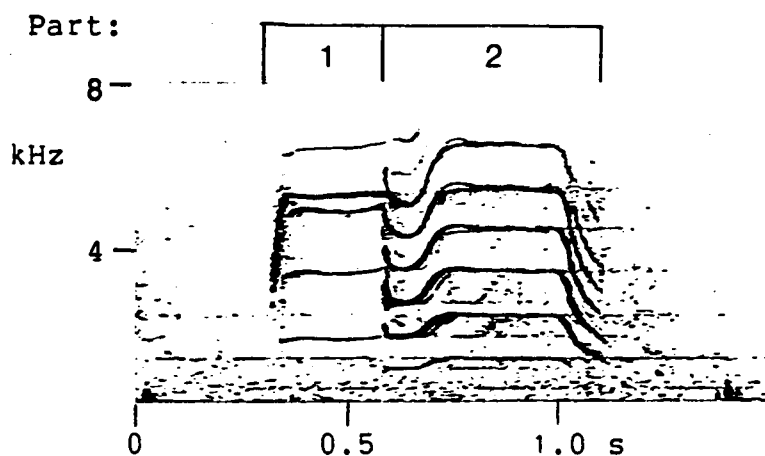
Measurement	B vs C	B vs D	C vs D
Duration (ms)	<0.001	<0.001	ns
Time to PRL (ms)	<0.01	<0.001	ns
SBI, start (Hz)	ns	ns	ns
SBI, peak (Hz)	<0.001	<0.001	ns
SBI, end (Hz)	<0.01	<0.001	ns

CALL N21



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	B	381	10.8	302	444	20
<u>Part 1:</u>						
Dur (ms)	B	125	23.2	49	181	20
<u>Part 2:</u>						
Dur (ms)	B	54	14.5	42	74	20
SBI, peak (Hz)	B	795	23.0	367	1015	20
<u>Part 3:</u>						
Dur (ms)	B	201	13.8	145	256	20
Tone: f, start (Hz)	B	3442	11.6	2330	3922	20

CALL N23i



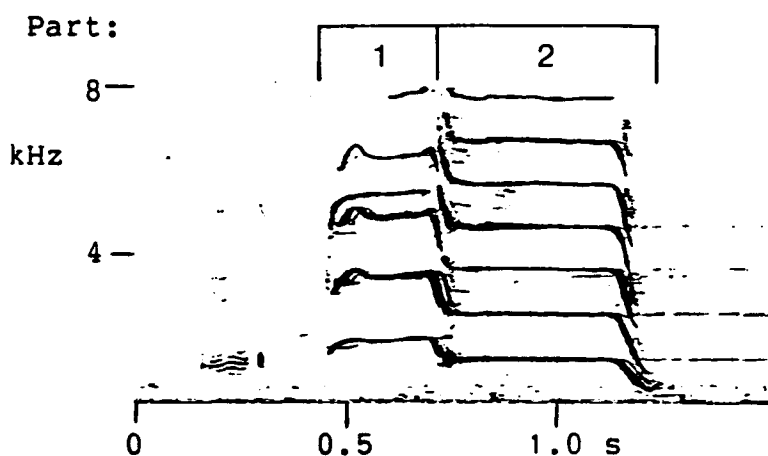
Measurement	Pod	Mean	C.V.	Min	Max	n	p
Duration (ms)	I11	908	8.2	782	1045	29	<0.001
	I31	819	7.2	743	957	26	
<u>Part 1:</u>							
Dur (ms)	I11	397	18.3	298	557	29	ns
	I31	372	17.7	266	478	26	
SBI, start (Hz)	I11	1476	9.5	1185	1665	28	ns
	I31	1476	7.7	1191	1648	25	
SBI, mid (Hz)	I11	1771	7.9	1452	1949	29	ns
	I31	1785	8.6	1510	1994	26	
<u>Part 2:</u>							
Dur (ms)	I11	510	14.3	375	640	29	<0.001
	I31	447	11.6	358	545	26	
Dur, downsweep at end (ms)	I11	128	30.7	64	196	29	<0.001
	I31	97	25.4	49	147	26	
SBI, start (Hz)	I11	847	9.2	748	1056	29	ns
	I31	844	11.4	695	1096	26	
SBI, peak (Hz)	I11	1247	9.9	1042	1482	29	ns
	I31	1258	12.8	1066	1592	26	

continued...

CALL N23i - continued...

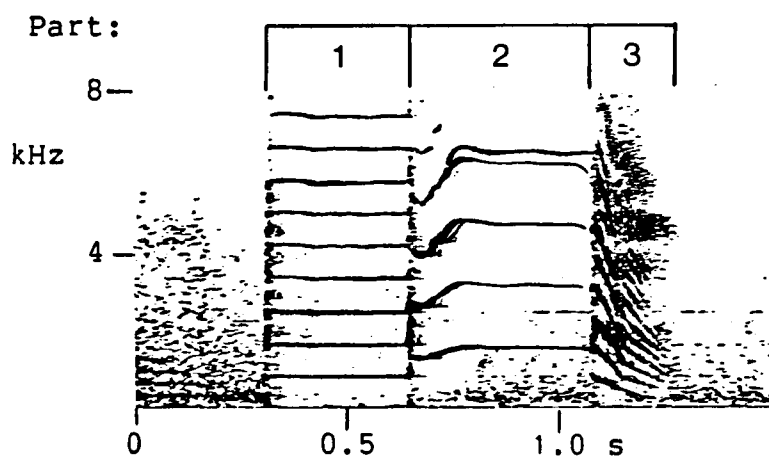
Measurement	Pod	Mean	C.V.	Min	Max	n	p
SBI, end (Hz)	I11	390	26.5	242	656	29	<0.01
	I31	477	20.5	323	788	26	
Tone: f, start (Hz)	I11	5328	4.0	4845	5682	29	ns
	I31	5334	3.8	5044	5633	26	

CALL N23ii



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (Hz)	G	802	15.9	438	1053	33
<u>Part 1:</u>						
Dur (ms)	G	349	23.0	237	528	33
SBI, start (Hz)	G	1452	6.9	1171	1609	33
SBI, mid (Hz)	G	1562	5.2	1447	1828	33
<u>Part 2:</u>						
Dur (ms)	G	452	20.6	154	639	33
Dur, downsweep at end (ms)	G	59	33.5	10	104	33
SBI, start (Hz)	G	1058	7.1	833	1208	33
SBI, peak (Hz)	G	1050	6.6	879	1190	33
SBI, end (Hz)	G	726	26.1	306	1121	33
Tone: f, start (Hz)	G	5147	2.8	4939	5526	33

CALL N24



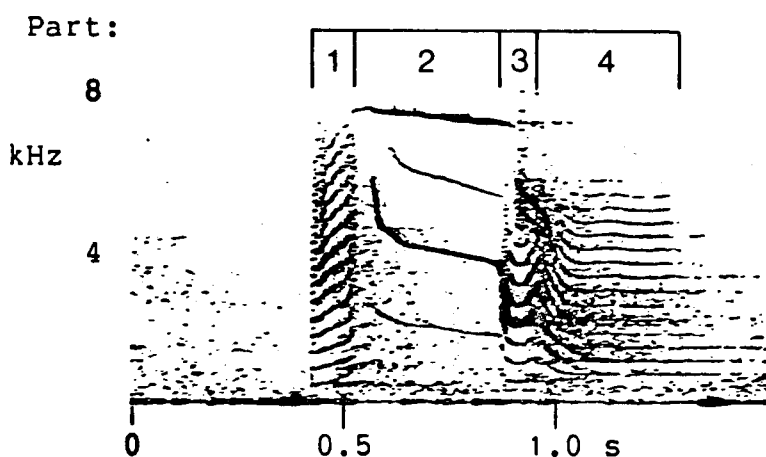
Measurement	Pod	Mean	C.V.	Min	Max	n	p
Duration (ms)	I11	950	18.1	621	1399	21	ns
	I31	938	19.7	641	1313	10	
<u>Part 1:</u>							
Dur (ms)	I11	339	37.5	115	707	21	ns
	I31	365	21.9	223	483	10	
SBI (Hz)	I11	828	7.3	709	1004	21	ns
	I31	791	5.0	711	863	10	
<u>Part 2:</u>							
Dur (ms)	I11	441	26.0	155	584	21	ns
	I31	470	17.5	365	663	10	
SBI, start (Hz)	I11	1238	18.1	947	1762	20	<0.01
	I31	1514	14.1	1243	1916	10	
SBI, peak (Hz)	I11	1579	9.4	1356	1906	21	<0.05
	I31	1465	8.2	1354	1762	10	

continued...

 CALL N24 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n	p
<u>Part 3:</u>							
Dur (ms)	I11	156	37.6	75	300	21	<0.05
	I31	98	36.3	50	309	10	
SBI, start (Hz)	I11	792	30.6	454	1176	21	ns
	I31	506	43.6	202	1047	10	
SBI, end (Hz)	I11	378	46.9	191	786	21	<0.01
	I31	228	44.9	132	495	10	
Tone: f, start (Hz)	I11	6691	7.5	6223	7990	20	<0.01
	I31	6187	2.0	5977	6362	9	

CALL N25



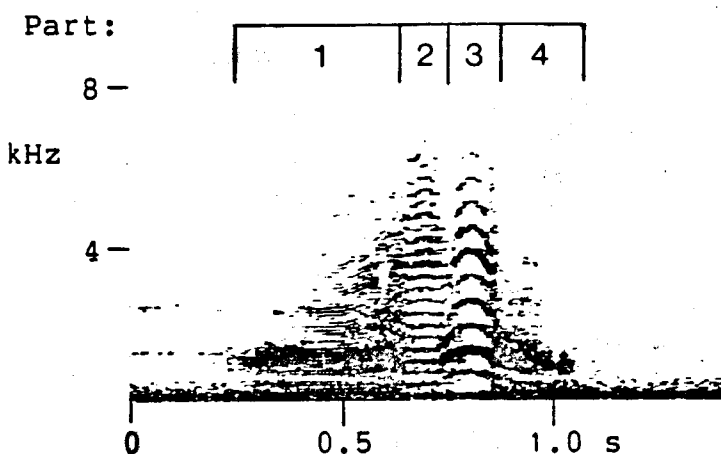
Measurement	Pod	Mean	C.V.	Min	Max	n	p
Duration (ms)	G	932	11.8	782	1230	28	<0.001
	I11	1123	17.8	682	1667	32	
<u>Part 1:</u>							
Dur (ms)	G	122	12.5	98	160	28	<0.001
	I11	95	18.4	61	147	32	
SBI (Hz)	G	725	11.3	561	866	28	<0.001
	I11	555	22.7	239	833	32	
<u>Part 2:</u>							
Dur (ms)	G	518	19.6	381	749	28	<0.001
	I11	324	41.6	94	513	32	
SBI, start (Hz)	G	2017	10.5	1719	2519	28	<0.001
	I11	2340	13.5	1708	3001	32	
SBI, end (Hz)	G	1774	8.6	1485	2172	28	ns
	I11	1815	14.6	1278	2332	32	

continued...

CALL N25 - continued...

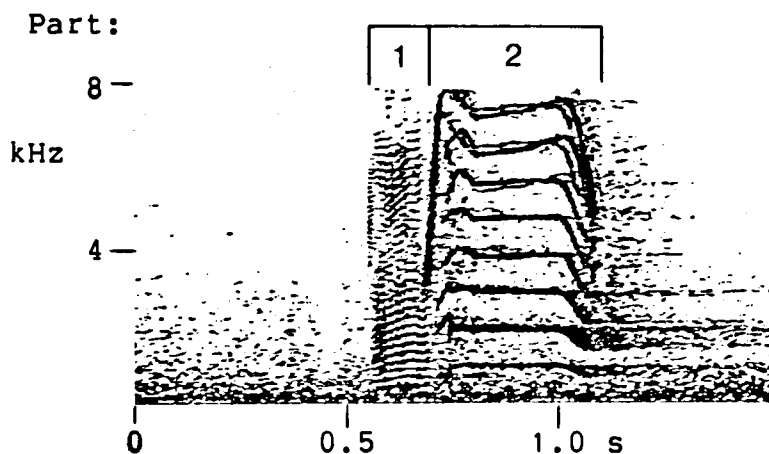
Measurement	Pod	Mean	C.V.	Min	Max	n	p
<u>Part 3:</u>							
Dur (ms)	G	111	19.6	78	158	28	<0.001
	I11	66	41.1	15	124	32	
SBI (Hz)	G	682	21.1	431	1012	28	ns
	I11	721	46.1	373	1321	32	
<u>Part 4:</u>							
Dur (ms)	G	185	26.5	115	335	26	<0.001
	I11	637	48.4	222	1205	32	
SBI, start (Hz)	G	701	23.6	470	1083	28	ns
	I11	795	42.5	384	1295	32	
SBI, peak (Hz)	G	1120	20.7	639	1486	28	ns
	I11	1066	44.3	486	1755	32	
SBI, end (Hz)	G	377	32.6	251	875	26	ns
	I11	352	15.8	252	466	32	
Tone: f, start (Hz)	G	7600	3.1	7342	7918	6	ns
	I11	7416	4.7	6890	7994	20	

CALL N26



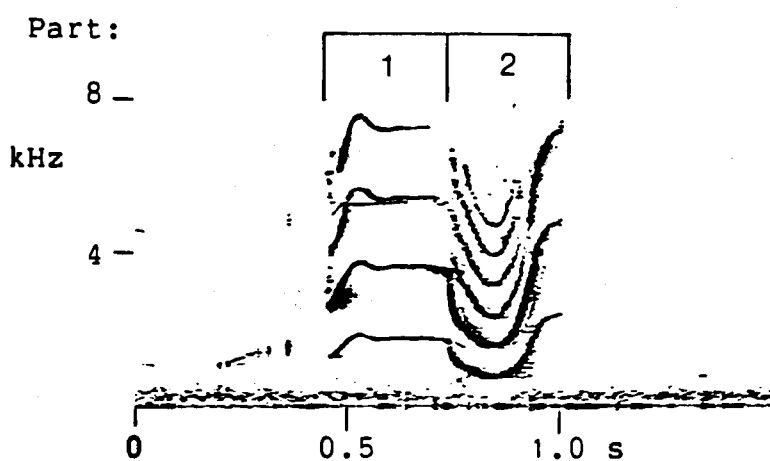
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	I11	788	10.9	627	884	10
<u>Part 1:</u>						
Dur (ms)	I11	194	23.5	93	264	10
SBI (Hz)	I11	107	9.4	96	120	10
<u>Part 2:</u>						
Dur (ms)	I11	148	16.1	103	176	10
SBI (Hz)	I11	447	18.9	348	595	10
<u>Part 3:</u>						
Dur (ms)	I11	97	24.9	66	129	10
SBI (Hz)	I11	1767	11.0	1450	2019	9
<u>Part 4:</u>						
Dur (ms)	I11	349	18.6	202	420	10
IPI, start (ms)	I11	25	17.4	19	33	10
IPI, end (ms)	I11	83	10.9	66	97	10

CALL N27



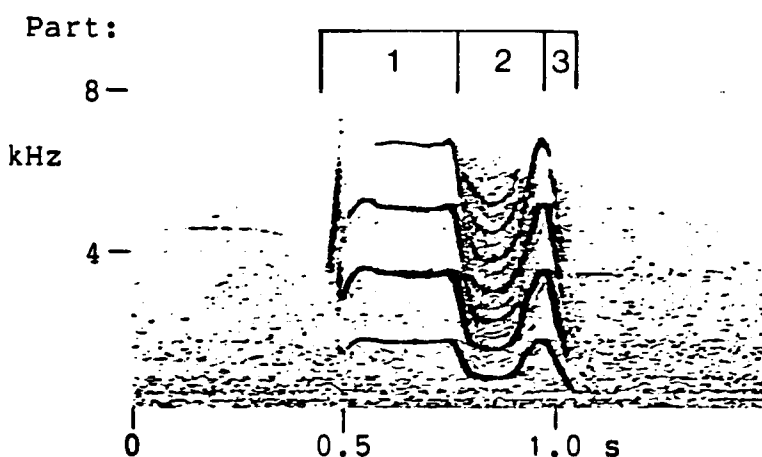
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	A1	498	17.8	365	663	13
<u>Part 1:</u>						
Dur (ms)	A1	191	13.4	140	242	13
SBI (Hz)	A1	183	24.1	96	238	12
<u>Part 2:</u>						
Dur (ms)	A1	306	29.8	161	421	13
SBI, start (Hz)	A1	865	8.8	681	950	13
SBI, mid (Hz)	A1	928	7.6	832	1055	13
SBI, end (Hz)	A1	611	16.8	413	750	13
Tone: f, start (Hz)	A1	3217	16.0	2511	4366	12

CALL N28



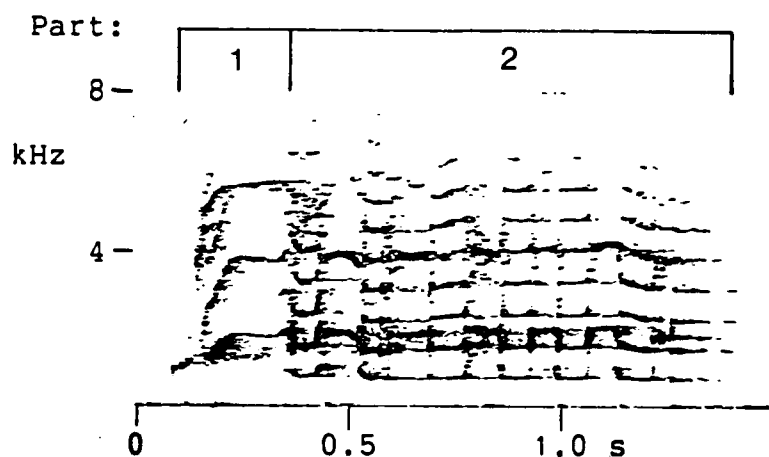
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	G	587	15.6	442	737	22
<u>Part 1:</u>						
Dur (ms)	G	315	25.3	184	460	22
SBI, start (Hz)	G	1380	12.3	1149	1795	22
SBI, mid (Hz)	G	1659	7.9	1341	1875	22
<u>Part 2:</u>						
Dur (ms)	G	405	14.3	324	516	22
SBI, start (Hz)	G	1704	6.4	1477	1894	22
SBI, dip (Hz)	G	746	6.2	662	843	22
SBI, end (Hz)	G	2001	14.9	1490	2621	22
Tone: f, start (Hz)	G	5237	4.5	4894	5742	22

CALL N29



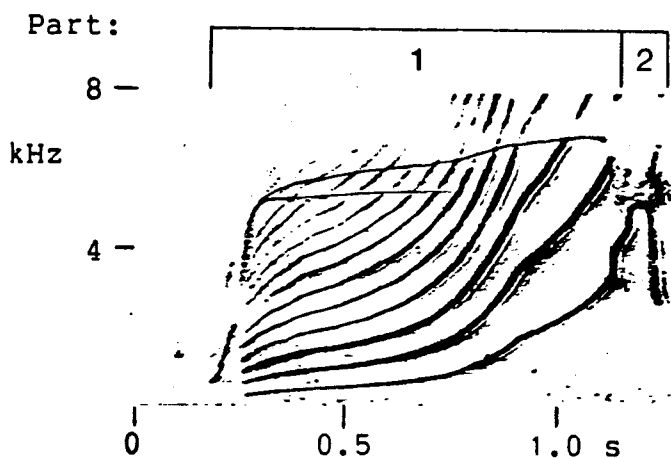
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	G	637	13.2	485	773	31
<u>Part 1:</u>						
Dur (ms)	G	362	24.0	211	533	31
SBI, start (Hz)	G	1423	15.1	849	1811	31
SBI, mid (Hz)	G	1711	8.6	1449	1972	31
<u>Part 2:</u>						
Dur (ms)	G	201	11.2	139	235	31
SBI, start (Hz)	G	1681	15.4	809	2032	31
SBI, dip (Hz)	G	728	11.3	552	895	28
SBI, end (Hz)	G	1696	25.4	723	2821	30
<u>Part 3:</u>						
Dur (ms)	G	76	22.8	53	133	30
SBI, end (Hz)	G	691	32.3	334	1379	31
Tone: f, start (Hz)	G	5316	3.8	4915	5741	25

CALL N30



Measurement	Pod	Mean	C.V.	Min	Max	n	
Duration (ms)	I11	1074	18.8	841	1566	12	ns
	I31	1130	20.5	699	1574	10	
<u>Part 1:</u>							
Dur (ms)	I11	289	33.3	184	532	12	<0.05
	I31	425	43.3	103	648	10	
<u>Part 2:</u>							
Dur (ms)	I11	785	19.7	505	1034	12	ns
	I31	705	14.4	585	931	10	
Dur, lo parts (ms)	I11	78	19.4	38	106	36	<0.05
	I31	66	24.2	32	107	30	
Dur, hi parts (ms)	I11	81	21.5	43	115	36	ns
	I31	92	14.0	29	73	29	
f, lo parts (Hz)	I11	728	13.7	513	945	36	<0.001
	I31	1566	11.0	1198	1983	30	
f, hi parts (Hz)	I11	2015	11.5	1417	2554	36	<0.05
	I31	2718	29.1	1901	4578	29	

CALL N32i



Measurement	Pod	Mean	C.V.	Min	Max	n	p
Duration (ms)	R	1206	13.6	853	1449	15	<0.05*
	W	1045	17.8	620	1330	19	
	64	936	12.4	801	1146	8	
	73	1018	6.2	933	1082	5	
<u>Part 1:</u>							
Dur (ms)	R	1094	15.4	695	1321	15	<0.01
	W	921	18.3	553	1187	19	
	64	897	10.2	781	1066	8	
	73	970	3.8	933	1030	5	
SBI, start (Hz)	R	391	16.5	266	502	15	ns
	W	352	13.1	263	428	19	
	64	400	16.6	310	483	8	
	73	289	16.4	235	339	5	
SBI, mid (Hz)	R	1132	31.4	583	1756	15	ns
	W	1190	25.0	753	1917	19	
	64	920	15.3	707	1108	8	
	73	1110	40.5	654	1669	5	
SBI, end (Hz)	R	2925	8.2	2482	3414	15	ns
	W	2960	11.0	2339	3640	19	
	64	2661	14.9	1912	2987	8	
	73	2761	13.7	2350	3192	5	

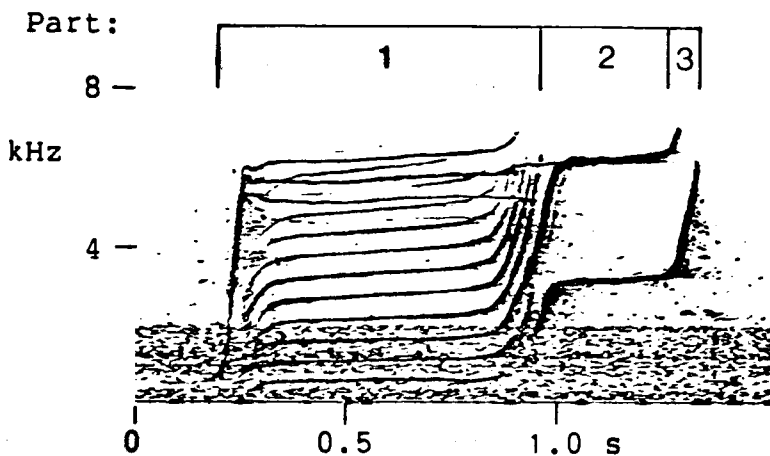
continued...

CALL N32i - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n	p
<u>Part 2:</u>							
Dur (ms)	R	111	35.1	42	158	15	ns
	W	123	36.7	51	229	19	
	64	96	28.3	80	128	3	
	73	120	5.9	115	125	2	
f, SB1, peak (Hz)	R	5811	11.5	4635	6699	15	<0.01
	W	5169	9.0	4439	6035	19	
	64	4521	7.5	4064	4785	4	
	73	5383	10.2	4995	5771	2	
f, SB1, end (Hz)	R	3072	13.8	2456	3808	10	ns
	W	2913	10.4	2441	3571	18	
	64	2930	1.3	2904	2957	2	
	73	2259	----	----	----	1	
<u>Tone:</u>							
f, start (Hz)	R	1769	36.8	607	3010	12	ns
	W	2285	31.4	879	3341	18	
	64	3005	32.4	1700	4644	8	
	73	1072	48.3	686	1959	5	
f, end (Hz)	R	6939	9.3	5682	7549	10	ns
	W	6397	11.6	5427	7979	19	
	64	6347	3.4	6097	6778	8	
	73	5066	6.6	4715	5500	4	

* ANOVA comparisons between R and W pods only.

CALL N32ii



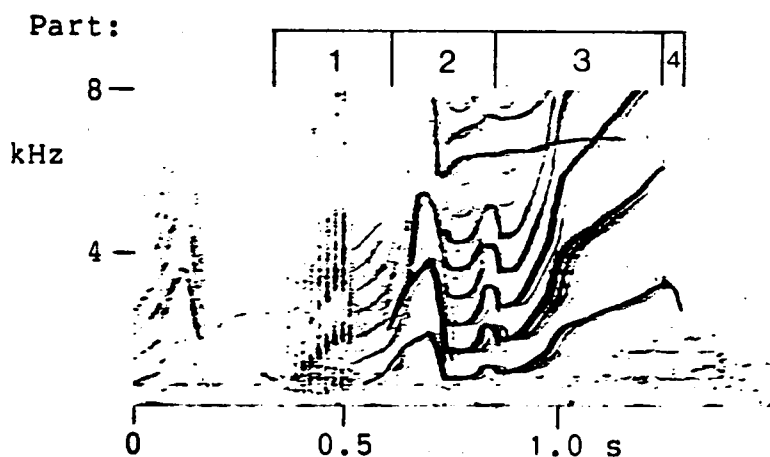
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	R	1353	20.4	958	1856	18
	73	1103	11.7	989	1243	3
<u>Part 1:</u>						
Dur (ms)	R	902	25.4	539	1266	18
	73	512	23.9	387	632	3
SBI, start (Hz)	R	470	14.0	389	620	18
	73	388	6.6	368	417	3
SBI, mid (Hz)	R	557	13.0	352	679	18
	73	891	8.8	801	938	3
<u>Part 2:</u>						
Dur (ms)	R	376	15.6	303	500	18
	73	496	6.6	464	530	3
SBI, end (Hz)	R	3201	4.1	2870	3396	18
	73	3314	5.8	2850	3661	3

continued...

 CALL N32ii - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
<u>Part 3:</u>						
Dur (ms)	R	78	32.0	36	139	17
	73	95	23.2	73	116	3
f, SB1, end (Hz)	R	5862	8.7	4897	6661	18
	73	5583	2.5	5479	5739	3
<u>Tone:</u>						
f, start (Hz)	R	1936	41.5	818	3394	11
	73	857	1.6	848	867	2
f, level (Hz)	R	5993	7.6	5382	6914	17
	73	5718	3.6	5571	5865	2
f, end (Hz)	R	6382	4.0	5872	6768	15
	W	6219	----	----	----	--

CALL N33



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	R	949	10.5	750	1154	22
	W	889	10.1	717	1039	14
	64	923	13.0	742	1108	20
	73	1063	13.5	755	1273	11

Part 1:

Dur (ms)	R	178	27.4	90	282	22
	W	190	39.2	85	370	14
	64	179	22.8	128	286	20
	73	226	27.1	103	317	11

IPI (ms)	R	21	17.4	15	28	20
	W	21	12.8	16	25	14
	64	20	15.8	15	27	20
	73	20	15.0	16	28	11

Part 2:

Dur (ms)	R	204	8.9	159	243	22
	W	230	11.2	179	272	14
	64	252	16.1	171	337	20
	73	297	13.1	231	372	11

continued...

CALL N33 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
Dur, 1st hi part (ms)	R	114	16.6	60	151	22
	W	132	16.0	88	166	14
	64	158	19.6	112	217	20
	73	195	17.4	132	255	11
Dur, 1o part (ms)	R	54	21.1	23	77	22
	W	195	13.7	138	236	14
	64	48	18.0	27	64	20
	73	52	15.7	39	64	11
Dur, 2nd hi part (ms)	R	35	26.8	21	54	22
	W	35	24.2	17	46	14
	64	44	30.3	21	73	20
	73	49	15.7	37	60	11
SBI, 1st peak (Hz)	R	1793	8.8	1521	2059	22
	W	1773	7.2	1538	1962	14
	64	1696	8.8	1481	1912	20
	73	1709	9.6	1439	2007	11
SBI, dip (Hz)	R	712	14.3	578	1024	22
	W	668	9.1	589	778	14
	64	680	9.4	542	791	20
	73	621	7.0	570	715	11
SBI, 2nd peak (Hz)	R	1142	11.4	853	1373	22
	W	1045	11.7	817	1308	14
	64	962	11.9	789	1220	20
	73	978	11.0	759	1131	11
<u>Part 3:</u>						
Dur (ms)	R	486	16.2	343	647	22
	W	432	11.3	316	517	14
	64	472	20.1	341	694	20
	73	405	16.4	263	502	11
SBI, start (Hz)	R	925	15.3	621	1162	22
	W	833	14.5	703	1068	14
	64	778	10.2	625	937	20
	73	750	10.5	646	869	11

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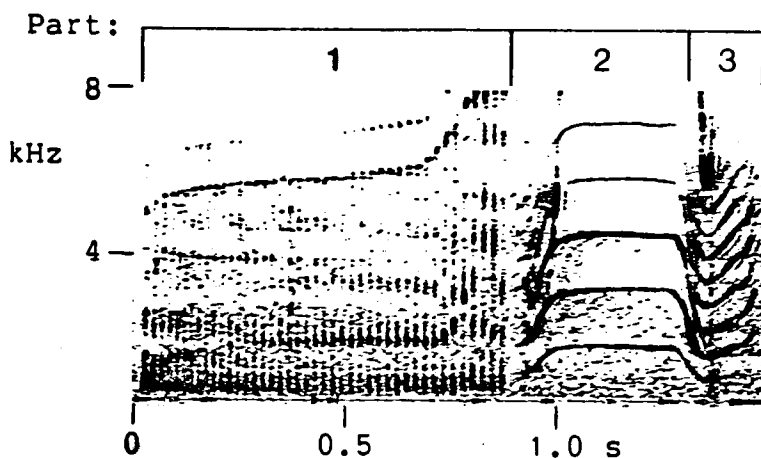
CALL N33 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
SBI, end (Hz)	R	2997	11.3	2266	3774	22
	W	2892	12.0	2305	3504	14
	64	2550	13.2	1922	3065	20
	73	2683	16.4	2062	3501	11
<u>Part 4:</u>						
Dur (ms)	R	148	20.1	119	210	7
	W	109	25.2	81	147	4
	64	173	----	---	---	1
	73	164	19.0	133	235	9
f, SB1, peak (Hz)	R	5379	18.2	3993	7066	20
	W	4663	8.4	4000	5279	7
	64	4352	14.9	3943	5422	5
	73	4455	17.9	3211	5619	11
f, SB1, end (Hz)	R	2718	16.1	2320	3335	7
	W	2985	9.0	2723	3326	4
	64	4056	----	----	----	1
	73	2590	3.8	2492	2763	9
Tone: f, start (Hz)	R	5288	27.3	2088	7281	15
	W	4527	32.9	1957	5940	10
	64	4041	25.8	2389	6324	18
	73	2896	27.5	2028	3987	7

 CALL N33 - Measurement Comparisons

Measurement	R vs W	R vs 64	W vs 64
Duration (ms)	ns	ns	ns
<u>Part 1:</u>			
Dur (ms)	ns	ns	ns
IPI (ms)	ns	ns	ns
<u>Part 2:</u>			
Dur (ms)	ns	<0.001	ns
Dur, 1st hi (ms)	ns	<0.001	ns
Dur, lo (ms)	<0.001	ns	<0.001
SBI, 1st peak (Hz)	ns	ns	ns
SBI, dip (Hz)	ns	ns	ns
SBI, 2nd peak (Hz)	ns	<0.001	ns
<u>Part 3:</u>			
Dur (ms)	ns	ns	ns
SBI, start (Hz)	ns	<0.001	ns
SBI, end (Hz)	ns	<0.01	ns
<u>Part 4:</u>			
Dur (ms)	ns	----	----
f, SB1, peak (Hz)	ns	ns	ns
f, SB1, end	ns	----	----
Tone: f, start (Hz)	ns	ns	ns

CALL N34



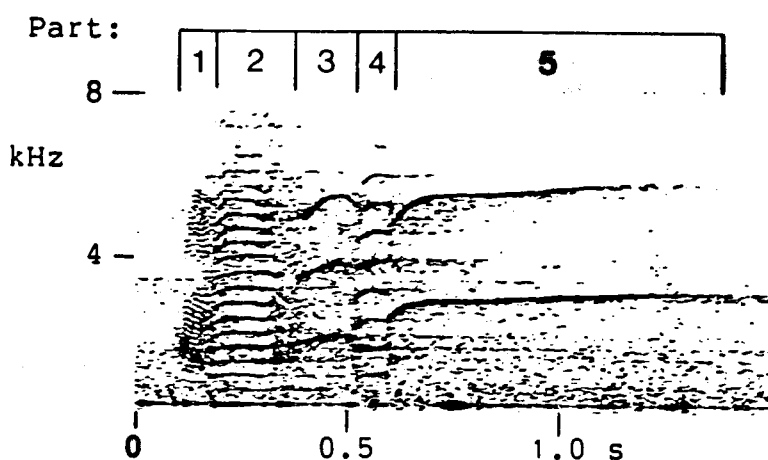
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	R	1320	17.9	987	1768	11
	W	1335	12.8	1022	1498	8
	64	1324	13.3	1086	1689	14
	73	1085	6.6	1034	1136	2
<u>Part 1:</u>						
Dur (ms)	R	778	29.8	434	1215	11
	W	799	23.8	433	961	8
	64	673	24.4	420	1012	14
	73	457	7.1	434	480	2
IPI (ms)	R	20	12.0	16	25	11
	W	21	9.8	19	26	8
	64	19	8.7	17	23	13
	73	21	6.7	20	22	2
<u>Part 2:</u>						
Dur (ms)	R	421	8.0	335	462	11
	W	423	6.0	396	480	8
	64	451	21.7	236	642	14
	73	488	7.0	464	512	2

continued...

CALL N34 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
SBI, start (Hz)	R	1226	16.3	960	1636	11
	W	989	22.0	799	1392	8
	64	1285	13.5	993	1643	14
	73	946	4.0	920	973	2
SBI, peak (Hz)	R	1492	5.6	1390	1698	11
	W	1434	3.6	1381	1519	8
	64	1416	17.1	628	1717	14
	73	1380	1.5	1366	1395	2
<u>Part 3:</u>						
Dur (ms)	R	120	18.5	85	161	11
	W	112	13.6	96	143	8
	64	199	48.9	127	515	14
	73	140	4.0	136	144	2
SBI, start (Hz)	R	671	3.9	626	722	11
	W	669	7.1	628	771	8
	64	673	10.6	586	891	14
	73	642	5.1	619	665	2
SBI, end (Hz)	R	955	13.2	827	1268	11
	W	905	17.0	712	1185	8
	64	923	12.7	692	1093	14
	73	922	4.1	895	949	2

Call N35



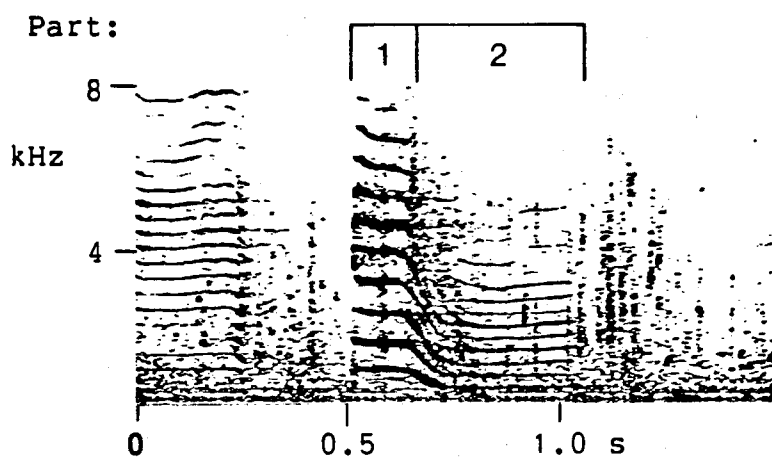
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	R	1056	16.5	648	1275	10
	W	612	5.1	571	668	6
<u>Part 1:</u>						
Dur (ms)	R	86	18.1	58	109	10
	W	68	5.0	63	72	5
SBI (Hz)	R	129	21.5	96	179	10
	W	122	17.8	91	144	6
<u>Part 2:</u>						
Dur (ms)	R	143	13.8	124	182	10
	W	90	22.7	61	118	5
SBI (Hz)	R	303	11.6	249	357	10
	W	299	11.9	255	350	5
<u>Part 3:</u>						
Dur (ms)	R	202	16.5	123	238	10
	W	167	15.5	122	185	5
SBI (Hz)	R	1790	10.5	1483	2108	10
	W	1982	9.2	1797	2232	6

continued...

 CALL N35 - continued...

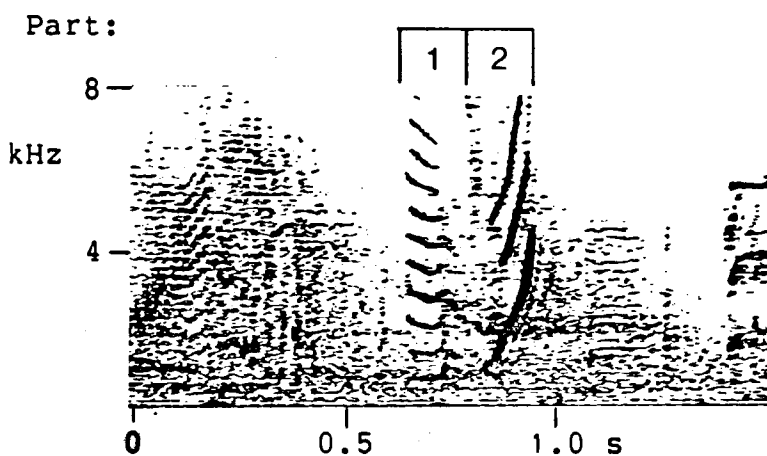
Measurement	Pod	Mean	C.V.	Min	Max	n
<u>Part 4:</u>						
Dur (ms)	R	115	26.3	85	182	9
	W	117	32.6	84	183	5
SBI (Hz)	R	698	10.1	623	795	8
	W	842	10.4	741	945	5
<u>Part 5:</u>						
Dur (ms)	R	518	34.3	189	746	9
	W	157	37.7	65	228	5
SBI, start (Hz)	R	2207	16.8	1659	2771	10
	W	2376	7.4	2103	2525	5
SBI, end (Hz)	R	2534	11.6	2026	2836	10
	W	3024	8.6	2588	3273	5

CALL N38



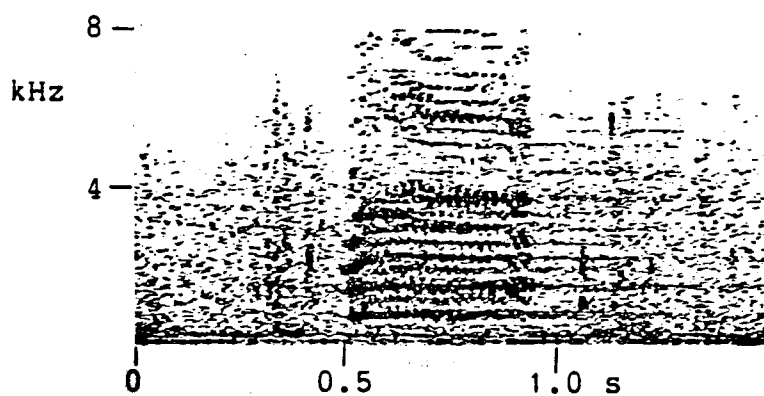
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	G	576	15.8	412	707	9
<u>Part 1:</u>						
Dur (ms)	G	244	23.5	181	330	9
SBI (Hz)	G	827	8.7	739	978	9
<u>Part 2:</u>						
Dur (ms)	G	331	17.2	231	412	9
SBI (Hz)	G	314	18.5	229	395	7

CALL N39



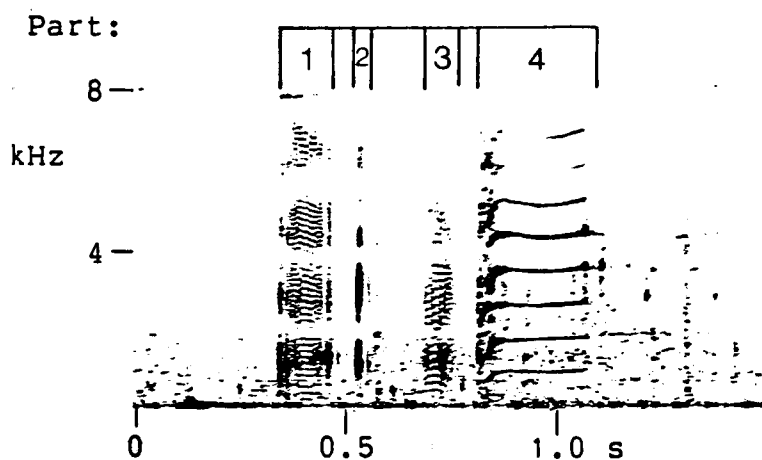
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	I 11	305	15.0	223	381	12
<u>Part 1:</u>						
Dur (ms)	I 11	97	21.4	70	150	12
SBI (Hz)	I 11	845	9.5	716	977	11
<u>Part 2:</u>						
Dur (ms)	I 11	208	18.8	122	267	12
SBI, start (Hz)	I 11	1693	22.9	896	2318	12
SBI, end (Hz)	I 11	2953	25.3	1857	4523	12

Part: CALL N40



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	G	401	30.5	229	695	12
SBI, start (Hz)	G	563	21.8	390	803	12
SBI, peak (Hz)	G	715	12.2	611	870	12
SBI, end (Hz)	G	535	26.1	293	766	12
IPI (ms)	G	23	13.6	18	28	12

CALL N41



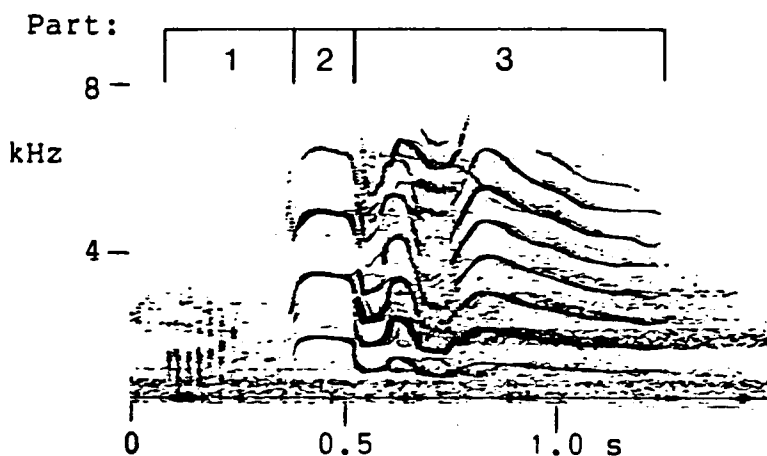
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	G	789	6.6	713	876	15
	I11	705	23.5	532	957	6
<u>Part 1:</u>						
Dur (ms)	G	134	10.3	109	163	15
	I11	137	17.9	117	179	6
SBI (Hz)	G	120	25.5	72	183	15
	I11	120	17.7	96	144	6
Dur, gap between Pts. 1 & 2 (ms)	G	84	28.7	49	128	15
	I11	116	50.3	59	224	6
Dur, gap between Pts. 2 & 3 (ms)	G	126	28.0	64	189	15
	I11	139	38.3	92	235	6
<u>Part 3:</u>						
Dur (ms)	G	65	15.1	48	84	15
	I11	60	22.6	43	82	6
SBI (Hz)	G	139	25.3	85	191	15
	I11	131	42.4	62	204	6
Dur, gap between Pts. 3 & 4 (ms)	G	72	19.1	45	97	15
	I11	79	26.2	51	109	6

continued...

CALL N41 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
<u>Part 4:</u>						
Dur (ms)	G	308	15.3	232	409	15
	I11	172	47.9	63	272	6
SBI, start (Hz)	G	509	18.7	393	757	15
	I11	654	14.0	507	781	6
SBI, end (Hz)	G	854	6.8	752	944	15
	I11	858	22.8	546	1115	6

CALL N42



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	R	1272	7.3	1089	1460	20
	64	1265	4.0	1233	1323	3
<u>Part 1:</u>						
Dur (ms)	R	419	22.9	281	614	20
	64	407	18.5	322	464	3

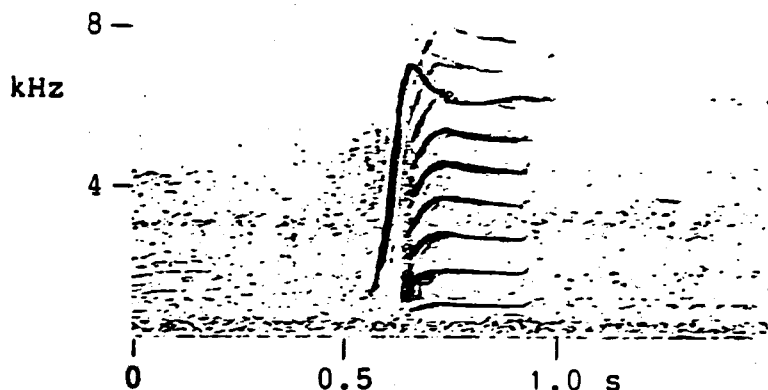
continued...

CALL N42 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
IPI (ms)	R	24	19.4	16	30	14
	64	21	18.9	17	25	3
<u>Part 2:</u>						
Dur (ms)	R	228	26.6	151	354	20
	64	245	24.3	177	287	3
SBI (Hz)	R	1513	6.2	1351	1693	20
	64	1427	1.4	1405	1443	3
<u>Part 3:</u>						
Dur (ms)	R	625	17.9	444	749	20
	64	613	17.4	533	734	3
SBI, start (Hz)	R	677	10.5	563	788	20
	64	734	5.7	689	772	3
SBI, peak (Hz)	R	986	9.6	735	1130	20
	64	1076	9.3	994	1187	3
SBI, dip (Hz)	R	572	14.9	451	766	20
	64	596	5.8	557	620	3
SBI, end (Hz)	R	782	15.7	609	1110	20
	64	780	15.7	669	911	3

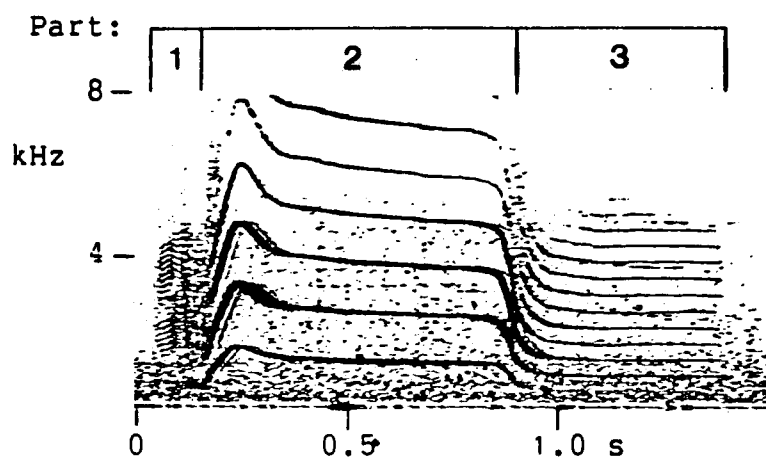
CALL N43

Part:

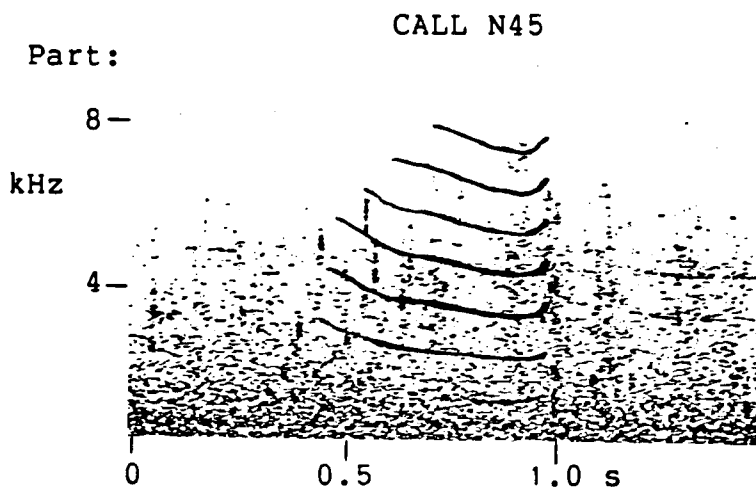


Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	R	345	12.7	281	435	20
	W	293	8.9	269	331	5
	64	445	18.3	388	503	2
	73	399	----	---	---	1
SBI, start (Hz)	R	776	10.6	657	984	20
	W	726	7.0	681	809	5
	64	911	3.0	892	931	2
	73	691	----	---	---	1
SBI, end (Hz)	R	745	7.8	536	817	20
	W	770	7.9	709	859	5
	64	781	4.1	759	804	2
	73	710	----	---	---	1
Tone: f, start (Hz)	R	1607	30.0	931	2986	20
	W	1416	23.7	1022	1830	5
	64	1902	11.3	1750	2054	2
	73	1376	----	----	----	1
f, peak (Hz)	R	6307	2.6	5969	6564	20
	W	6470	1.7	6346	6636	5
	64	6466	2.6	6348	6585	2
	73	5596	---	----	----	1
f, end (Hz)	R	5607	2.0	5380	5744	20
	W	5700	2.8	5470	5850	5
	64	5620	2.2	5531	5709	2
	73	4989	---	----	----	1

CALL N44

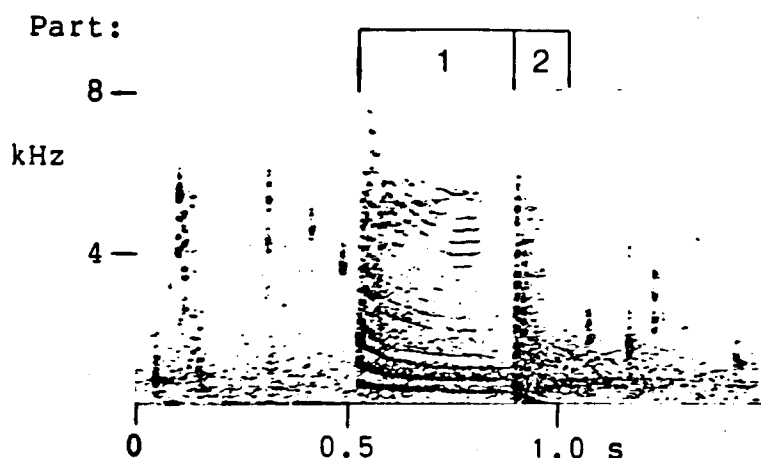


Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	G	1396	14.0	1054	1736	23
<u>Part 1:</u>						
Dur (ms)	G	118	29.6	68	219	23
SBI (Hz)	G	126	19.0	58	171	23
<u>Part 2:</u>						
Dur (ms)	G	859	17.6	592	1218	23
SBI, start (Hz)	G	675	24.2	434	1015	23
SBI, peak (Hz)	G	1914	10.1	1501	2140	23
SBI, end (Hz)	G	1157	10.8	901	1479	23
<u>Part 3:</u>						
Dur (ms)	G	418	16.8	235	571	23
SBI, start (Hz)	G	479	16.8	314	607	23
SBI, end (Hz)	G	497	14.9	314	579	23



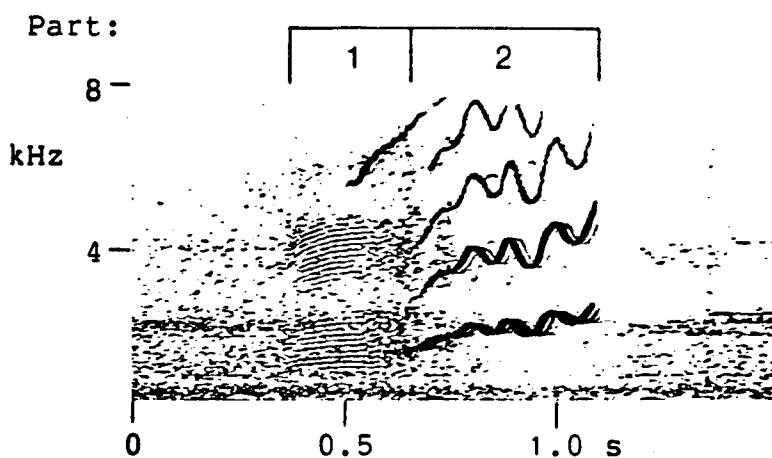
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	G	208	47.9	87	414	12
	I11	238	----	--	---	1
SBI, start (Hz)	G	1172	6.9	1025	1315	12
	I11	1086	---	-----	-----	1
SBI, end (Hz)	G	1201	6.8	1076	1305	12
	I11	1211	---	-----	-----	1

CALL N46



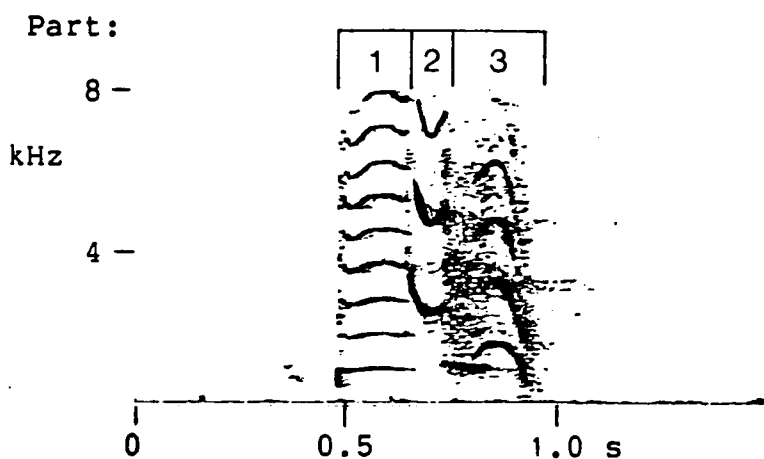
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	G	356	8.6	320	383	4
	I11	427	7.9	349	488	15
<u>Part 1:</u>						
Dur (ms)	G	241	2.8	238	252	4
	I11	355	6.3	305	389	15
SBI, start (Hz)	G	578	22.4	388	664	4
	I11	563	17.6	433	762	15
SBI, end (Hz)	G	228	11.2	192	251	4
	I11	280	11.6	240	328	15
Dur, gap between Pts. 1 & 2 (ms)	G	84	31.0	56	113	4
	I11	47	47.2	16	86	15
<u>Part 2:</u>						
Dur (ms)	G	30	13.6	25	35	4
	I11	24	23.3	18	39	15
f, peak emphasis (Hz)	G	799	14.3	681	953	4
	I11	1059	13.1	818	1233	15

CALL N47



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	A1	838	17.7	612	1243	26
<u>Part 1:</u>						
Dur (ms)	A1	385	34.1	217	742	26
SBI (Hz)	A1	141	12.8	105	176	26
<u>Part 2:</u>						
Dur (ms)	A1	453	24.2	225	693	26
SBI, start (Hz)	A1	1139	18.4	700	1477	26
SBI, end (Hz)	A1	2390	16.9	1800	3338	26
Tone: f, start (Hz)	A1	4762	15.8	2959	6324	24

CALL N48



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	G	505	4.5	481	526	3
	I11	640	19.5	488	787	9
<u>Part 1:</u>						
Dur (ms)	G	175	5.0	166	183	3
	I11	180	16.3	129	219	9
SBI, start (Hz)	G	797	16.0	652	891	3
	I11	711	27.8	446	1002	9
SBI, end (Hz)	G	2764	9.6	2492	3020	3
	I11	3011	10.7	2425	3360	9
<u>Part 2:</u>						
Dur (ms)	G	109	11.9	96	122	3
	I11	118	23.0	82	180	9
SBI (Hz)	G	1846	52.3	731	2421	3
	I11	1704	39.9	692	2357	9

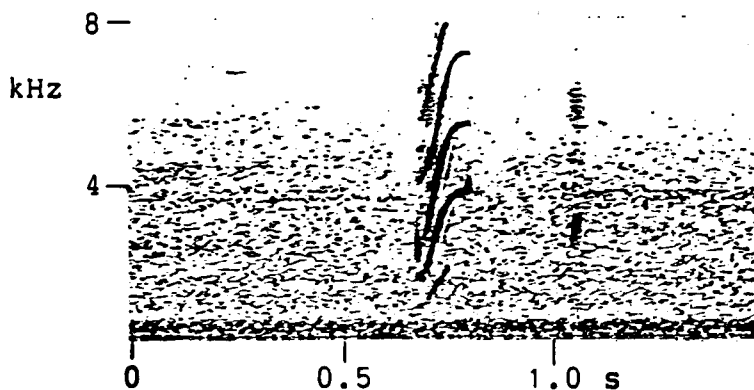
continued...

 CALL N48 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
<u>Part 3:</u>						
Dur (ms)	G	220	12.3	205	252	3
	I11	340	30.0	239	500	9
SBI, peak (Hz)	G	1279	19.7	1018	1520	3
	I11	1454	18.0	1018	1773	9
SBI, end (Hz)	G	970	14.8	822	1109	3
	I11	674	30.5	387	1014	9

CALL N50

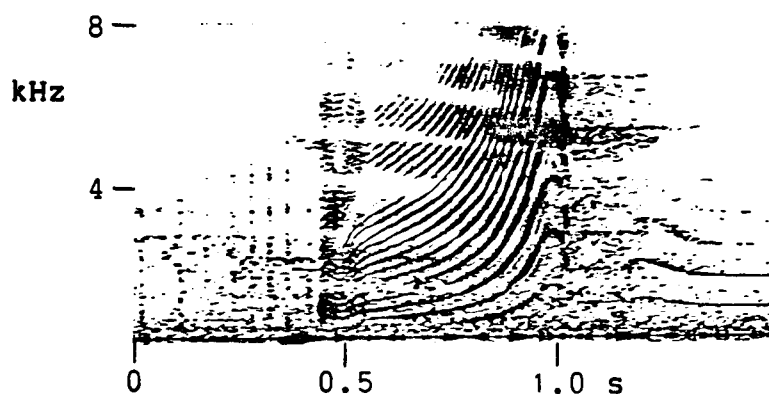
Part:



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	R	146	15.1	124	200	10
	W	167	11.4	154	181	2
	64	180	----	----	----	1
	73	207	----	----	----	1
SBI, start (Hz)	R	849	33.6	483	1199	10
	W	498	41.7	351	645	2
	64	816	----	----	----	1
	73	603	----	----	----	1
SBI, peak (Hz)	R	1478	6.2	1275	1579	10
	W	1402	7.4	1329	1475	2
	64	1522	---	----	----	1
	73	1517	---	----	----	1
SBI, end (Hz)	R	1489	5.2	1381	1633	10
	W	1414	3.8	1376	1453	2
	64	1448	---	----	----	1
	73	1545	---	----	----	1

CALL N51

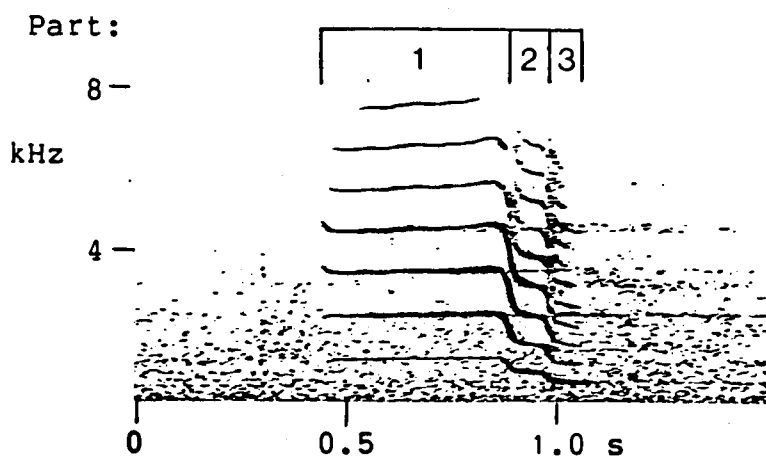
Part:



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	R	828	27.8	385	1212	11
	W	576	1.8	565	585	3
	73	624	17.0	511	721	3
SBI, start (Hz)	R	182	32.8	85	273	11
	W	145	17.9	121	173	3
	73	224	23.5	170	275	3
SBI, end (Hz)	R	1281	15.6	1063	1751	11
	W	1355	4.0	1308	1414	3
	73	1193	10.7	1068	1323	3

SOUTHERN COMMUNITY CALLS:

CALL S1



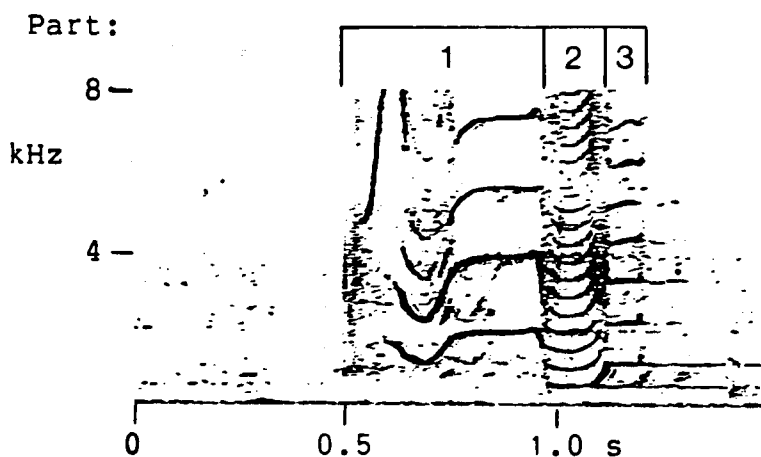
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	J	884	38.5	527	1986	52
	MD	736	6.9	649	815	9
	Sh	803	21.6	500	955	6
Part 1:						
Dur (ms)	J	629	44.5	341	1464	48
	MD	596	7.3	526	678	9
	Sh	509	24.4	306	667	6
SBI, start (Hz)	J	1020	6.1	885	1178	52
	MD	1184	4.2	1099	1245	9
	Sh	1162	9.1	1023	1329	6

continued...

 CALL S1 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
SBI, end (Hz)	J	1065	11.6	880	1515	52
	MD	1195	4.6	1122	1275	9
	Sh	1140	7.0	1033	1224	6
<u>Part 2:</u>						
Dur (ms)	J	99	34.5	42	234	48
	MD	77	21.9	45	100	9
	Sh	151	52.2	95	308	6
SBI, start (Hz)	J	693	19.4	546	1370	48
	MD	1027	5.5	954	1113	9
	Sh	771	11.0	669	911	6
SBI, end (Hz)	J	573	13.4	403	733	48
	MD	1026	8.8	816	1118	9
	Sh	523	10.1	461	589	6
<u>Part 3:</u>						
Dur (ms)	J	118	32.7	63	295	48
	MD	64	16.0	46	77	9
	Sh	142	45.0	41	219	6
SBI, end (Hz)	J	413	13.0	270	550	52
	MD	735	10.1	615	810	9
	Sh	447	5.6	418	483	6

CALL S2i



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	J	844	23.8	575	1615	34
	MD	954	22.3	745	1500	21
	Sh	912	11.3	690	1168	23
Part 1:						
Dur (ms)	J	577	31.5	325	1308	34
	MD	499	39.6	343	1062	21
	Sh	572	14.1	447	746	23
SBI, start (Hz)	J	1176	25.8	605	1737	34
	MD	1767	10.7	1459	2026	9
	Sh	1394	13.0	1021	1733	9
SBI, dip (Hz)	J	1012	17.4	624	1387	34
	MD	1187	38.6	548	1876	20
	Sh	1296	13.5	857	1542	23
SBI, end (Hz)	J	1929	9.5	1605	2243	34
	MD	2174	9.2	1831	2474	20
	Sh	2051	7.9	1803	2359	23

continued...

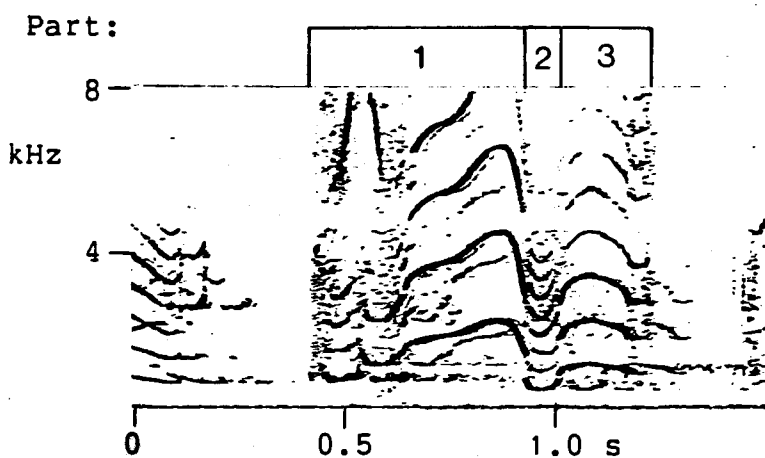
 CALL S2i - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
<u>Part 2:</u>						
Dur (ms)	J	141	14.1	108	191	34
	MD	325	22.7	212	464	21
	Sh	239	30.9	135	407	23
SBI, start (Hz)	J	497	18.0	323	694	34
	MD	607	12.0	407	743	20
	Sh	499	12.0	379	653	23
SBI, dip (Hz)	J	459	15.2	359	692	34
	MD	627	10.2	500	724	20
	Sh	518	9.3	459	660	23
SBI, end (Hz)	J	2118	17.9	1364	2881	34
	MD	2589	22.2	1520	3365	21
	Sh	2523	21.2	1555	3852	23
<u>Part 3:</u>						
Dur (ms)	J	125	27.0	82	223	34
	MD	129	38.7	62	259	21
	Sh	100	23.5	52	152	23
SBI, end (Hz)	J	1017	10.4	830	1300	34
	MD	1744	19.5	822	2110	20
	Sh	1141	13.7	824	1391	23
Tone: f, start (Hz)	J	4683	13.7	3772	6484	29
	MD	4254	30.9	2561	5750	4
	Sh	4258	6.5	3994	4848	9

 CALL S2i - Measurement Comparisons

Measurement	J vs MD	J vs Sh	MD vs Sh
Duration (ms)	ns	ns	ns
<u>Part 1:</u>			
Dur (ms)	ns	ns	ns
SBI, start (Hz)	--	--	--
SBI, dip (Hz)	ns	<0.001	ns
SBI, end (Hz)	<0.001	ns	ns
<u>Part 2:</u>			
Dur (ms)	<0.001	<0.001	<0.001
SBI, start (Hz)	<0.001	ns	<0.001
SBI, dip (Hz)	<0.001	<0.01	<0.001
SBI, end (Hz)	<0.01	<0.05	ns
<u>Part 3:</u>			
Dur (ms)	ns	<0.05	<0.05
SBI, end (Hz)	<0.001	ns	<0.001
Tone: f, start	ns	ns	ns

CALL S2ii



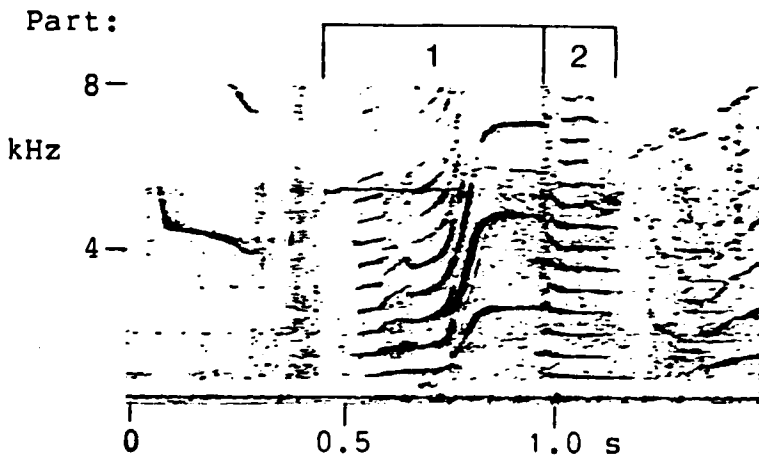
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	J	840	15.2	642	1040	13
	MD	839	14.9	637	980	9
<u>Part 1:</u>						
Dur (ms)	J	572	27.5	370	965	13
	MD	423	20.3	308	531	9
SBI, start (Hz)	J	1229	20.7	733	1587	13
	MD	1944	11.7	1783	2105	2
SBI, dip (Hz)	J	1057	15.1	622	1266	13
	MD	966	48.1	435	1780	9
SBI, end (Hz)	J	2063	9.1	1770	2400	13
	MD	2264	18.1	1863	2835	9
<u>Part 2:</u>						
Dur (ms)	J	133	17.5	88	172	13
	MD	190	29.7	110	252	9
SBI, start (Hz)	J	519	13.6	359	615	13
	MD	616	9.1	488	676	9
SBI, dip (Hz)	J	466	35.5	270	958	13
	MD	634	12.6	494	722	9

continued...

 CALL S2ii - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
<u>Part 2:</u>						
SBI, end (Hz)	J	2159	13.6	1490	2461	11
	MD	2769	21.8	2104	3982	9
<u>Part 3:</u>						
Dur (ms)	J	166	33.7	109	306	12
	MD	225	13.1	182	280	9
SBI, peak (Hz)	J	1138	19.8	684	1600	13
	MD	2398	18.3	1824	3001	9
SBI, end (Hz)	J	878	16.4	681	1076	13
	MD	1546	19.2	1226	2124	9
Tone: start (Hz)	J	4413	10.3	3693	5056	10

CALL S2iii



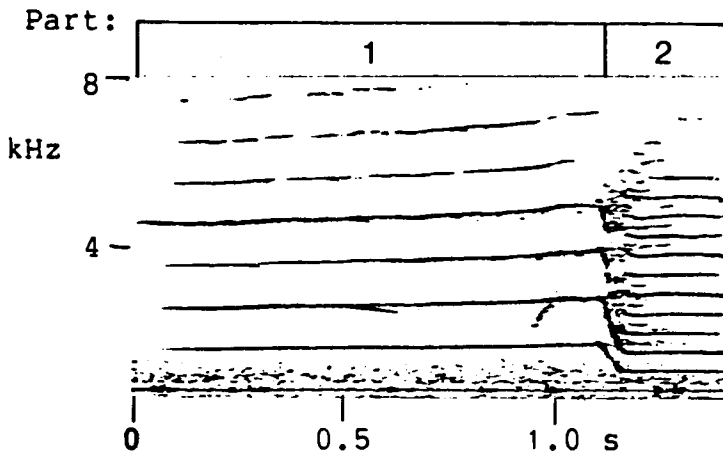
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	L	617	23.8	384	982	26
	73	741	1.9	731	751	2
<u>Part 1:</u>						
Dur (ms)	L	466	29.5	216	873	26
	73	624	2.5	613	635	2
Time to upsweep (ms)	L	304	32.0	194	613	24
	73	356	4.8	344	368	2
SBI, start (Hz)	L	554	9.9	464	688	26
	73	435	24.7	359	511	2
SBI, end (Hz)	L	2649	10.1	2358	3686	25
	73	2769	6.0	2651	2887	2

continued...

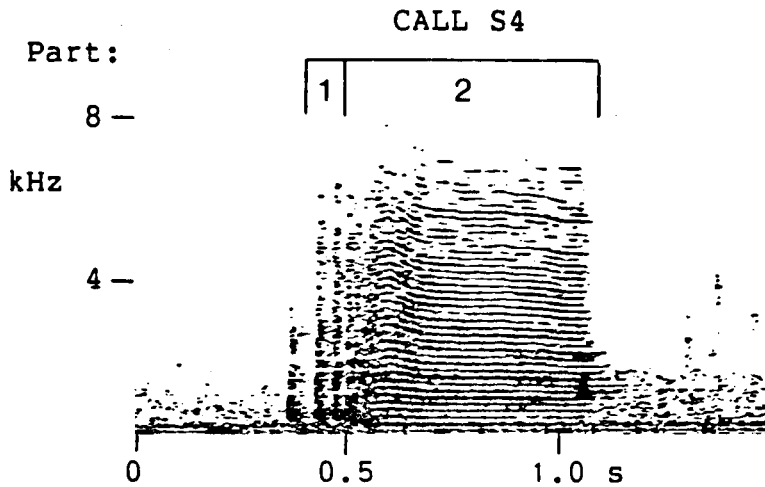
 CALL S2iii - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
<u>Part 2:</u>						
Dur (ms)	L	150	30.7	79	268	26
	73	117	1.2	116	118	2
SBI, start (Hz)	L	606	18.8	408	828	26
	73	548	6.7	522	574	2
SBI, end (Hz)	L	542	20.4	336	793	26
	73	522	20.6	446	598	2
<u>Tone:</u>						
f, start (Hz)	L	5557	4.5	5103	6033	25
	73	6247	6.9	5943	6551	2
f, end (Hz)	L	6419	11.1	5398	7813	24
	73	6791	12.2	6207	7375	2

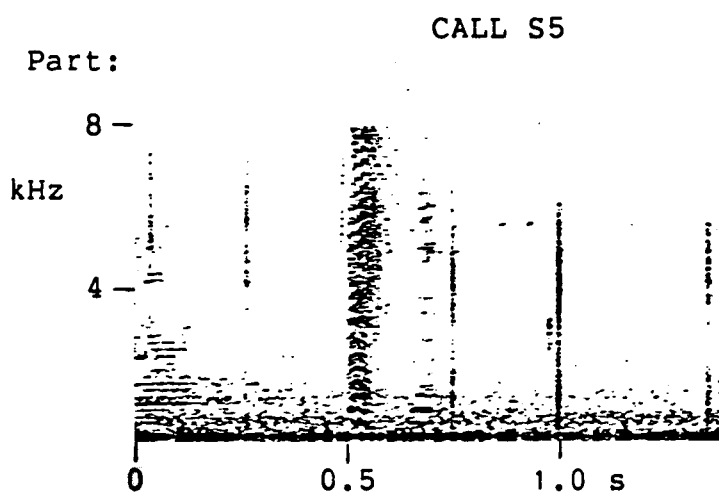
CALL S3



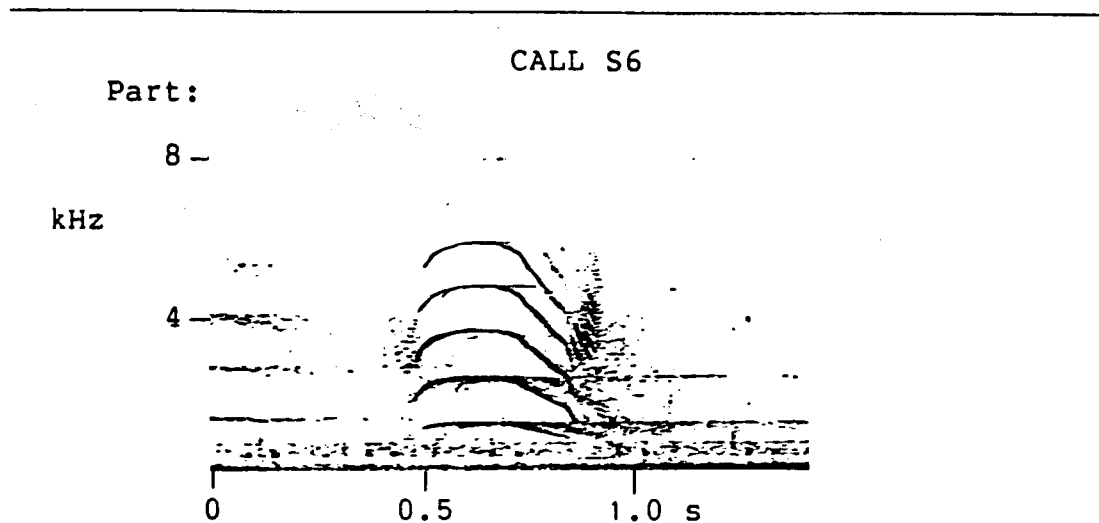
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	J	1195	24.3	598	1649	21
	MD	1079	3.6	1025	1135	10
<u>Part 1:</u>						
Dur (ms)	J	964	30.4	433	1449	21
	MD	909	3.8	872	952	10
SBI, start (Hz)	J	1068	4.0	994	1166	21
	MD	955	4.6	868	1028	10
SBI, end (Hz)	J	1068	6.6	972	1245	21
	MD	898	5.6	831	982	10
<u>Part 2:</u>						
Dur (ms)	J	231	17.5	165	313	21
	MD	169	6.8	153	189	10
SBI, start (Hz)	J	453	6.3	395	500	21
	MD	408	5.0	377	431	10
SBI, end (Hz)	J	455	6.8	396	516	21
	MD	400	6.7	356	435	10



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	J	758	26.8	484	1269	29
<u>Part 1:</u>						
Dur (ms)	J	188	39.6	87	425	29
IPI, start (ms)	J	52	24.0	30	75	29
<u>Part 2:</u>						
Dur (ms)	J	570	26.8	380	968	29
SBI (Hz)	J	159	11.5	120	191	29

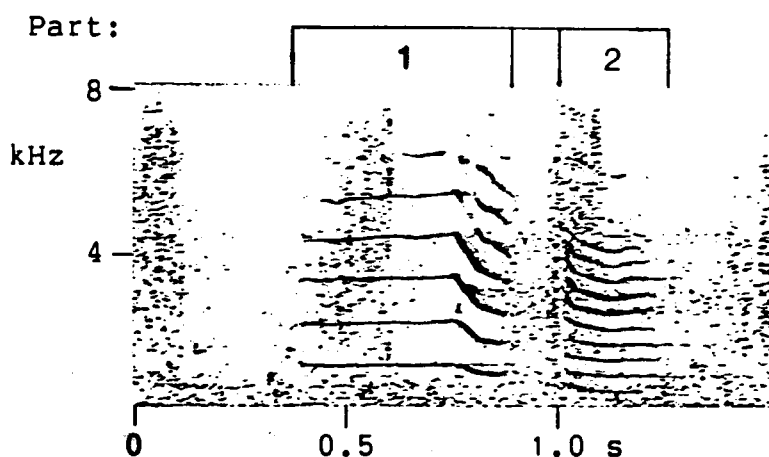


Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	J	81	25.1	45	116	16
	Sh	123	8.7	107	130	4
SBI (Hz)	J	294	9.2	235	331	16
	Sh	364	3.5	351	381	4



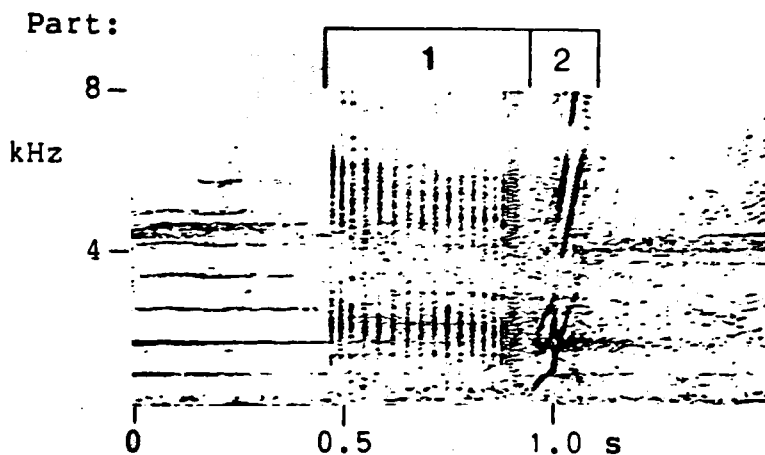
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	J	466	17.4	315	580	21
SBI, start (Hz)	J	950	15.1	686	1176	21
SBI, peak (Hz)	J	1033	12.5	861	1336	21
SBI, end (Hz)	J	251	16.4	170	343	21

CALL S7



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	J	905	15.7	706	1246	23
<u>Part 1:</u>						
Dur (ms)	J	607	22.7	427	957	23
Time to down-sweep (ms)	J	470	28.8	278	839	23
SBI, start (Hz)	J	1023	4.7	933	1137	23
SBI, end (Hz)	J	613	12.7	452	739	23
Dur, gap between Pts. 1 & 2 (ms)	J	135	29.9	74	283	23
<u>Part 2:</u>						
Dur (ms)	J	163	15.3	122	216	23
SBI, start (Hz)	J	444	12.1	375	574	23
SBI, end (Hz)	J	393	7.8	348	451	23

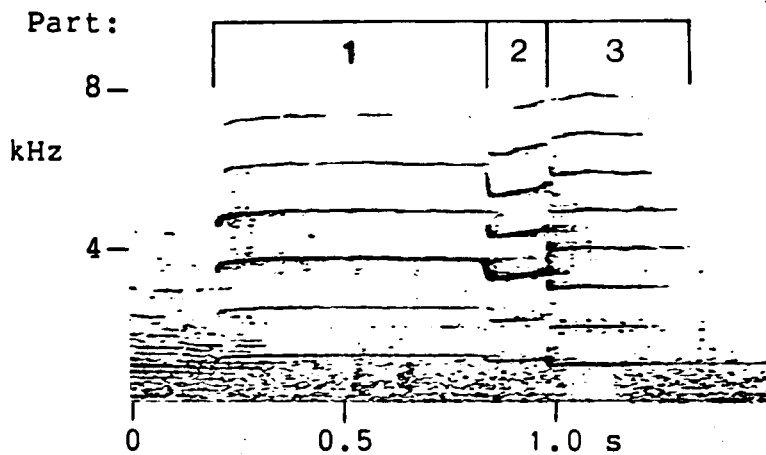
CALL S8 i & ii



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	J	221	63.4	78	459	17
	L	501	13.1	399	642	14
<u>Part 1:</u>						
Dur (ms)	J	123	98.3	14	337	17
	L	409	16.5	280	523	14
IPI, start (ms)	J	34	38.1	22	61	7
	L	29	18.7	21	42	14
<u>Part 2:</u>						
Dur (ms)	J	98	37.5	49	178	17
	L	92	14.5	73	119	14
SBI, start (Hz)	J	2542	15.6	1653	3223	17
	L	734	9.4	667	924	14
SBI, end (Hz)	J	6432	19.0	4099	7854	17
	L	5495	18.3	4300	7330	14

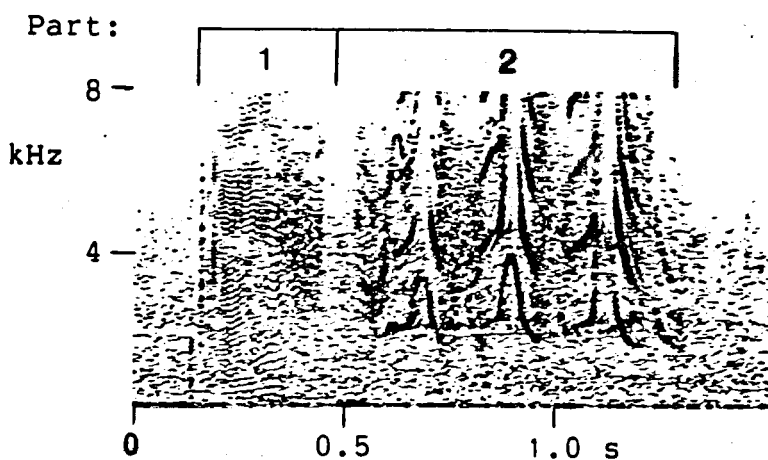
N.B.: Subtype S8i given by J pod, and S8ii by L pod.

CALL S9



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	J	1069	8.7	952	1249	11
<u>Part 1:</u>						
Dur (ms)	J	636	16.5	502	803	11
SBI, start (Hz)	J	1189	4.3	1136	1282	11
SBI, end (Hz)	J	1170	4.3	1107	1265	11
<u>Part 2:</u>						
Dur (ms)	J	173	11.9	131	200	11
SBI (Hz)	J	1046	5.6	975	1151	11
<u>Part 3:</u>						
Dur (ms)	J	258	13.0	214	315	11
SBI (Hz)	J	937	4.6	882	1002	11

CALL S10

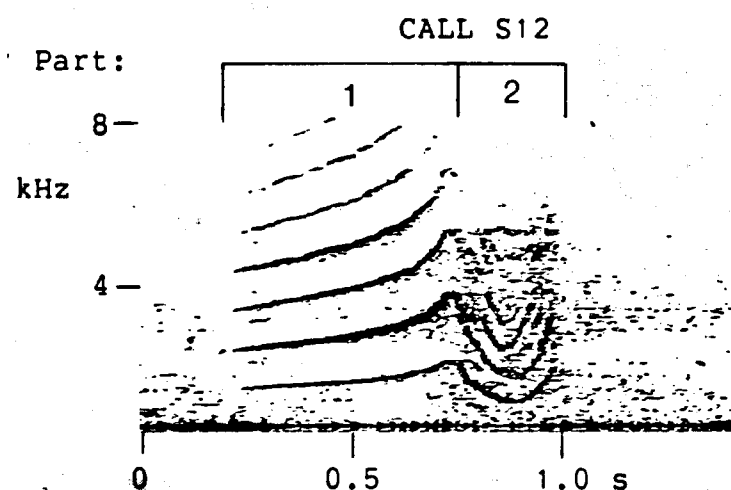


Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	J	958	9.8	887	1103	5
	K	1035	4.4	992	1083	3
	L	1610	17.6	1160	1975	6
<u>Part 1:</u>						
Dur (ms)	J	369	14.6	305	431	5
	K	428	13.2	373	486	3
	L	451	15.3	356	519	6
SBI, start (Hz)	J	102	22.7	72	135	5
	K	107	22.0	84	131	3
	L	94	20.0	73	127	6
SBI, end (Hz)	J	229	38.6	177	387	5
	K	175	6.4	162	182	3
	L	196	18.6	149	230	6
<u>Part 2:</u>						
Dur (ms)	J	589	22.7	474	798	5
	K	606	9.5	544	657	3
	L	1159	20.7	804	1530	6
Dur, pulses (ms)	J	119	14.8	73	210	15
	K	113	34.2	67	180	9
	L	137	34.3	68	284	18

continued...

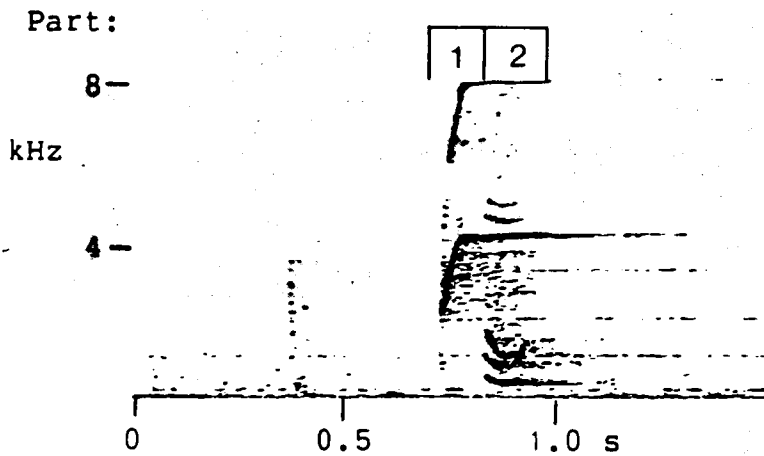
CALL S10 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n
Dur, IPI's (ms)	J	77	8.1	49	120	15
	K	89	38.7	48	159	9
	L	132	38.6	77	233	11



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	J	954	25.4	726	1549	14
<u>Part 1:</u>						
Dur (ms)	J	650	36.0	400	1246	14
SBI, start (Hz)	J	1047	6.1	894	1119	14
SBI, end (Hz)	J	1944	16.3	1290	2515	14
<u>Part 2:</u>						
Dur (ms)	J	303	12.4	193	353	14
SBI, dip (Hz)	J	539	25.5	440	926	14
SBI, end (Hz)	J	1627	20.9	961	2260	14

CALL S13



Measurement	Pod	Mean	C.V.	Min	Max	n	p*
Duration (ms)	J	231	17.4	189	329	14	<0.001
	L	163	15.1	124	222	16	
	73	305	7.4	273	339	7	
<u>Part 1:</u>							
Dur (ms)	J	126	28.0	98	210	14	<0.001
	L	63	12.4	48	78	16	
	73	160	13.4	118	183	7	
Dur, level part (ms)	J	71	41.3	38	134	14	<0.001
	L	26	22.5	17	43	16	
	73	127	17.7	90	157	7	
SBI, start (Hz)	J	2688	10.4	1989	3083	14	ns
	L	2375	16.4	1405	2859	16	
	73	2791	25.2	1841	3662	7	
SBI, mid (Hz)	J	3938	3.5	3506	4089	14	<0.001
	L	3124	3.4	2905	3331	16	
	73	3179	5.2	2927	3421	7	
SBI, end (Hz)	J	3863	3.4	3453	3992	14	<0.001
	L	3140	3.6	2941	3367	16	
	73	3289	4.4	3124	3528	7	

continued...

CALL S13 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n	p*
<u>Part 2:</u>							
Dur (ms)	J	105	14.1	87	130	14	ns
	L	100	19.0	76	144	16	
	73	145	21.8	93	196	7	
SBI, start (Hz)	J	480	16.9	362	678	14	ns
	L	465	15.0	375	595	16	
	73	597	37.1	343	1024	7	
SBI, dip (Hz)	J	434	16.9	351	618	14	ns
	L	479	12.1	375	559	16	
	73	591	33.1	408	967	7	
SBI, end (Hz)	J	493	17.4	378	661	14	ns
	L	536	22.4	348	813	16	
	73	555	37.7	270	924	7	

* ANOVA comparison between J and L pods only.

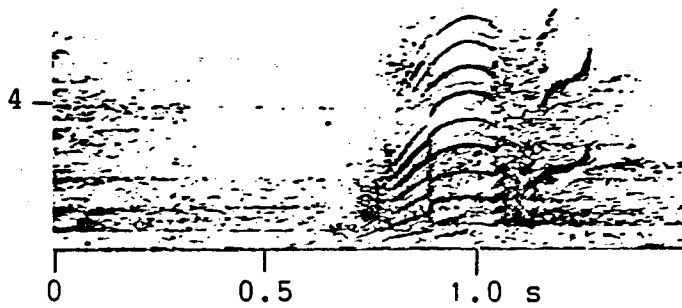
CALL S14

Part:

1	2	3
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8—

kHz



Measurement	Pod	Mean	C.V.	Min	Max	n	p*
Duration (ms)	J	539	5.9	518	587	4	<0.001
	MD	635	5.7	567	712	14	
	Sh	716	6.7	651	787	13	

Part 1:

Dur (ms)	J	303	11.2	264	347	4	<0.01
	MD	372	8.2	322	416	14	
	Sh	439	15.5	352	604	14	
SBI, start (Hz)	J	266	21.2	215	337	4	ns
	MD	331	23.2	245	525	14	
	Sh	304	16.3	227	405	14	
SBI, mid (Hz)	J	512	12.8	454	582	4	ns
	MD	631	7.2	576	720	14	
	Sh	643	7.3	594	749	14	
SBI, end (Hz)	J	653	6.9	595	693	4	ns
	MD	642	6.6	568	705	14	
	Sh	684	12.2	583	853	13	

Part 2:

Dur (ms)	J	108	11.1	91	121	4	<0.001
	MD	116	13.8	90	149	14	
	Sh	148	12.8	122	185	14	

continued...

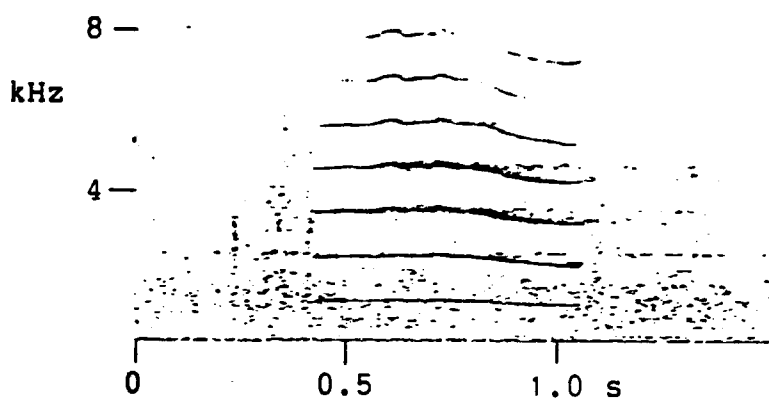
 CALL S14 - continued...

Measurement	Pod	Mean	C.V.	Min	Max	n	p*
<u>Part 3:</u>							
Dur (ms)	J	128	10.7	109	141	4	ns
	MD	147	14.3	115	196	14	
	Sh	139	13.3	104	170	13	
SBI, start (Hz)	J	1721	7.0	1553	1815	4	ns
	MD	2290	6.0	2070	2529	14	
	Sh	2254	3.8	2128	2400	14	
SBI, end (Hz)	J	2185	3.3	2089	2247	4	ns
	MD	2316	5.1	2129	2516	14	
	Sh	2284	4.8	2110	2520	13	

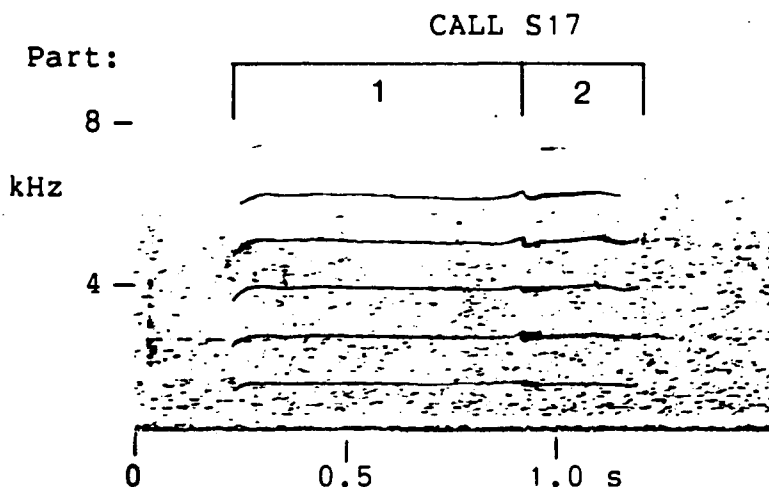
* ANOVA comparison between MD and Sh only.

CALL S16

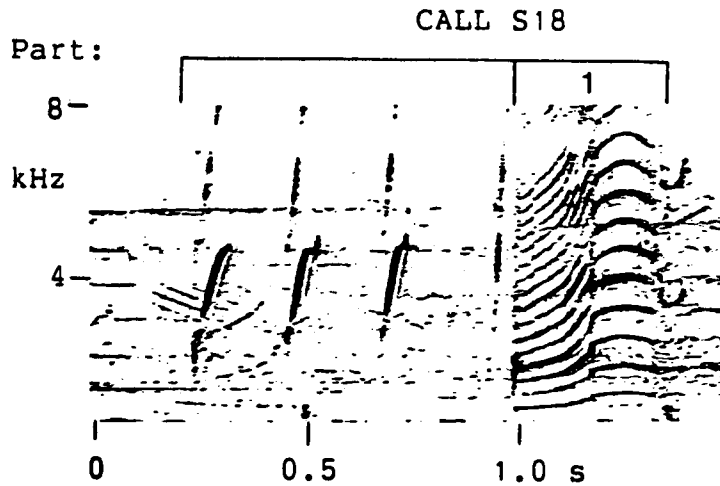
Part:



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	K	729	31.4	350	1264	15
	L	1088	30.6	709	1333	3
Time to downsweep (ms)	K	540	40.6	237	1102	15
	L	857	29.7	564	1023	3
SBI, start (Hz)	K	1138	6.2	962	1226	15
	L	1258	7.9	1147	1336	3
SBI, start of downsweep (Hz)	K	1123	10.3	881	1270	15
	L	1228	6.6	1160	1317	3
SBI, end (Hz)	K	950	9.7	732	1114	15
	L	984	10.5	870	1071	3

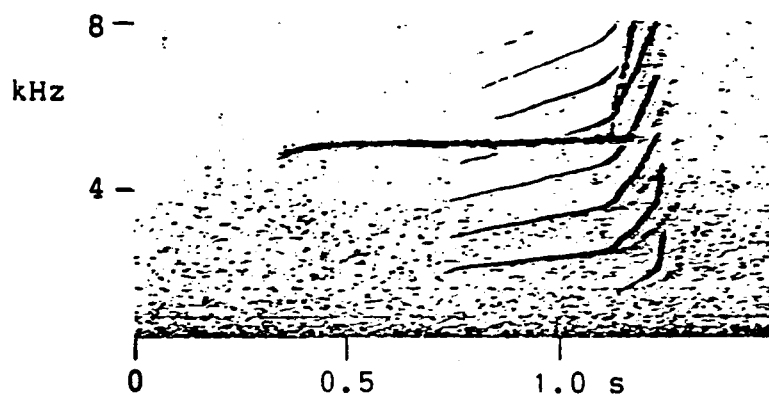


Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	K	857	11.0	743	980	7
	L	870	----	---	---	1
<u>Part 1:</u>						
Dur (ms)	K	609	15.9	483	727	7
	L	717	----	---	---	1
SBI, start (Hz)	K	1219	3.7	1159	1283	7
	L	1201	---	----	----	1
SBI, mid (Hz)	K	1216	3.8	1166	1297	7
	L	1270	---	----	----	1
SBI, end (Hz)	K	1158	5.2	1076	1231	7
	L	1177	---	----	----	1
<u>Part 2:</u>						
Dur (ms)	K	247	14.2	184	292	7
	L	153	----	---	---	1
SBI, end (Hz)	K	1223	2.9	1187	1292	7
	L	1262	---	----	----	1

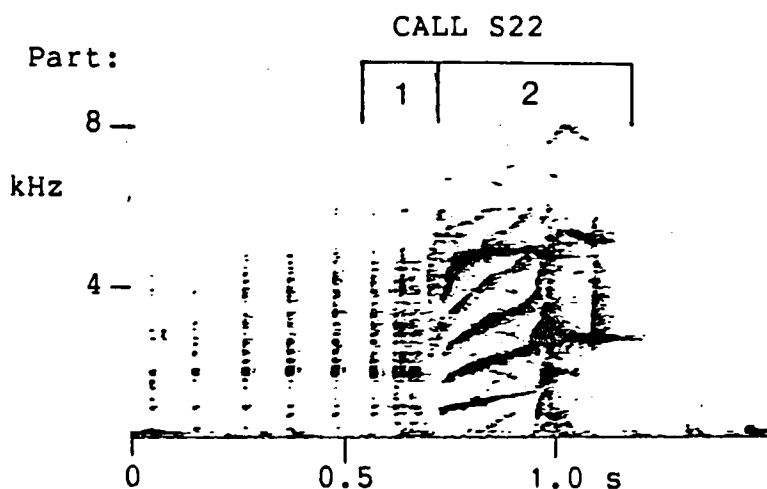


Measurement	Pod	Mean	C.V.	Min	Max	n	p
<u>'Chirps:</u>							
No./call	L	3	41.6	0	4	26	
	73	3	18.1	2	4	15	
Dur (ms)	L	80	17.5	47	97	23	ns
	73	87	14.9	66	116	30	
f, start (Hz)	L	1745	18.1	1208	2479	23	<0.001
	73	2312	9.9	1980	3001	30	
f, end (Hz)	L	4463	8.3	3321	4996	23	ns
	73	4400	5.2	4083	5008	30	
<u>Part 1:</u>							
Dur (ms)	L	418	21.6	256	568	16	ns
	73	422	20.9	342	597	11	
SBI, start (Hz)	L	377	8.6	327	427	16	ns
	73	383	9.6	332	455	11	
SBI, end (Hz)	L	703	10.3	575	810	16	ns
	73	757	6.9	685	846	11	

Part: CALL S19



Measurement	Pod	Mean	C.V.	Min	Max	n	p
Duration (ms)	L	730	22.1	330	1099	35	ns
	73	844	28.9	559	1475	15	
<u>Pulsed part:</u>							
Dur (ms)	L	485	28.1	169	833	35	<0.01
	73	625	23.4	390	1048	15	
SBI, start (Hz)	L	827	23.5	471	1365	35	<0.001
	73	1103	13.0	812	1368	15	
SBI, end (Hz)	L	2004	23.5	1303	3128	35	ns
	73	2056	17.5	1468	2816	15	
<u>Tone:</u>							
Dur (ms)	L	682	24.8	240	1063	35	ns
	73	729	36.7	354	1367	15	
f, start (Hz)	L	4874	2.9	4562	5127	35	ns
	73	4906	5.0	4483	5447	15	
f, end (Hz)	L	5885	11.1	4976	7751	35	ns
	73	5655	10.0	4848	6828	15	



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	L	428	24.1	294	565	11
	73	585	10.7	509	733	12
<u>Part 1:</u>						
Dur (ms)	L	128	35.6	79	211	14
	73	152	24.3	92	199	12
SBI (Hz)	L	127	14.7	108	174	14
	73	96	15.7	72	117	10
<u>Part 2:</u>						
Dur (ms)	L	299	23.8	196	417	11
	73	433	11.9	381	556	12
Dur, level part (ms)	L	79	56.6	42	177	14
	73	134	48.5	71	300	12
SBI, start (Hz)	L	1029	21.8	806	1628	14
	73	908	13.0	720	1129	12
SBI, mid (Hz)	L	2356	14.8	1515	2669	14
	73	2656	4.8	2442	2824	12
SBI, end (Hz)	L	2442	15.7	1694	2975	11
	73	2721	5.1	2421	2909	12

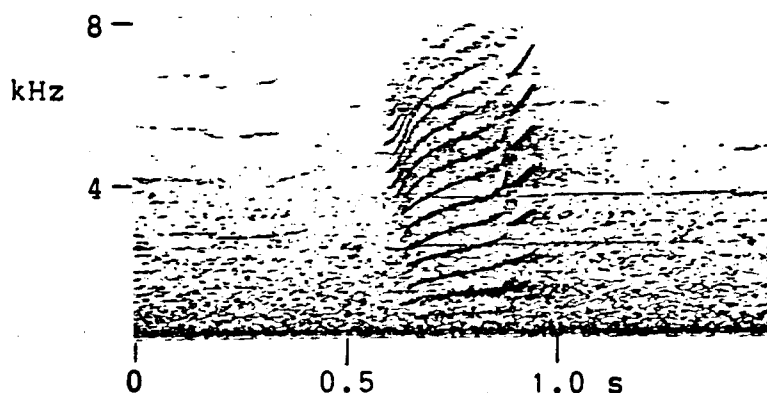
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CALL S22 - continued...

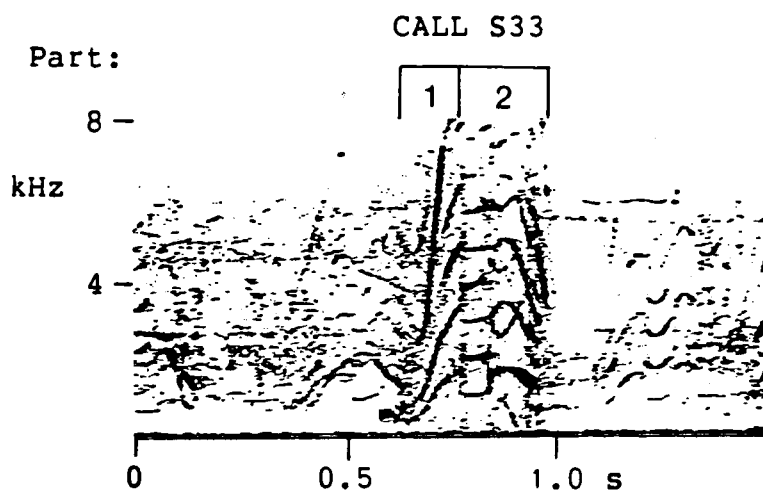
Measurement	Pod	Mean	C.V.	Min	Max	n
<u>Tone:</u>						
f, start (Hz)	L	4388	17.6	3064	5546	14
	73	4028	10.8	3252	4745	11
f, level part (Hz)	L	5798	7.6	4961	6579	14
	73	5685	8.7	4607	6436	11
f, end (Hz)	L	5879	7.4	5062	6696	14
	73	5744	7.4	4801	6338	11

CALL S31

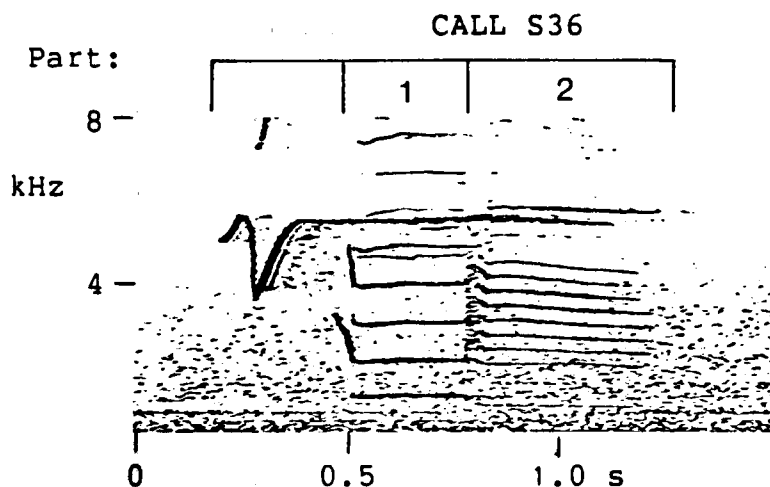
Part:



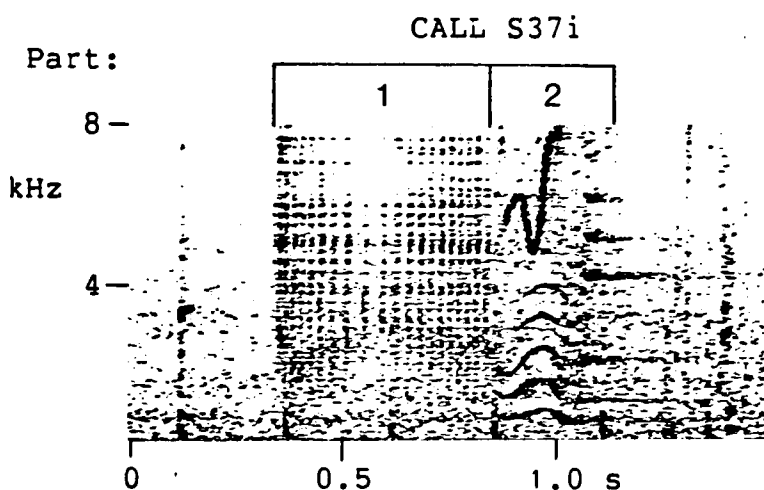
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	L	481	26.5	338	738	23
SBI, start (Hz)	L	148	28.2	62	238	23
SBI, end (Hz)	L	706	27.6	382	1073	23



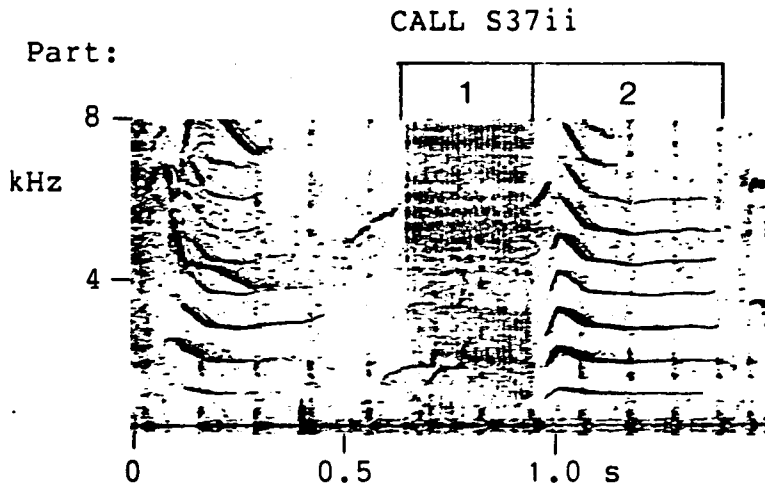
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	L	566	20.4	440	825	14
	73	586	60.3	321	1079	6
<u>Part 1:</u>						
Dur (ms)	L	166	21.5	93	239	15
	73	237	59.5	120	449	6
<u>Part 2:</u>						
Dur (ms)	L	396	27.0	299	654	14
	73	349	61.4	195	630	6
Dur, lo parts (ms)	L	66	25.7	29	108	34
	73	70	9.7	58	79	10
Dur, hi parts (ms)	L	85	18.5	44	107	24
	73	93	15.1	77	110	6
f, lo parts (Hz)	L	866	18.0	556	1099	37
	73	879	5.9	813	967	10
f, hi parts (Hz)	L	1695	6.7	1470	1869	34
	73	1685	5.8	1551	1805	10



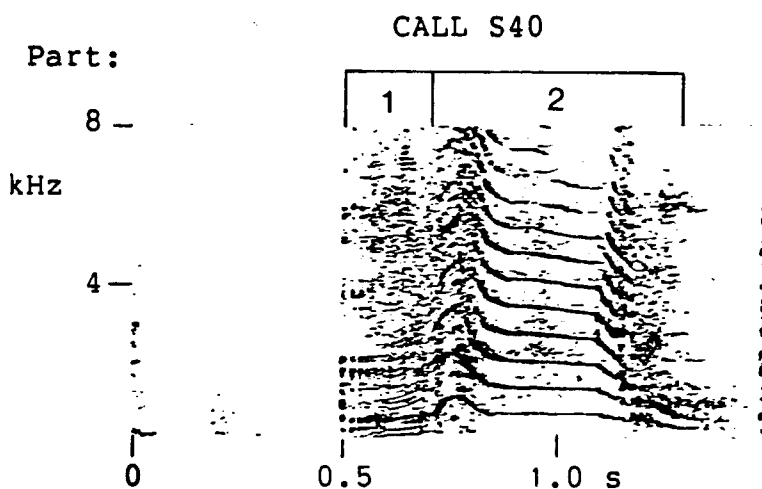
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	L	951	11.0	750	1135	21
<u>Part 1:</u>						
Dur (ms)	L	302	12.7	223	378	28
SBI, start (Hz)	L	900	6.0	779	981	28
SBI, end (Hz)	L	848	6.7	750	955	28
<u>Part 2:</u>						
Dur (ms)	L	324	20.3	200	443	19
SBI, start (Hz)	L	333	16.4	244	452	21
SBI, end (Hz)	L	214	38.8	86	402	21
<u>Tone:</u>						
Dur (ms)	L	932	11.6	722	1182	28
f, start (Hz)	L	4751	9.5	3469	5485	27
f, peak (Hz)	L	5847	5.9	5371	6603	27
f, min (Hz)	L	3847	7.3	3441	4394	27
f, end (Hz)	L	5439	2.8	5128	5719	28



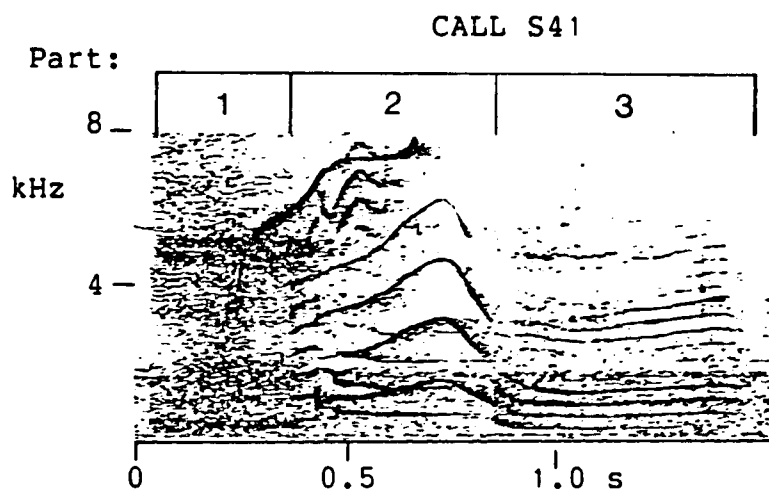
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	J	609	25.5	380	977	20
<u>Part 1:</u>						
Dur (ms)	J	368	40.6	141	613	17
SBI (Hz)	J	45	20.3	35	85	20
<u>Part 2:</u>						
Dur (ms)	J	253	22.2	187	416	17
SBI, start (Hz)	J	488	16.1	367	647	20
SBI, peak (Hz)	J	864	26.0	587	1518	20
SBI, end (Hz)	J	526	19.4	386	726	20
<u>Tone:</u>						
f, start (Hz)	J	4605	11.2	3206	5116	17
f, 1st peak (Hz)	J	6098	4.9	5514	6648	17
f, dip (Hz)	J	5226	6.8	4800	5989	17



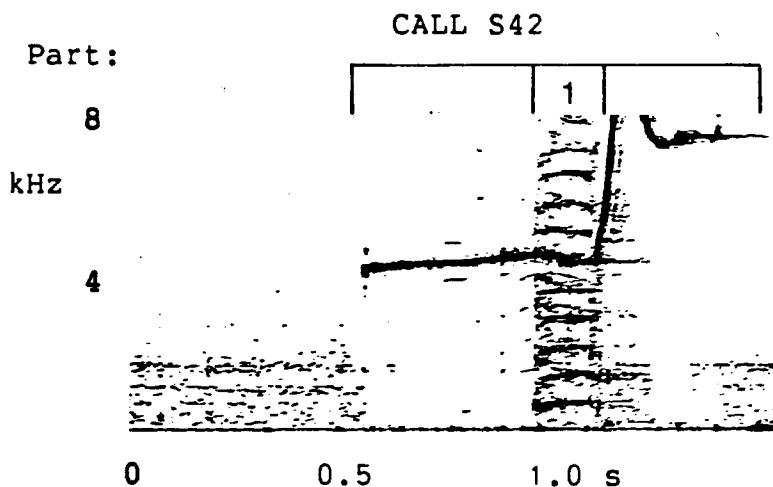
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	L	765	16.7	654	1042	13
<u>Part 1:</u>						
Dur (ms)	L	444	26.6	332	635	11
SBI (Hz)	L	77	18.7	48	95	13
<u>Part 2:</u>						
Dur (ms)	L	389	34.1	298	685	13
SBI, start (Hz)	L	1056	14.7	905	1462	13
SBI, end (Hz)	L	795	6.4	719	909	13
<u>Tone:</u>						
f, start (Hz)	L	5871	5.8	5135	6254	11
f, 1st peak (Hz)	L	6657	2.7	6411	6959	11
f, dip (Hz)	L	5963	4.4	5577	6348	11



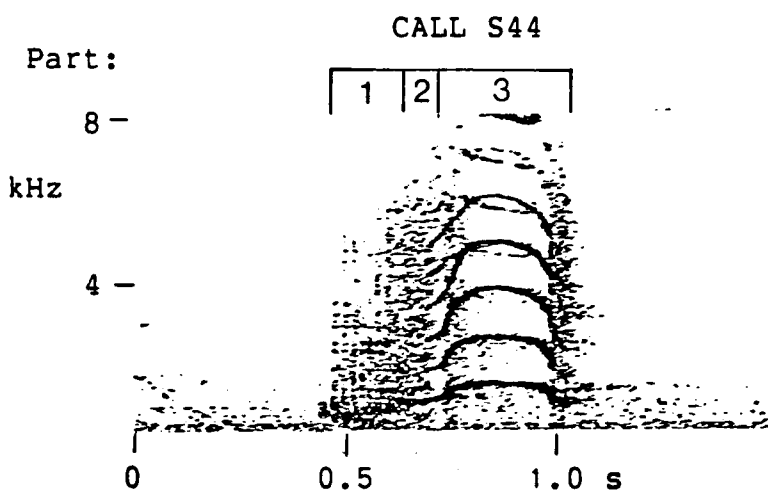
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	L	601	14.6	519	843	18
<u>Part 1:</u>						
Dur (ms)	L	111	34.5	19	205	18
IPI, start (ms)	L	17	30.8	5	26	18
<u>Part 2:</u>						
Dur (ms)	L	490	15.1	410	679	18
SBI, start (Hz)	L	580	13.0	421	661	18
SBI, peak (Hz)	L	1118	9.9	705	1223	18
SBI, mid (Hz)	L	659	11.9	511	770	18
SBI, end (Hz)	L	283	14.3	206	345	18



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	J	1318	17.0	904	1731	19
<u>Part 1:</u>						
Dur (ms)	J	213	47.3	42	380	19
SBI (Hz)	J	102	18.0	71	145	19
<u>Part 2:</u>						
Dur (ms)	J	538	23.4	365	776	19
SBI, start (Hz)	J	1037	24.5	439	1380	19
SBI, peak (Hz)	J	2118	10.4	1539	2638	19
SBI, end (Hz)	J	1164	18.8	754	1534	19
<u>Part 3:</u>						
Dur (ms)	J	566	23.6	302	761	19
SBI, start (Hz)	J	379	9.6	311	441	19
SBI, end (Hz)	J	361	8.4	311	403	19
Tone: f, start (Hz)	J	5208	11.8	4039	6196	19

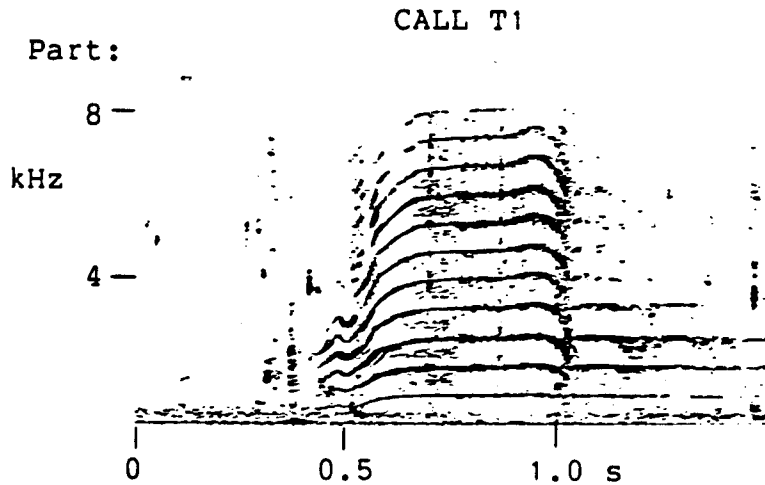


Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	J	898	18.3	618	1261	26
	L	775	12.8	705	889	3
	73	730	----	---	----	1
<u>Part 1:</u>						
Dur (ms)	J	251	37.9	146	566	26
	L	287	28.1	239	380	3
	73	375	----	---	---	1
SBI (Hz)	J	723	5.0	645	794	26
	L	761	6.4	726	817	3
	73	767	---	---	---	1
<u>Tone:</u>						
f, start (Hz)	J	4142	2.3	3983	4345	26
	L	4227	5.5	3977	4441	3
	73	4355	---	----	----	1
f, at end of Pt. 1 (Hz)	J	4490	4.4	4197	4878	26
	L	4757	2.6	4651	4890	3
	73	4820	---	----	----	1
f, end (Hz)	J	7475	2.3	7238	7903	26
	L	7352	0.3	7329	7368	3
	73	----	---	----	----	-

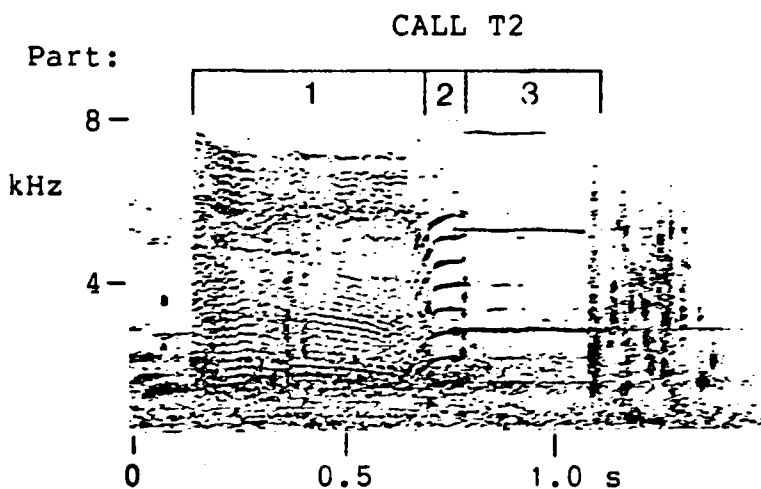


Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	J	631	16.7	469	893	29
<u>Part 1:</u>						
Dur (ms)	J	183	31.6	70	326	29
IPI (ms)	J	30	22.8	21	55	29
<u>Part 2:</u>						
Dur (ms)	J	62	25.9	27	98	29
SBI (Hz)	J	610	16.0	399	772	29
<u>Part 3:</u>						
Dur (ms)	J	385	24.4	236	603	29
SBI, start (Hz)	J	648	17.3	351	800	29
SBI, mid (Hz)	J	1009	8.5	833	1219	29
SBI, end (Hz)	J	588	21.5	352	1031	29

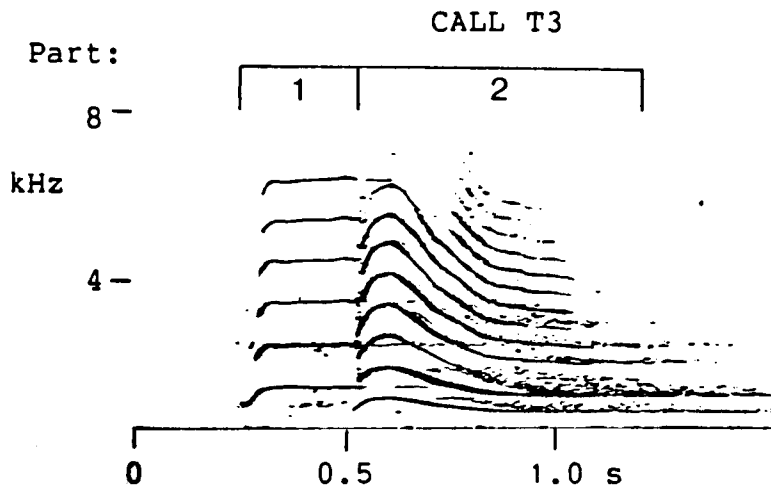
 TRANSIENT COMMUNITY CALLS:



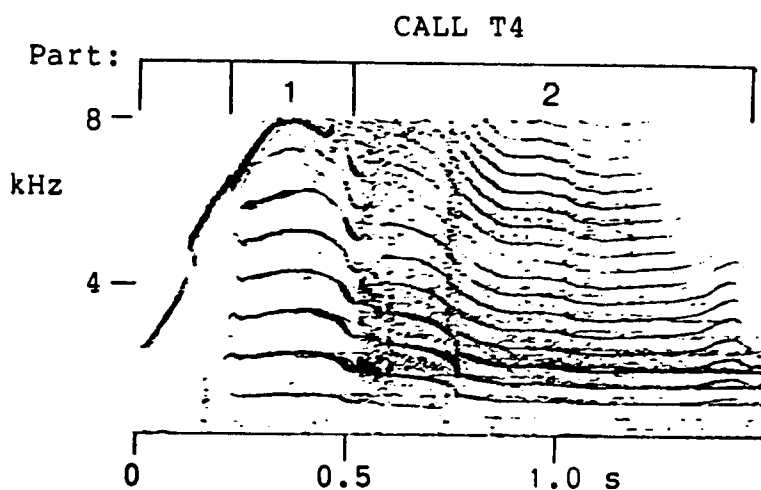
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	04	702	30.7	501	930	3
	X	571	18.0	444	714	8
	Y	803	22.3	514	957	5
Time to peak SBI (ms)	04	691	29.6	501	908	3
	X	541	20.4	411	708	8
	Y	779	20.2	516	890	5
SBI, start (Hz)	04	401	16.5	334	466	3
	X	372	11.6	322	433	8
	Y	397	8.2	354	439	5
SBI, peak (Hz)	04	726	7.6	675	785	3
	X	658	16.9	485	819	8
	Y	622	8.6	568	675	5
SBI, end (Hz)	04	679	21.6	513	788	3
	X	620	19.1	445	785	8
	Y	581	10.1	513	667	5



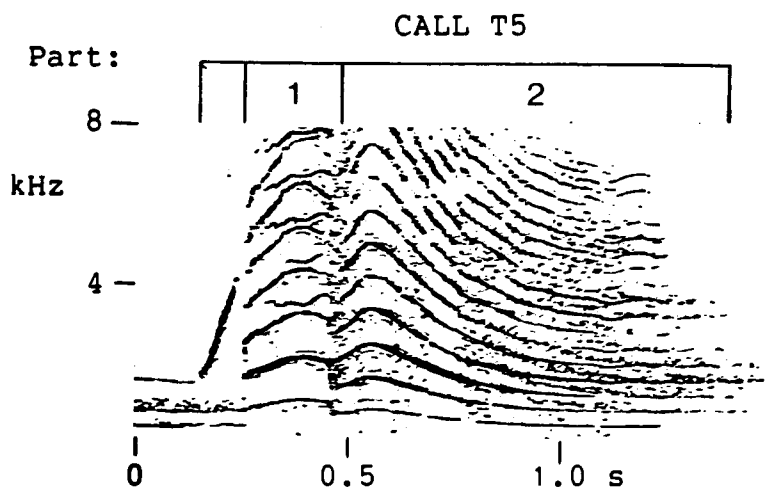
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	X	901	25.5	636	1040	3
<u>Part 1:</u>						
Dur (ms)	X	453	40.7	243	589	3
SBI (Hz)	X	163	6.8	151	172	3
<u>Part 2:</u>						
Dur (ms)	X	115	21.2	91	140	3
SBI (Hz)	X	560	2.1	551	573	3
<u>Part 3:</u>						
Dur (ms)	X	333	14.7	278	372	3
SBI (Hz)	X	2583	4.4	2479	2705	3



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	X	917	7.3	840	1012	7
<u>Part 1:</u>						
Dur (ms)	X	333	19.6	284	474	7
SBI, start (Hz)	X	663	12.7	547	815	7
SBI, mid (Hz)	X	1033	3.2	978	1079	7
<u>Part 2:</u>						
Dur (ms)	X	583	9.0	532	679	7
SBI, start (Hz)	X	666	7.2	593	714	7
SBI, peak (Hz)	X	788	5.8	742	856	7
SBI, end (Hz)	X	388	10.0	345	438	7



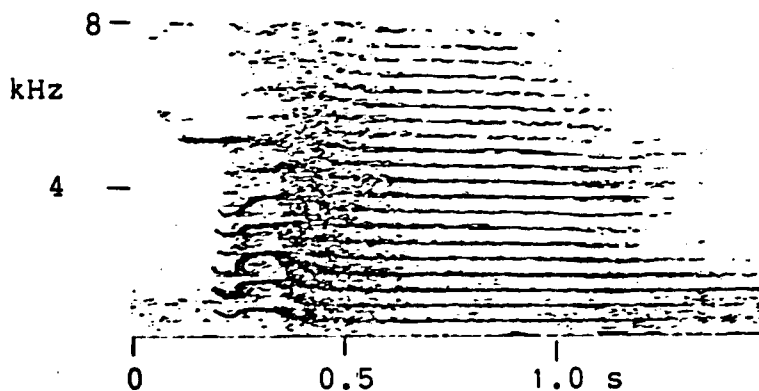
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	X	1392	10.2	1139	1574	7
<u>Part 1:</u>						
Dur (ms)	X	326	20.5	264	407	7
SBI, start (Hz)	X	1012	10.0	877	1139	7
SBI, end (Hz)	X	762	21.2	529	1068	7
<u>Part 2:</u>						
Dur (ms)	X	842	19.2	555	999	7
SBI, peak (Hz)	X	712	7.9	655	825	7
SBI, mid (Hz)	X	420	11.3	361	495	7
SBI, end (Hz)	X	421	15.3	287	484	7
Tone: f, start (Hz)	X	1759	17.3	1220	2259	7



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	X	1131	5.8	1030	1209	5
<u>Part 1:</u>						
Dur (ms)	X	192	8.3	164	202	5
SBI, start (Hz)	X	878	8.8	777	985	5
SBI, peak (Hz)	X	1072	5.3	1024	1169	5
<u>Part 2:</u>						
Dur (ms)	X	823	5.9	763	871	5
SBI, start (Hz)	X	749	5.7	687	799	5
SBI, peak (Hz)	X	819	7.2	741	886	5
SBI, end (Hz)	X	368	5.9	346	391	5

CALL T7

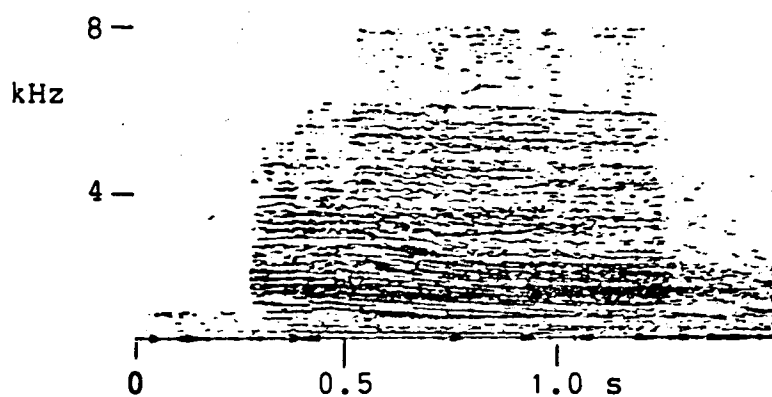
Part:



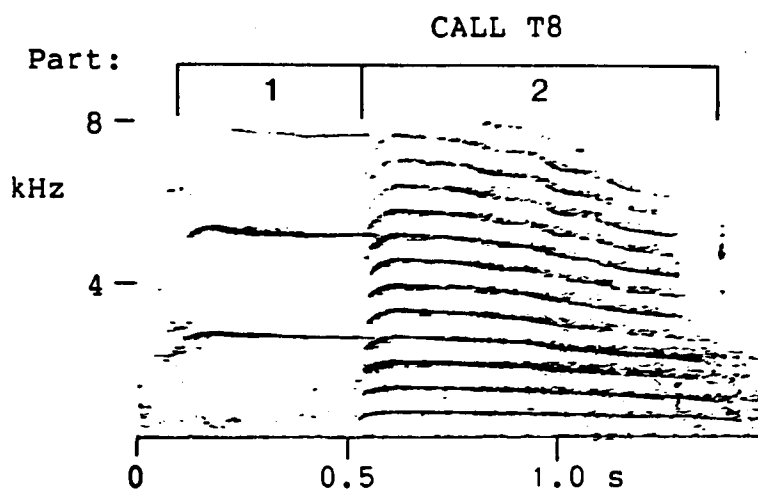
Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	O4	946	9.1	874	1042	3
	Y	1087	4.1	1050	1149	4
SBI, start (Hz)	O4	454	16.1	378	524	3
	Y	487	8.4	430	517	4
SBI, peak (Hz)	O4	707	4.5	685	744	3
	Y	668	4.1	632	695	4
SBI, mid (Hz)	O4	467	2.1	456	475	3
	Y	409	7.2	369	439	4
SBI, end (Hz)	O4	390	3.4	383	406	3
	Y	353	6.2	330	373	4
<u>Tone:</u>						
Dur (ms)	O4	230	13.3	199	260	3
	Y	228	8.6	206	249	4
f, start (Hz)	O4	5178	0.6	5153	5213	3
	Y	5011	2.3	4899	5173	4

CALL T6

Part:



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	X	999	16.9	868	1190	3
SBI, start (Hz)	X	183	25.0	138	230	3
SBI, end (Hz)	X	101	16.4	88	120	3



Measurement	Pod	Mean	C.V.	Min	Max	n
Duration (ms)	O4	726	----	---	---	1
	Y	1271	----	---	---	1
<u>Part 1:</u>						
Dur (ms)	O4	264	----	---	---	1
	Y	442	----	---	---	1
SBI, start (Hz)	O4	2551	----	---	---	1
	Y	2534	----	---	---	1
SBI, end (Hz)	O4	2656	----	---	---	1
	Y	2539	----	---	---	1
<u>Part 2:</u>						
Dur (ms)	O4	462	----	---	---	1
	Y	829	----	---	---	1
SBI, start (Hz)	O4	634	----	---	---	1
	Y	532	----	---	---	1
SBI, peak (Hz)	O4	685	----	---	---	1
	Y	640	----	---	---	1
SBI, end (Hz)	O4	306	----	---	---	1
	Y	463	----	---	---	1