REPRODUCTIVE STRATEGIES OF WEDDELL SEALS IN McMURDO SOUND, ANTARCTICA: RELATIONSHIP AMONG VOCALIZATIONS, BEHAVIORS, AND SOCIAL INTERACTIONS

A Thesis

by

LUDIVINE BLANDINE ROUSSEAU

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2006

Major Subject: Wildlife and Fisheries Sciences

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ABSTRACT

Reproductive Strategies of Weddell Seals in McMurdo Sound, Antarctica:

Relationship among Vocalizations, Behaviors, and Social Interactions. (May 2006)

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Phocid seals (true seals, Order Carnivora, Family Phocidae) use a diverse array of breeding habitats and strategies, and produce many vocalizations. Therefore, phocids are well suited as subjects for study of reproductive strategies and the role of vocalizations in species mating at sea. However, the amount of information is still limited for aquatically breeding pinnipeds. Using underwater audio and video recordings of Weddell seals (*Leptonychotes weddellii*) interacting in McMurdo Sound, I compared the frequencies of vocalizations and behaviors of males and females during the mating season. I also investigated differences in these frequencies based on the social context. Finally, I identified patterns of vocalizations and behaviors to help determine the behavioral context of calls and used this information as a basis for considering the degree of ritualization in Weddell seal displays. Mews, growls, knocks, and trills were found to be almost exclusively male-specific. The territorial male produced chirps more often when another male was present in its territory; whereas, mews and growls were more frequent when one or more free-ranging females were present. Several vocal and behavioral patterns were also detected, including trills announcing the arrival or departure of the territorial male into or from the breathing hole. In the context of an evolutionary-based model of communication, these findings suggest that low-frequency vocalizations and stereotyped displays produced by territorial males may have been favored by sexual selection: they may provide reliable information to females about the fitness of the signaler and influence their choice of mate. They may also help in limiting conflicts between the territorial male and females over access to the breathing hole.

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INTRODUCTION

Sexual Selection and the Evolution of Reproductive Strategies

In many species, females invest more time and energy in their offspring than males. In such species, sexual selection, defined as the differential success of getting mates, will favor the evolution of polygynous systems: males try to mate with multiple females, and females try to mate with a single male of good quality (Freeman & Herron 2001). Such reproductive asymmetries between sexes lead to the following prediction: males that are successful at attracting females, and females that are selective about choosing their mate, will have a greater chance to mate and to produce successful offspring.

Polygynous systems are common in pinnipeds and are characterized by seasonal and synchronized reproductive cycles, and the production of only one offspring per reproductive event (Wells et al. 1999; Van Parijs 2003). Given the short breeding season and the limited number of pups that females can produce, male pinnipeds should be highly efficient at attracting multiple females, and females should be highly efficient at choosing a mate of good quality (Le Boeuf 1991). Wells et al. (1999) reviewed all the reproductive strategies found in phocids. Their review shows that female spatial patterns, movements, as well as mating locations, greatly vary among species: some mate on land,

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This thesis follows the style and format of Animal Behaviour.

others at sea, females may be clustered, mildly clustered, or dispersed. The review also highlights the diversity in primary male tactics of phocids, ranging from scramble competition, lekking, sequential defense, to resource defense and female defense.

When females are dispersed, one way for males to be successful at attracting females is to establish and defend territories that include a resource exploited by females; this strategy is termed resource-defense polygyny (Freeman & Herron 2001). It seems to be the predominant strategy in phocids (Wells et al. 1999): females are widely dispersed in the aquatic environment, so males cannot directly monopolize females. Instead, they monopolize resources needed by females. Resource-defense polygyny has been identified in Atlantic walruses (Stirling et al. 1987), bearded seals (Van Parijs et al. 2003, 2004), harbor seals (Van Parijs et al. 1999, 2000; Nicholson 2000), and Weddell seals (Thomas & Kuechle 1982; Thomas & Stirling 1983; Le Boeuf 1991).

Sexual Selection and the Evolution of Communication

Communication plays a role in defending territories, as well as in attracting females. Territorial defense signals give information on the identity and location of territorial males and their territories; whereas, mate attraction signals indicate the location and availability of potential mates (Bradbury & Vehrencamp 1998a). Males that are able to influence the behaviors and decisions of conspecifics by emitting such signals, and individuals that are able to assess the most relevant cues in these signals, will have a greater fitness (Owings & Morton 1998; Tyack 1999). Therefore, sexual selection will drive the evolution of vocal and behavioral patterns that directly increase individual fitness, and that increase the chance of finding mates. Such patterns would also involve a certain degree of ritualization to ensure that a given signal or pattern will not be confused with another signal (Rogers & Kaplan 2002:1-25). Ritualization involves (1) a limited number of components in signals, (2) mostly attention-getting components, (3) repeated sequences in signals, and/or (4) stereotyped patterns of signals (Bradbury & Vehrencamp 1998b).

Sounds have the advantage of traveling long distances, especially in aquatic environments, and require little energy expenditure. Therefore, acoustic displays have great potential for territory defense and mate attraction in pinnipeds (Miller 2002; Stirling & Thomas 2003). All species of phocids mating at sea produce underwater vocalizations (Wartzok & Ketten 1999). Stirling and Thomas (2003) showed that the underwater vocal repertoire of aquatic-mating species of pinnipeds was correlated to their mating system. Additionally, Van Parijs et al. (2003) found that stereotyped acoustic displays in male bearded seals reflected male status. They found that territorial males produced longer and louder trills, with a higher start frequency and a greater number of steps, than roaming males. Territorial males were thought to be successful males; whereas, roaming males were thought to be younger males or males in poorer condition. Trill duration was also correlated to dive display parameters. This study suggests that trills may indicate male quality. Therefore, the acoustic qualities (amplitude, frequency, etc.) of trills could be used by females to select their mate.

Other pinniped species also use stereotyped vocalizations during the breeding season. For example, Atlantic walruses regularly emit stereotyped vocal patterns at specific locations, close to groups of females and calves (Stirling et al. 1987). In the northern elephant seal, males produce two types of threat calls within breeding areas on the beach: the clap threats, made of very short pulses regularly spaced, and the burst threats, made of a cluster of harsh roars (Shipley et al. 1980).

The Reproductive System of Weddell Seals

Weddell seals occur around the coast of Antarctica, but are also found in pack ice (Stirling 1969). Their movements and distribution, as well as their breeding season, are determined primarily by changes in fast ice (sea ice that is attached to the shore) and the location of breathing holes (Stirling 1969; Thomas 2002). In McMurdo Sound, located in the southern Ross Sea, females start regularly hauling out on the ice in September. Most males arrive at the breeding areas between mid-October and the beginning of November. Males establish underwater territories that they defend throughout the reproductive season, until mid-December (Thomas & Stirling 1983). Copulation occurs from the end of November to mid-December (Thomas & Kuechle 1982; Green & Burton 1988a; Bartsh et al. 1992). The development of the fertilized egg is delayed until mid-January or February; pups are born in October and the weaning period lasts about 50 days (Kooyman 1981).

Territories of male Weddell seals are 15–50 m wide and 50–400 m long, generally along a tidal crack (Kooyman 1981). They contain one or more breathing holes, a resource needed by males and females (Miller 2002; Thomas 2002). However, not all males establish territories. Bartsh et al. (1992) classified male Weddell seals as territorial, transitional, or non-territorial. Territorial males are ≥ 7 years old. They are successful at establishing and defending territories, as well as copulating. They are initially heavier, more active, and lose more weight throughout the breeding season than transitional and non-territorial males. Transitional males are 5–7 years old and are unsuccessful at defending territories. Non-territorial males are the smallest, not necessarily the youngest though. They do not exhibit territorial behavior. Bartsh et al. (1992) suggested that defending territories to increase reproductive success is very energetically costly, and that only large males would be able to incur such costs. Indeed, territorial fights between males occur frequently during the breeding season and involve pushing, striking, wrestling, and biting (Miller 2002). Fights may even become bloody, and individuals that are defeated lose their territory (Thomas 2002).

Vocalizations in Weddell Seals

Generalities.--Weddell seals are more vocal during the breeding season than at any other time of the year (Green & Burton 1988a), and males are more vocal than females (Thomas & Stirling 1983). This suggests that vocalizations play a role in their mating system. Weddell seal vocalizations in McMurdo Sound have a frequency of

0.1–12.8 kHz and a duration of 0.8–35.6 sec (Thomas & Stirling 1983). Source sound-pressure levels of Weddell seal vocalizations are high: 148–193 dB re: 1 μPa at 1 m (Thomas & Kuechle 1982). High source levels allow vocalizations to be detected by conspecifics at a great distance underwater or when hauling out on the ice. Thomas and Kuechle (1982) established a repertoire of Weddell seal vocalizations including 12 broad categories they designated by letters: continuous and long-duration vocalizations (e.g. T, R, G, M, E and L), and short-duration vocalizations (e.g. P, C, A, Z, K, and H). They also identified 34 sound subtypes and nine auxiliary sounds that are always produced in association with other sounds. They tentatively concluded that T (e.g. trill) vocalizations were only produced by males, and suspected that R (e.g. cricket call), E (e.g. eeyoo call), G (e.g. guttural glug), and A (e.g. click) vocalizations were also produced by males only.

Functions of Vocalizations.--Several functions have been proposed for Weddell seal vocalizations. These include attraction of dispersed females, territory defense, and association with aggressive and submissive behaviors (Thomas & Stirling 1983; Thomas et al. 1988; Thomas 1991; Miller 2002). For example, trills are thought to be important in male-specific advertisement, defense, dominance, and warning (Thomas et al. 1983; Thomas 1991). Thomas et al. (1988) found that the daily frequencies of several types of vocalizations produced by Weddell seals were affected by the haul-out patterns of females and pups, whereas the weekly frequencies depended on the period in the reproductive season (e.g. pupping, mating, weaning, dispersing). However, researchers have not quantitatively investigated the underwater behavioral and social contexts of most Weddell seal vocalizations.

Degree of Ritualization.--Stereotypy, repetition of components over time, is one characteristic of ritualized displays (Bradbury & Vehrencamp 1998b). Weddell seal vocalizations are not highly stereotyped. They differ between populations, probably due to learning, fidelity to breeding sites, and isolation of breeding sites (Thomas & Stirling 1983; Pahl et al. 1997; Terhune et al. 2001). Additionally, Terhune et al. (1994) found that Weddell seals change the amplitude and the duration of their calls when they are overlapped by conspecifics' vocalizations: individuals seem to increase the duration of overlapped calls made of multiple elements by adding more elements to the sequence. Moreover, Thomas and Stirling (1983) suggested that plasticity occurred during the learning process, as pups appeared to mimic several adult vocalizations.

However, there is evidence that Weddell seal vocalizations are ritualized to some degree. Green and Burton (1988b) identified some stereotyped, repetitive, and seasonal sequences of vocalizations. They called these sequences songs, according to the definition of Thorpe (1964). Moors and Terhune (2004) investigated the repetition patterns of Weddell seal calls made of at least three elements. They found three patterns of duration (constant, increasing, or decreasing duration for elements or intervals throughout the call), and three frequency patterns (constant, increasing, or decreasing frequency throughout the call). The most common patterns used by Weddell seals are constant duration for both elements and intervals, and decreasing frequency. Calls with constant rhythm patterns tend to have the same duration. Overall, Weddell seals mainly produce vocalizations of stable duration and stable rhythm patterns.

Moors and Terhune (2004) suggested several functions for the regular repetition of elements in Weddell seal calls. Repetition may enhance the detectability of calls in environments with high levels of background noise. Second, it may increase the ability of conspecifics to predict successive elements in the calls. Third, it may allow for individual or species recognition. Finally, it may provide information on the emotional state of the individual emitting the call. These functions are consistent with the assessment/management approach developed by Owings and Morton (1998). This approach states that individuals that can successfully assess reliable cues and manage the behaviors of conspecifics will have a greater reproductive success. However, more behavioral research is needed to obtain stronger evidence of the functional role of ritualized vocalizations in Weddell seals.

Problem Statement and Objectives

The great diversity in reproductive habitats and strategies of phocids makes them appropriate subjects for studying the evolution of breeding strategies of mammals that mate at sea. Given that all aquatically mating pinnipeds produce underwater vocalizations, studying these species can also provide insights on the role of vocalizations in animal reproduction.

Vocalizations in terrestrial species of mammals and birds have been intensively studied (e.g. Tyack 1999; Rogers & Kaplan 2002:70-127), but information on aquatic species is much more limited. Most studies that have been conducted on Weddell seals and other pinnipeds suggest that vocalizations play a role in mating, are also often associated with greater reproductive success, and would therefore be favored by sexual selection. However, previous studies have not clearly determined the behavioral and social contexts of vocalizations produced by individuals. The purpose of this study was to increase our knowledge of reproductive strategies in pinnipeds, and of interactions between vocalizations, behaviors, and social contexts during the reproductive season of animal species mating at sea.

I compared the relative frequencies (% of all vocalizations or behaviors) of each vocalization and behavior type produced by male and female Weddell seals during the mating season. Second, I investigated differences in these frequencies based on the social context (e.g. presence, number, and sex of conspecifics within the territory and in the breathing hole, presence of free-ranging females versus captured females, etc.). I also identified patterns of vocalizations and behaviors to help determine the behavioral context of calls and assess the degree of ritualization of Weddell seal displays. I tested the following hypotheses: roar-like vocalizations, especially trills, are male-specific; trills are the most frequent vocalization type produced by the territorial male; chirps and mews are submissive, but growls are aggressive; finally, Weddell seal displays are stereotyped.

METHODS

Data Collection

The data were collected in McMurdo Sound, Antarctica (Fig. 1), October–December 2002, by researchers who conducted a parallel study on hunting and diving behaviors and energetics of free-ranging Weddell seals (e.g. Davis et al. 2003). An artificial breathing hole of 1.5 x 2.75 m was drilled in the ice 1.2 km from Tent Island. A research hut with a trap door was placed above this hole. Weddell seals hauling out on the ice along the Southwestern shore of Ross Island were captured, sedated, and transported into the research hut. Video cameras and recorders of dive depth, swim speed, heart-rate and tail strokes were mounted on the head and back of these free-ranging seals. After an 18-hour recovery period, seals were released into the artificial breathing hole located under the hut. In less than 24 hours after release, the captured individuals exhibited dives similar to free-ranging individuals (Davis et al. 2003). Captured seals were returned to their original site after 4 or 5 days of study.

Figure 1. Map of the U.S. stations in Antarctica. The data were collected near the McMurdo station. Seals were captured on the ice along the southwestern shore of Ross Island, along the Ross Sea. From the National Science Foundation, Polar Programs, UV Monitoring Network, by Biospherical Instruments Inc.

For the specific study of social and vocal interactions in Weddell seals, data on both free-ranging and captured individuals were used. One free-ranging male, named Pink (pink tag 841), established its territory around the artificial hole and stayed from 12 October 2002–10 December 2002. This male became the focal male of the study. Two free-ranging females, referred to as Yellow 1 (yellow tag 1346) and Yellow 2 (yellow tag 1575) often entered the territory of the focal male. None of these females were ever observed in the company of pups. The captured individuals consisted of three males and seven females (Table 1).

Table 1. Morphology of the captured seals.

Seal	Gender	Mass (kg)	Length, straight (cm)
A3	Male	392.4	238
A4	Male	426.6	239
A5	Male	512	259
S27	Female	459.2	232
S28	Female	466.6	245
S29	Female	559.8	253.5
S30	Female	461.6	240.5
S31	Female	476	244
M1	Female	366.6	224
M2	Female	435.6	253

Vocalizations were recorded with a general-purpose hydrophone (Reson TC 4032, frequency response: 5 Hz−120 kHz) that was suspended underwater, 6 m below the ice cover, and centered below the artificial breathing hole. The hydrophone was connected to an audio amplifier (Reson EC 6070), itself connected to an MP3 player-recorder (Creative Nomad Jukebox, sampling rate: 44 kHz) and to a VHS recorder.

Video recordings were obtained from both an underwater camera (Pisces Design, Inc.) that was suspended 15 m below the ice cover and centered below the artificial hole, and a camera placed above the hole. Video recordings were stored on VHS tapes with a Sony videocassette recorder. A total of 102 hours of recordings (51 two-hour recordings) were made on 26 different days from 25 October–5 December 2002. However, only 92 hours had both video and audio recordings. For two hours of these recordings, the camera was not well placed below the hole, making behavioral observations and individual identification impossible. Additionally, a problem was encountered when encoding four hours of these recordings into MPEG2 files. Therefore, only 86 hours of recordings were analyzed: 38 hours recorded by the underwater camera only, and 48 hours simultaneously recorded by the camera below the ice (24 hours) and by the camera above the ice (24 hours).

Classification of Vocalizations and Behaviors

Several classifications of Weddell seal vocalizations can be found in the literature (Terhune et al. 1994, 2001; Pahl et al. 1997). Thomas and Kuechle (1982) established the most detailed repertoire using frequency range, duration, repetition rate, number of elements per series, auxiliary sound usage, and harmonics, as criteria for classification of vocalizations. However, some calls lie along a continuum, and since I identified calls only by listening to them without the help of acoustic software, a simple classification was essential to limit sources of error. Terhune et al. (2001) proposed an alternative categorization system that includes only four main call types. Modifying Terhune et al.'s classification, I defined eight vocalization types that I grouped into two main categories: event calls (short duration) and state calls (long duration). Event calls last less than 2 sec and include chirps, jaw claps, knocks not associated with trills, growls, mews and whistles. Their duration was not recorded. However, I noted unusual duration for growls and mews (i.e. unusually short or unusually long). State calls last more than 2 sec and include trills associated with knocks, and trills not associated with knocks. Trills are characterized by a decrease in frequency.

I classified behaviors as swimming (i.e. "arrive", "leave", "swim toward the hole", "swim away from the hole", "swim toward a seal", or "swim away from a seal"), biting, breathing deeply, making bubbles, or resting. These behaviors are not exclusive. Therefore, I grouped them into two main categories: event and state behaviors. This system allows behaviors to be exclusive within each category. Event behaviors (e.g. "bite", "breathe deeply", and "bubble") are short-lasting and were always scored, even if a state behavior was concurrently occurring. State behaviors (e.g. all swimming behaviors and resting) are long-lasting. They were scored when the behavior was initiated and every time there was a change. The time at which the state behavior ended was also noted. I also made a distinction between arriving (or leaving) the hole and swimming toward (or away) from the hole. An individual arriving (or leaving) the hole had to be rapidly swimming into the hole (or out of view) following a relatively straight line. On the other hand, an individual swimming toward (or away from) the hole was swimming more slowly, not necessarily into the hole (or out of view), and was not following a straight line.

Data Extraction

I used a Sony videocassette recorder to play the VHS tapes. This recorder was linked to an external Canopus MPEG encoder that converted the VHS recordings into MPEG2 files using MediaCruise software. The MPEG2 files were then played back with The Observer Video-Pro 5.0, developed by Noldus. Advantages of The Observer Video-Pro 5.0 are described by Eckhardt and Waterman (2004). While watching the videos with The Observer, I noted the following information:

1. the time at which a seal produced a vocalization or exhibited a behavior,
2. the location of the seals (e.g. not on the screen, on the screen, in the breathing hole),
3. the sex of the individuals seen on the screen,
4. the identity of the individual seen on the screen when individual markings could be observed from the video recordings (especially from the above water recordings),
5. the type of vocalizations produced by individuals on the screen, or at close proximity to the hydrophone (e.g. very loud vocalizations),
6. the number of vocalizations in series when a series of chirps, jaw claps, or knocks was recorded,
7. the type of behaviors exhibited by individuals on the screen,

8. the direction of swimming (e.g. toward or away from the breathing hole, toward or away from a given seal),

9. if the behavior was biting, the part of the conspecifics body that was bitten (e.g. neck, fore flippers, hind flippers, or genital parts).

Data Analyses

I used The Observer Video-Pro 5.0 to obtain the overall total number of each vocalization and behavior type that was scored throughout the study period. I also computed the overall percentage of each vocalization and behavior type for males (including the territorial male), females, and seals whose sex was not identified, as well as for the focal male (e.g. Pink) and the wild female that was frequently observed in Pink's territory (e.g. Yellow 1).

To assess the effect of social context on the frequencies of vocalizations and behaviors, I divided the data into 15-min intervals and determined the social context for each of these intervals based on the identity of the seals that were observed or heard during the 15-min interval. I assumed that a seal had left the territory 30 min after its last behavior or vocalization was recorded. This assumption seemed reasonable based on the research on diving behavior of Weddell seals, where most dives have been found to last less than 30 min (Kooyman 1981; Davis et al. 2003). Therefore, if a seal did not return into, or close to the breathing hole within 30 min, it probably left the territory. I used six of the social context categories for analyses: “Pink”, “Male”, “CF”, “FF”, “2FF” and

"3FF" (Table 2). "Pink" meant that only Pink was present in its territory. "Male" and "CF" respectively meant that one captured male or one captured female was present in the territory, in addition to Pink. Finally, "FF", "2FF" and "3FF" respectively meant that one free-ranging female (e.g. Yellow 1), two free-ranging females (e.g. Yellow 1 and Yellow 2) or three free-ranging females (e.g. Yellow 1, Yellow 2, and a third female) were present in the territory, in addition to Pink.

Table 2. Total number of 15-min intervals in the original data.

Social context	Number of 15-min intervals
Pink	9
Male	15
CF	40
FF	93
2FF	59
3FF	9

I randomly selected 15 "Male", "CF", and "FF" intervals and nine "Pink", "FF", "2FF", and "3FF" intervals. For each of these intervals, I computed with Excel 2003 and SPSS 12.0.1 the mean frequency (% of all vocalizations or behaviors) and standard error for each vocalization and behavior type produced by Pink and by Yellow 1. I also obtained for each social context category the mean number of vocalizations per series and standard error for chirps, jaw claps, and knocks that were produced in series by Pink. At α=0.05, I found no significant differences between the social contexts “CF” and “FF” in the mean frequency of each vocalization and behavior type produced by Pink, nor in the mean number of vocalizations per series emitted by Pink. Therefore, “CF” and “FF” intervals were pooled together under the new social context “Female”. I compared the mean frequencies of each vocalization and behavior type, as well as the mean numbers of vocalizations per series for Pink, in the following situations: “Male” versus “Female”, and “Pink” versus “FF” versus “2FF” versus “3FF”. The same statistics were compared for the vocalizations and behaviors of Yellow 1 for “FF” versus “2FF” versus “3FF”. The distribution of the data were tested for normality using the Shapiro-Wilk test when degrees of freedom ≤ 50, or the Kolmogorov-Smirnov test when degrees of freedom > 50. In all cases, the data were not normally distributed. Therefore, I performed Kruskall-Wallis tests when I compared more than two social contexts and Mann-Whitney U tests when I compared only two social contexts. Mann-Whitney U tests were also used as post-hoc tests when needed.

I used the software Theme, designed by Noldus, to identify associations between vocalizations and behaviors produced by Weddell seals. This software uses a unique pattern detection algorithm to detect and analyze relationships in time-based data. I determined the social context for each two-hour recording based on the seals that were observed during these two hours: “male”, “captive female”, or “free-ranging female(s)”. Recordings that were assigned the same social context were pooled together and were considered as one sample for analysis by Theme. I also performed a search for patterns using each two-hour recording as a separate sample. The minimum number of times a pattern had to occur within a sample to be detected by Theme was set to 5, and the maximum accepted probability of any critical interval relationship to occur by chance alone was set to 0.05. The following search parameters were also included: (1) the lumping factor was set to 0.90; (2) the Fast Approximate Redundancy Reduction (FARR) was set to 90; (3) the "Exclude frequent event types" was set to 2.00; and (4) the simulation filter was activated. Consider the pattern AB formed by event A and event B. If N_{AB}/N_A was greater than the lumping factor, with N being the number of times a pattern or an event occurred, then A was eliminated. Similarly, if N_{AB}/N_B was greater than the lumping factor, B was eliminated. In both cases though, the pattern AB was added to the list of detected patterns. FARR corresponds to the maximum percentage of occurrences a newly-detected pattern may start and end at the same times as a pattern that has already been detected. If this percentage was exceeded, the new pattern was deleted. The "Exclude frequent event types" value corresponds to the number of standard deviations from the mean frequency above which events are excluded from the search process. Finally, when the simulation filter is activated, Theme tests every significant pattern AB by simulation before accepting it: events A are kept in the order they were recorded, whereas events B are randomized 200 times. Theme searches for patterns in the new data set. If the number of patterns AB detected in the new data set /200 is < 0.05, then the pattern AB from the real data set is accepted. The patterns that were detected were not submitted to further statistical analyses. Instead, they helped in determining the behavioral context of the vocalizations emitted by Weddell seals, and in discussing the degree of ritualization and sexual selection of vocal and behavioral displays.

RESULTS

Single Vocalizations and Behaviors: Sex Differences

A total of 10,474 vocalizations and 3,831 behaviors were scored during this study. Chirps were the most common vocalization, and only 0.17% of the vocalizations that were scored could not be identified or categorized within the established system of classification (Table 3). Resting and swimming behaviors were the most frequently observed behaviors, with seals mainly swimming toward or away from the breathing hole rather than toward or away from another seal (Table 4).

I found obvious sex differences in the use of vocalizations by Weddell seals when comparing the overall frequencies of each vocalization type produced by males and females (Fig. 2). Mews, growls, knocks, and trills associated or not with knocks, were almost exclusively emitted by males. These same differences were observed in the repertoires of Pink and Yellow 1, with the vocalizations of Yellow 1 being limited to chirps and jaw claps (Fig. 3). On the other hand, behavioral frequencies were very similar for both sexes (Fig. 4), and more specifically for Pink and Yellow 1 (Fig. 5).

Table 3. Number of vocalizations per type recorded during the study.

Vocalization type	Number
Chirps	6,431
Mews	1,077
Growls	885
Jaw claps	567
Knocks	548
Trills	524
Whistles	270
Trills + Knocks	154
Unknown	18
Total	10,474

Table 4. Number of behaviors per type recorded during the study.

Behavior type	Number
Rest	983
Swim toward hole	739
Swim away from hole	656
Arrive	490
Leave	523
Swim toward seal	100
Swim away from seal	38
Bite	89
Breathe	18
Bubble	106
Total	3,831

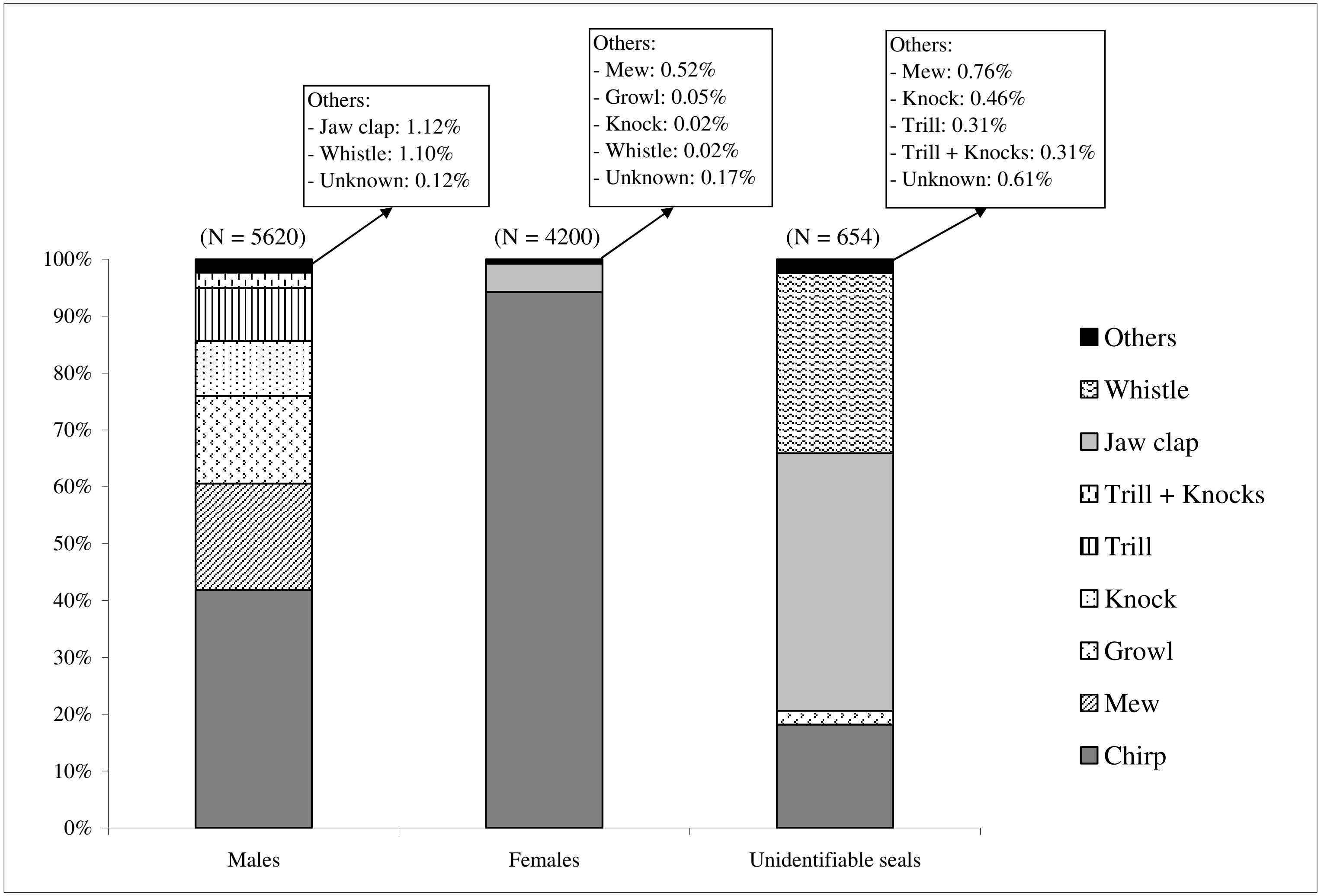

Figure 2. Overall frequencies of each vocalization type produced by males (including Pink), females, and unidentified seals. Vocalization types for which frequencies were < 2% were summed and grouped under the category "Others".

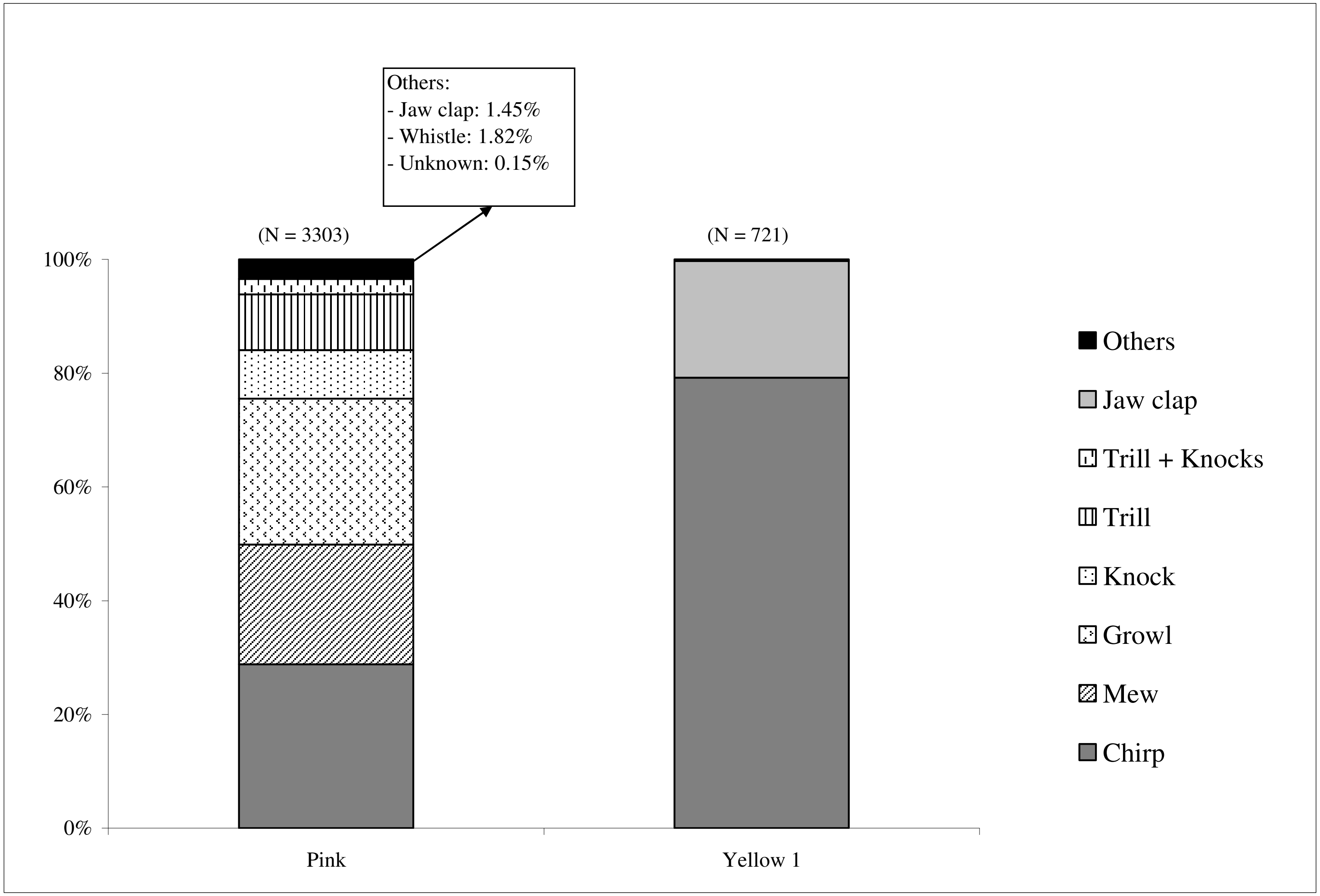

Figure 3. Frequencies of each vocalization type produced by the focal male Pink and the most frequently observed free-ranging female Yellow 1. Vocalization types for which frequencies were < 2% were summed and grouped under the category "Others".

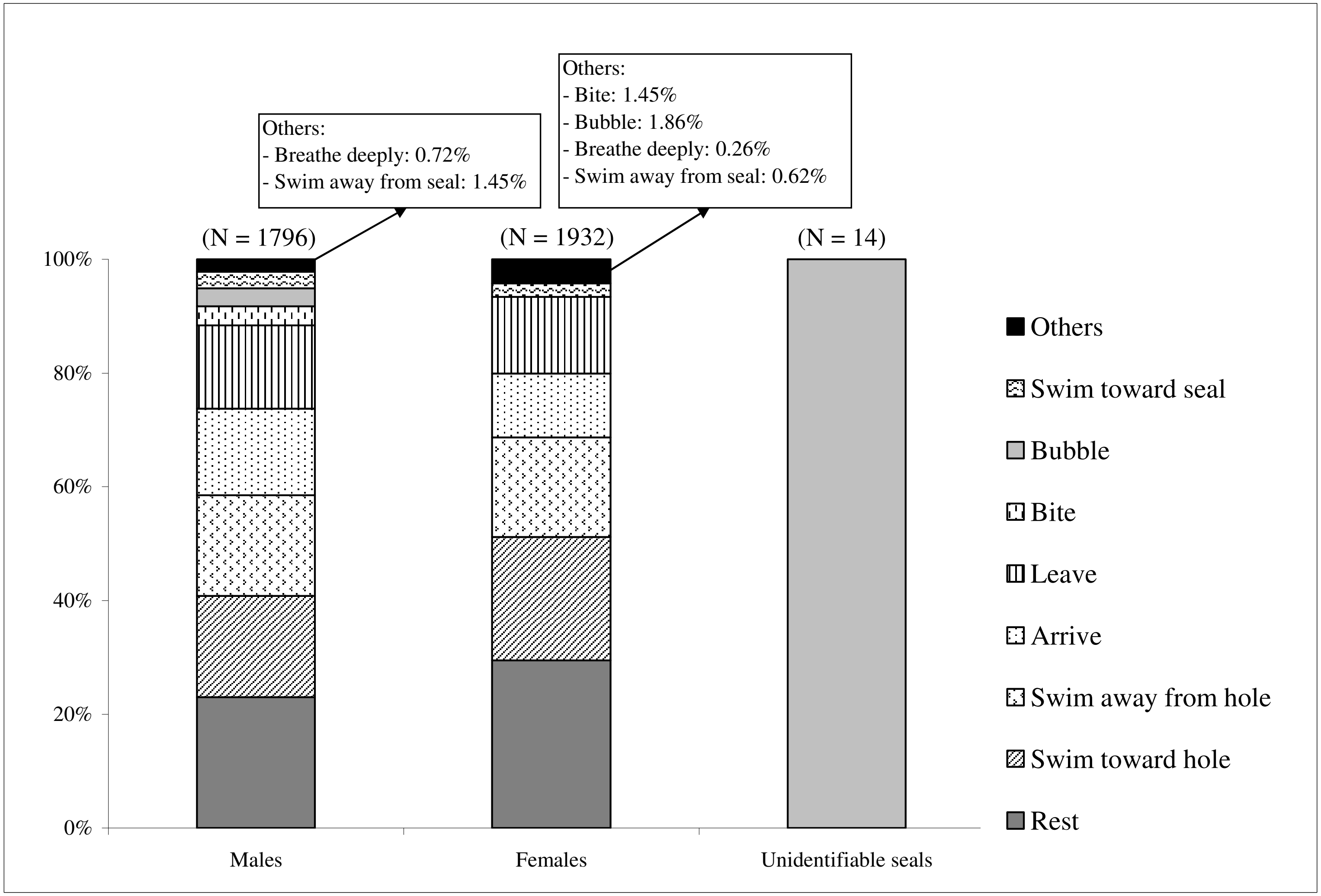

Figure 4. Overall frequencies of each behavior type produced by males (including Pink), females, and unidentified seals. Behavior types for which frequencies were < 2% were summed and grouped under the category “Others”.

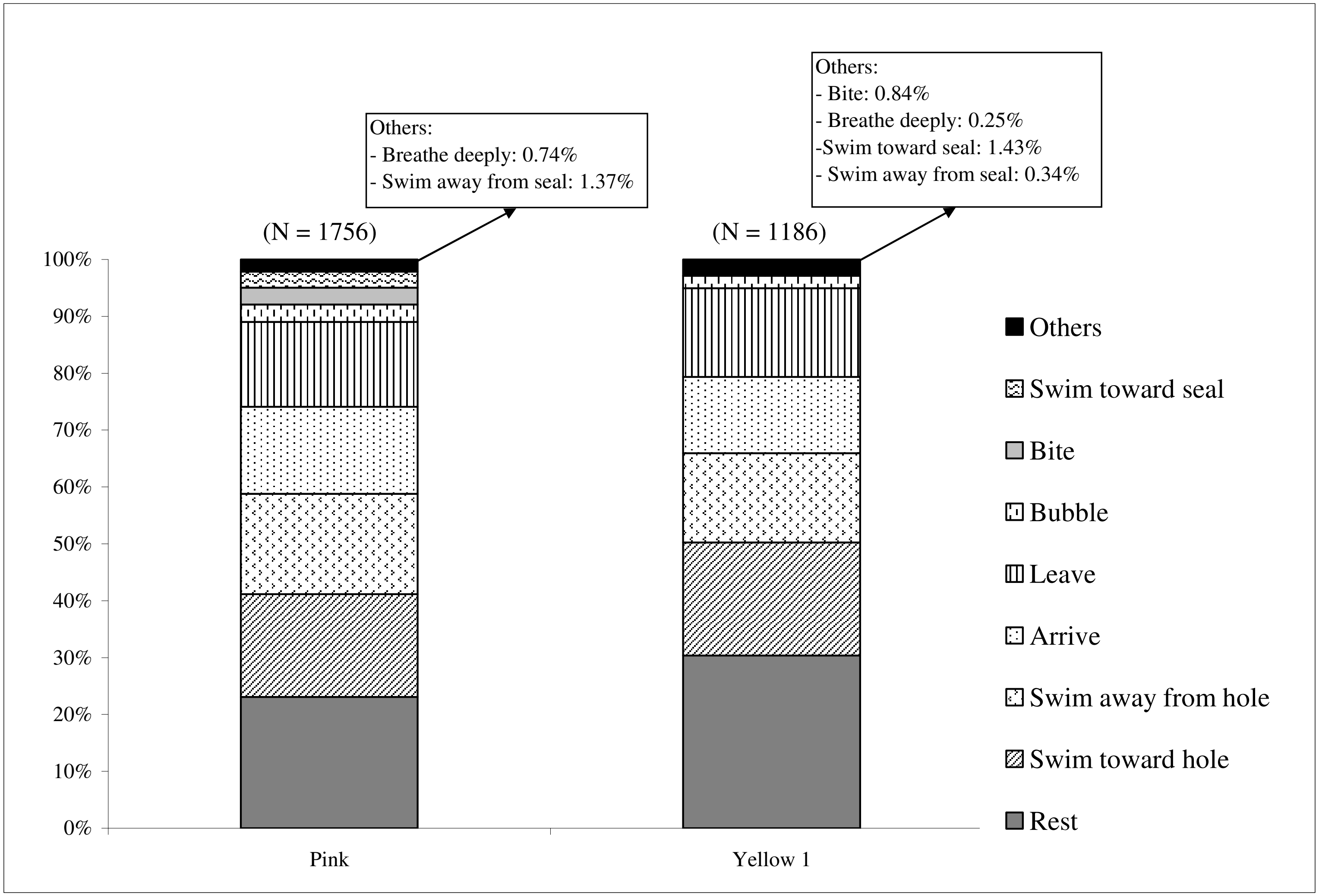

Figure 5. Frequencies of each behavior type produced by the focal male Pink and the most frequently observed free-ranging female Yellow 1. Behavior types for which frequencies were < 2% were summed and grouped under the category “Others”.

Effects of Social Context on Vocal and Behavioral Frequencies

Effect of the Sex of Seals Present in the Territory.--Statistical analyses showed that the sex of the conspecifics present in the territory of the focal male affected the frequencies at which Pink emitted chirps, growls, knocks, mews, trills associated with knocks, and whistles (Mann-Whitney U tests, $N1 = N2 = 15$ for all tests: for chirps: $U = 59.5$, $P = 0.028$; for mews: $U = 58.5$, $P = 0.015$; for growls: $U = 32.5$, $P = 0.0007$; for knocks: $U = 65.5$, $P = 0.020$; for trills associated with knocks: $U = 82.5$, $P = 0.035$; for whistles: $U = 77$, $P = 0.047$; for jaw claps: $U = 88$, $P = 0.118$; for trills: $U = 79$, $P = 0.143$). Pink emitted chirps more often when a male was present in the territory, whereas growls, knocks, mews, trills associated with knocks, and whistles were more frequent when a female was present (Table 5). The mean number of vocalizations per series, however, did not change whether the other seal was a male or a female (Mann-Whitney U tests for chirps: $U = 1987.5$, $N1 = N2 = 64$, $P = 0.536$; for jaw claps: $U = 29$, $N1 = N2 = 8$, $P = 0.798$). No tests were performed on the number of knocks per series, or knocks associated with trills because sample sizes were < 3.

Table 5. Mean frequencies per 15-min interval and standard errors of each vocalization type produced by Pink when a male or a female was present in its territory. Significant differences are indicated by an asterisk (*).

Vocalization type	Frequency (% of all vocalizations by Pink) X – SE	
	Male	Female
Chirps *	52.98 – 9.50	26.92 – 3.83
Mews *	8.13 – 5.34	19.96 – 4.51
Growls *	7.61 – 3.49	33.22 – 7.46
Knocks *	8.30 – 4.24	5.82 – 2.31
Trills + Knocks *	0	1.89 – 0.97
Whistles *	0.51 – 0.51	2.05 – 0.78
Jaw claps	8.30 – 4.24	0.16 – 0.16
Trills	8.27 – 3.93	9.98 – 2.22

The sex of the conspecifics present in the territory also affected the frequency at which Pink arrived into and left the breathing hole (Mann-Whitney U tests, $N1 = N2 = 15$ for all tests: for "arrive": $U = 62$, $P = 0.028$; for "leave": $U = 59.5$, $P = 0.020$; for "swim toward hole": $U = 98.5$, $P = 0.512$; for "swim away from hole": $U = 91.5$, $P = 0.313$; for "swim toward seal": $U = 112.5$, $P = 1.000$; for "swim away from seal": $U = 97.5$, $P = 0.150$; for "rest": $U = 73$, $P = 0.093$; for "bite": $U = 90$, $P = 0.073$; for “breathe”: $U = 112.5$, $P = 1.000$; for “bubble”: $U = 105$, $P = 0.317$). Pink arrived into and left the hole more often when a female was present in its territory (Table 6).

Table 6. Mean frequencies per 15-min interval and standard errors of each behavior type produced by Pink when a male or a female was present in its territory. Significant differences are indicated by an asterisk (*).

Behavior type	Frequency (% of all behaviors by Pink) X – SE	
	Male	Female
Rest	15.55 – 4.21	23.87 – 3.55
Swim toward hole	10.85 – 3.53	8.98 – 4.00
Swim away from hole	10.15 – 3.41	6.80 – 3.53
Arrive *	8.97 – 3.90	21.69 – 3.68
Leave *	11.76 – 6.81	29.55 – 4.35
Swim toward seal	1.41 – 1.18	1.90 – 1.30
Swim away from seal	0.85 – 0.58	0
Bite	6.62 – 3.99	0
Breathe	0	0
Bubble	0.51 – 0.51	0

Effect of the Presence and Number of Females in the Territory.--Kruskall-Wallis tests showed that the presence of free-ranging females in the territory of Pink affected the frequency at which Pink produced mews and growls (for mews: $H3 = 11.91$, $P = 0.008$; for growls: $H3 = 16.10$, $P = 0.001$; for chirps: $H3 = 5.32$, $P = 0.150$; for knocks: $H3 = 4.52$, $P = 0.211$; for trills associated with knocks: $H3 = 3.41$, $P = 0.333$; for whistles: $H3 = 3.18$, $P = 0.365$; for jaw claps: $H3 = 3.00$, $P = 0.392$; for trills: $H3 = 7.67$, $P = 0.053$). Pink emitted more mews and growls when females were present than when it was alone in its territory (Table 7). However, the frequency of mews and growls from Pink did not significantly differ based on the number of females in the territory (Mann-Whitney U tests, $N1 = N2 = 9$ for all tests: "FF" versus "2FF": $U = 28.5$, $P = 0.284$ for mews and $U = 35$, $P = 0.624$ for growls; "FF" versus "3FF": $U = 31$, $P = 0.397$ for mews and $U = 19$, $P = 0.057$ for growls; "2FF" versus "3FF": $U = 39.5$, $P = 0.928$ for mews and $U = 22$, $P = 0.100$ for growls). The number of chirps per series produced by Pink was not affected by the presence of free-ranging females in its territory, nor by the number of females (Kruskall-Wallis test for "Pink" versus "FF" versus "2FF" versus "3FF": $H3 = 5.85$, $P = 0.119$). No tests were performed on the number of jaw claps per series, knocks or knocks associated with trills because sample sizes were < 3.

Table 7. Mean frequencies per 15-min interval and standard errors of each vocalization type produced by Pink in the social contexts “Pink”, “FF”, “2FF” and “3FF”. Significant differences are indicated by an asterisk (*).

Vocalization type	Frequency (% of all vocalizations by Pink) X – SE			
	“Pink”	“FF”	“2FF”	“3FF”
Chirps	38.89 – 16.20	25.46 – 5.83	39.99 – 11.82	8.93 – 5.14
Mews *	0	20.62 – 5.39	12.49 – 4.20	15.47 – 6.55
Growls *	0	14.36 – 4.86	19.83 – 5.98	44.86 – 12.41
Knocks	1.85 – 1.85	5.12 – 2.25	6.72 – 3.03	9.91 – 4.03
Trills + Knocks	0	1.72 – 1.27	0.95 – 0.64	1.89 – 0.97
Whistles	1.85 – 1.85	1.36 – 0.90	0.51 – 0.51	2.59 – 1.48
Jaw claps	0	0	2.47 – 1.12	1.39 – 1.39
Trills	1.85 – 1.85	9.14 – 2.32	6.44 – 1.84	4.67 – 2.33

Furthermore, the presence or number of free-ranging females in the territory of Pink did not have any effect on its behavioral frequencies (Kruskall-Wallis tests for “arrive”: $H3 = 2.40$, $P = 0.494$; for “leave”: $H3 = 1.81$, $P = 0.612$; for “swim toward hole”: $H3 = 6.17$, $P = 0.103$; for “swim away from hole”: $H3 = 4.77$, $P = 0.189$; for “swim toward seal”: $H3 = 6.17$, $P = 0.104$; for “swim away from seal”: $H3 = 0.00$, $P = 1.000$; for “rest”: $H3 = 2.88$, $P = 0.410$; for “bite”: $H3 = 0.00$, $P = 1.000$; for “breathe”:

$H3 = 2.06$, $P = 0.560$; for “bubble”: $H3 = 6.19$, $P = 0.103$). It is important to note that no biting from Pink was scored when free-ranging females were present in its territory (Table 8).

Table 8. Mean frequencies per 15-min interval and standard errors of each behavior type produced by Pink in the social contexts “Pink”, “FF”, “2FF” and “3FF”.

Behavior type	Frequency (% of all behaviors by Pink) X – SE			
	“Pink”	“FF”	“2FF”	“3FF”
Rest	19.44 – 6.51	28.35 – 3.78	17.25 – 4.45	26.71 – 4.24
Swim toward hole	3.44 – 2.28	14.19 – 3.89	24.89 – 10.97	21.53 – 6.18
Swim away from hole	6.88 – 4.57	12.80 – 4.20	9.37 – 4.49	21.44 – 5.65
Arrive	19.18 – 5.91	24.18 – 4.70	13.46 – 4.66	14.95 – 5.84
Leave	17.72 – 7.20	20.48 – 4.43	15.04 – 4.34	9.68 – 4.64
Swim toward seal	0	0	0	1.78 – 1.19
Swim away from seal	0	0	0	0
Bite	0	0	0	0
Breathe	0	0	0.74 – 0.74	1.85 – 1.85
Bubble	0	0	8.15 – 8.15	2.06 – 1.25

Yellow 1, which often entered the territory of Pink during the breeding season, produced jaw claps only when Yellow 2 and a third free-ranging female were simultaneously present in the territory (X – SE = 18.66 – 7.95, $N = 9$). On the other hand, the frequency of chirps emitted by Yellow 1 remained unaffected by the number of other females in the territory (Kruskall-Wallis test: $H2 = 3.13$, $P = 0.209$). The frequencies of behaviors exhibited by Yellow 1 did not significantly differ either (Kruskall-Wallis tests: for “arrive”: $H2 = 1.98$, $P = 0.372$; for “leave”: $H2 = 5.61$, $P = 0.061$; for “swim toward hole”: $H2 = 0.77$, $P = 0.680$; for “swim away from hole”: $H2 = 0.64$, $P = 0.727$; for “swim toward seal”: $H2 = 4.15$, $P = 0.125$; for “swim away from seal”: $H2 = 2.00$, $P = 0.368$; for “rest”: $H2 = 4.79$, $P = 0.091$; for “bite”: $H2 = 4.15$, $P = 0.125$; for “breathe”: $H2 = 0.00$, $P = 1.000$; for “bubble”: $H2 = 1.04$, $P = 0.595$).

Patterns of Vocalizations and Behaviors

Theme detected many patterns, several of which were redundant. Some patterns were single-actor patterns, meaning that only one seal was involved, others were multi-actor, meaning that two or more seals were involved. I selected only eight patterns to discuss in this paper. Pattern 1 shows that Pink often emitted growls when a female was leaving or swimming away from the breathing hole (Fig. 6). Patterns including this specific sequence of behaviors and vocalizations were detected a total of 16 times, in three recordings. Pink also emitted mews as Yellow 1 arrived or was resting in the breathing hole (Fig. 7). This second pattern was detected 18 times, in three recordings. Patterns 3 and 4 show that Pink often emitted trills either before arriving into the breathing hole, or after leaving it (Figs. 8 and 9). The arrival of Pink was preceded by the production of trills 89 times, in 12 recordings, whereas its departure was followed by trills 51 times, in seven recordings. Also, females present in the breathing hole were found to leave the hole after Pink emitted a trill 20 times, in three recordings, as illustrated by pattern 5 (Fig. 10). Patterns 6 and 7 show that the trills emitted by Pink were often associated with other vocalization types. Pink's trills were followed by single knocks 16 times, in three recordings (Fig. 11), whereas mews, or combinations of mews, preceded Pink's trills 113 times, in 18 recordings (Fig. 12). Finally, when samples belonging to the same social context were pooled together, results from Theme revealed only one pattern of interest (Fig. 13). This pattern shows Pink coming into the breathing hole after Yellow 1 had left. This sequence was detected 64 times throughout the study period. Patterns are shown as tree diagrams, with each leaf of the tree describing an event type according to the following format: name of the seal producing the vocalization or behavior, vocalization or behavior type, location of the seal, and in some cases, comment on the duration of the vocalization.

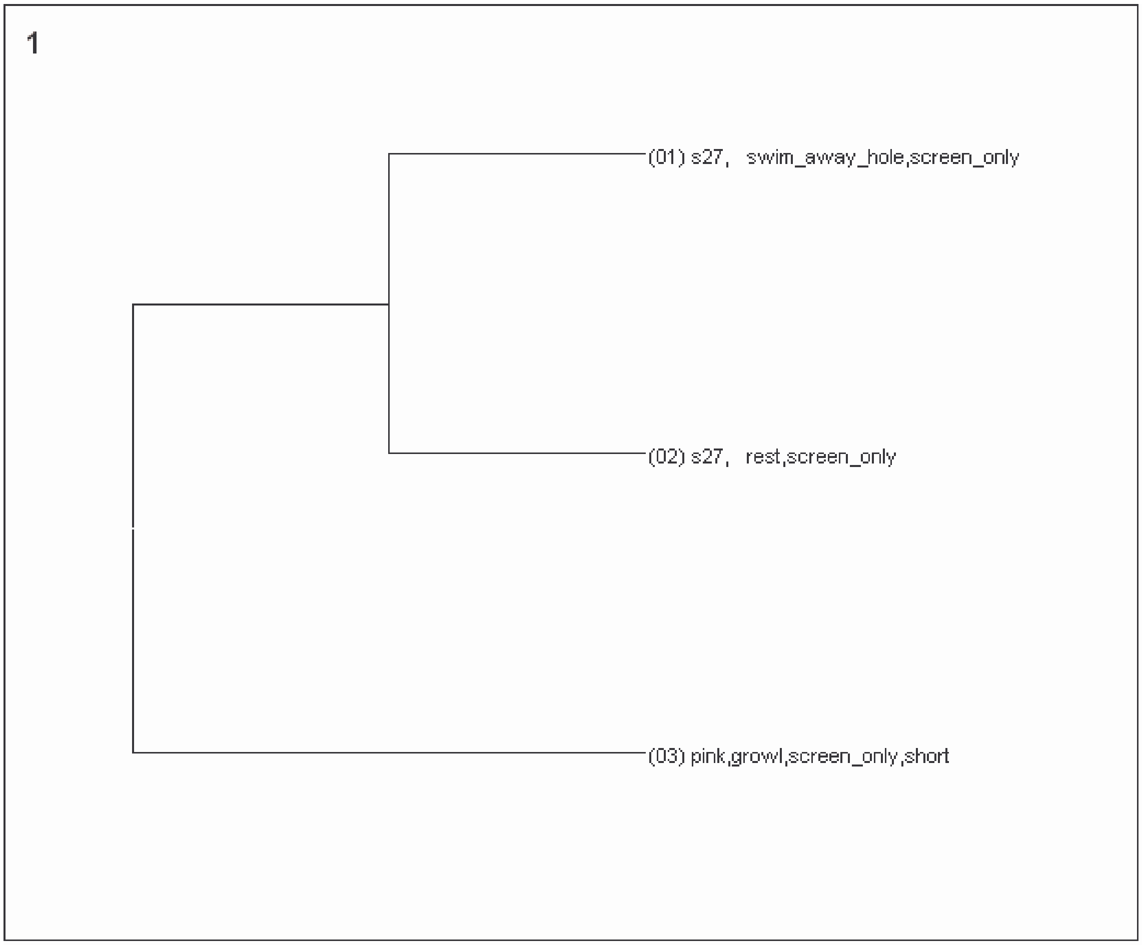

Figure 6. Tree diagram for pattern 1: Pink emits a growl as a female leaves or swims away from the breathing hole. The numbers in parentheses indicate the order of occurrence.

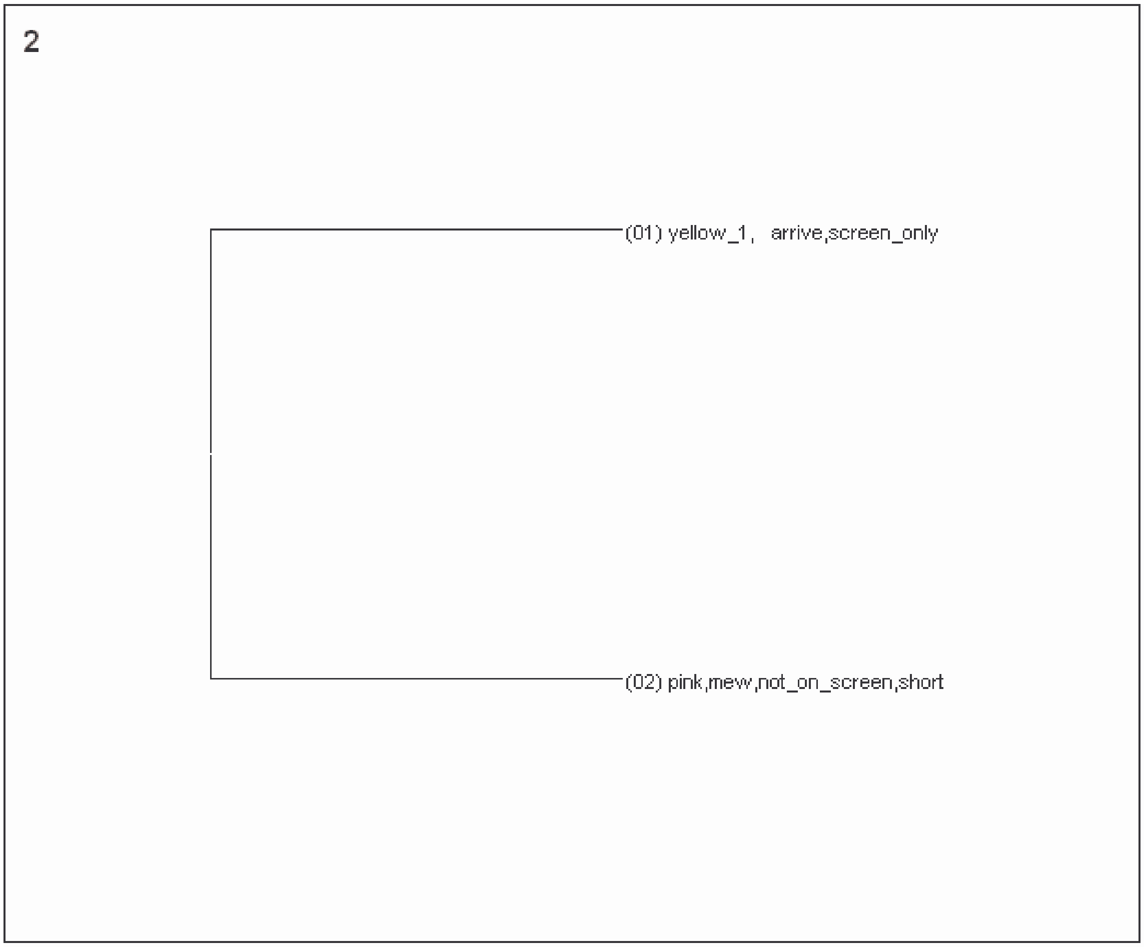

Figure 7. Tree diagram for pattern 2: Pink emits a mew when Yellow 1 arrives into or rests in the breathing hole. The numbers in parentheses indicate the order of occurrence.

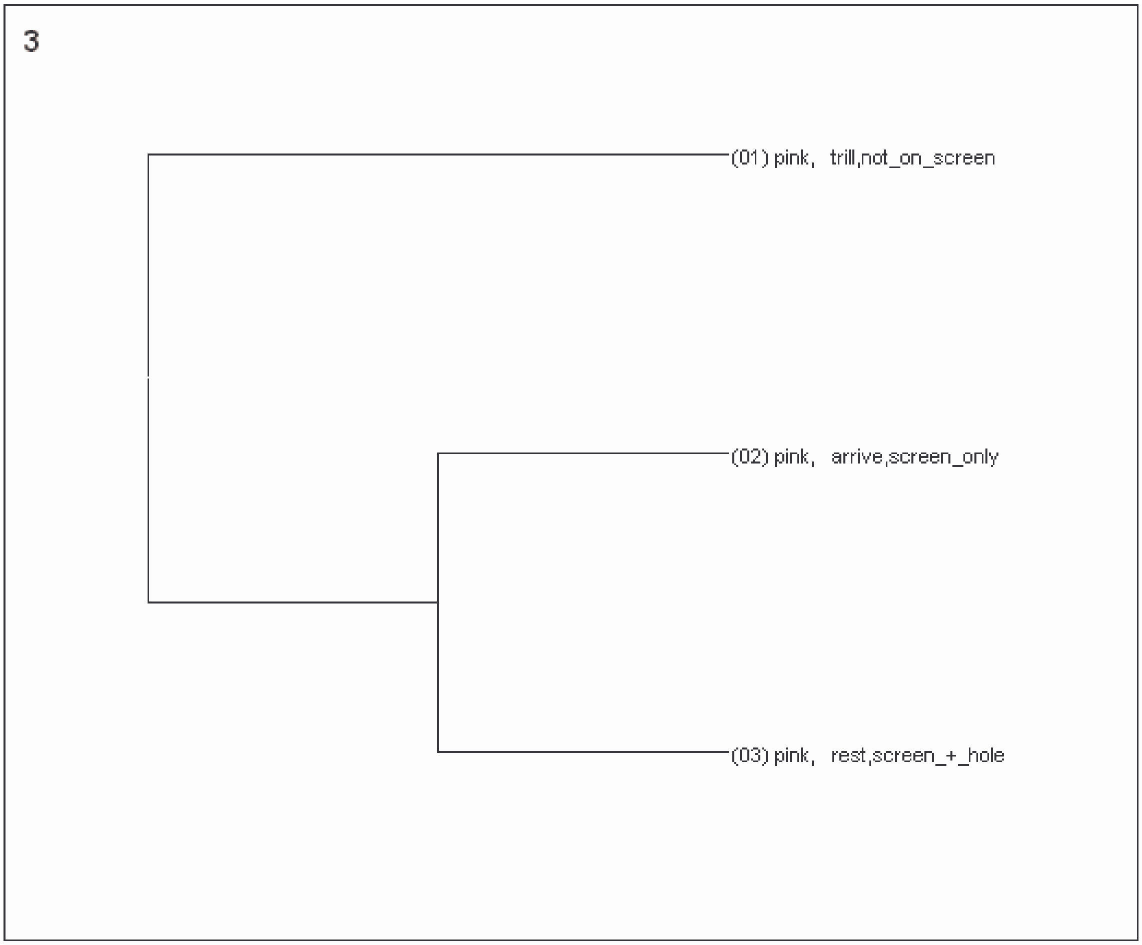

Figure 8. Tree diagram for pattern 3: Pink emits a trill before arriving into the breathing hole. The numbers in parentheses indicate the order of occurrence.

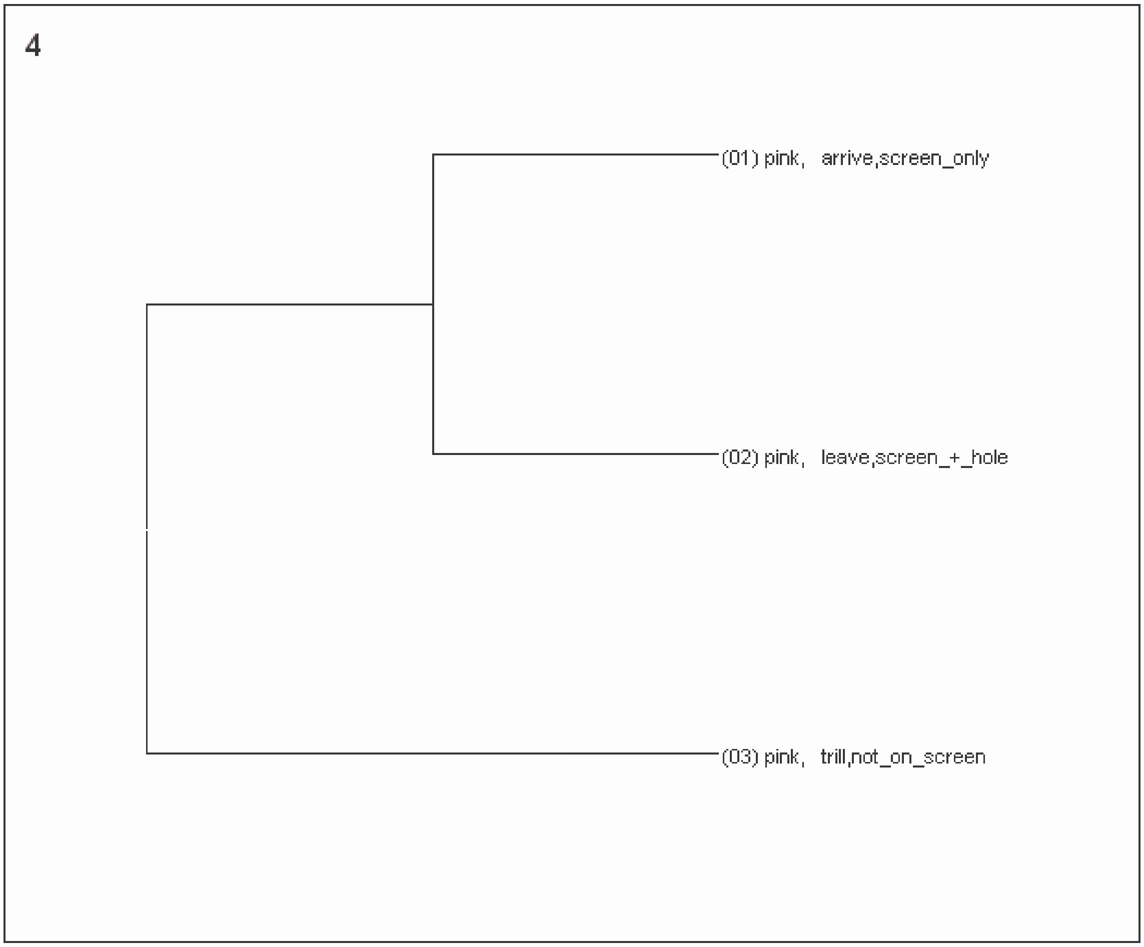

Figure 9. Tree diagram for pattern 4: Pink emits a trill after leaving the breathing hole. The numbers in parentheses indicate the order of occurrence.

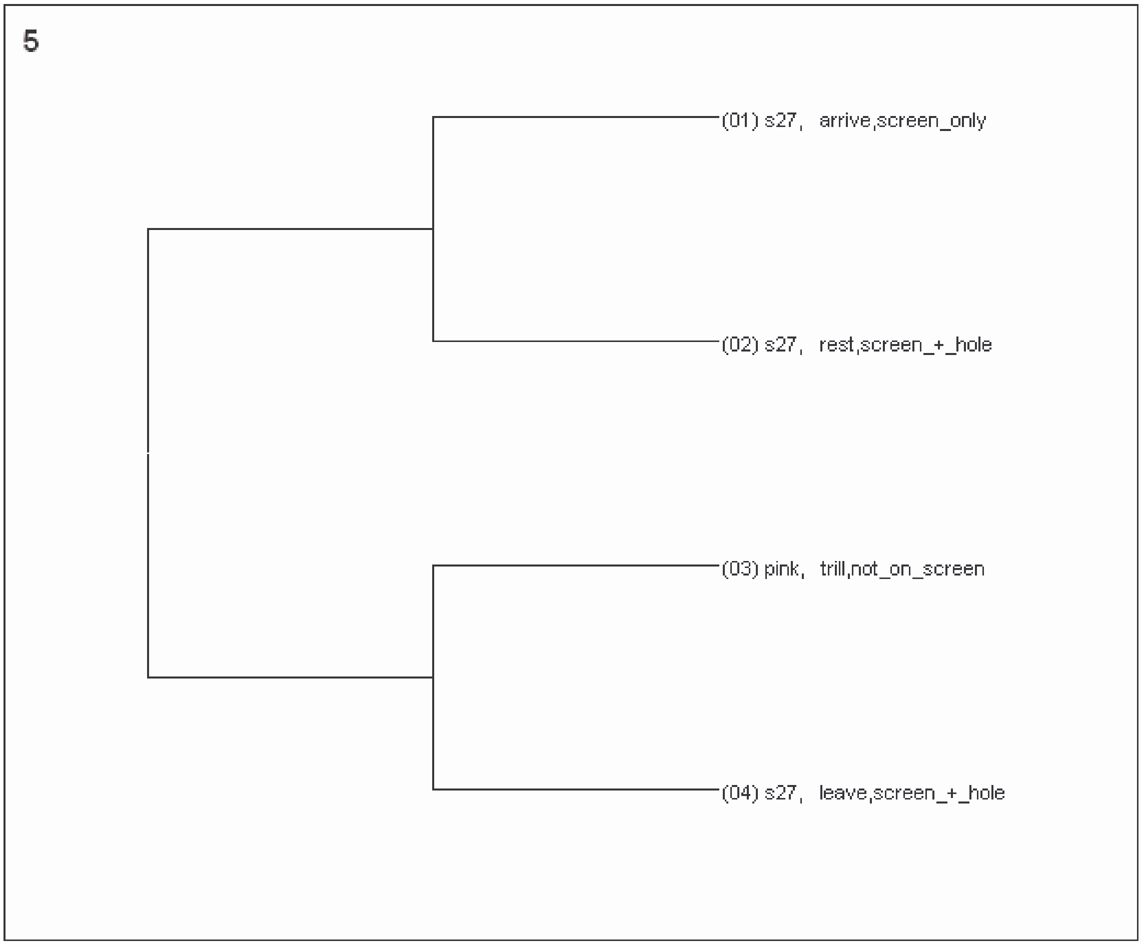

Figure 10. Tree diagram for pattern 5: a female leaves the breathing hole after Pink emitted a trill. The numbers in parentheses indicate the order of occurrence.

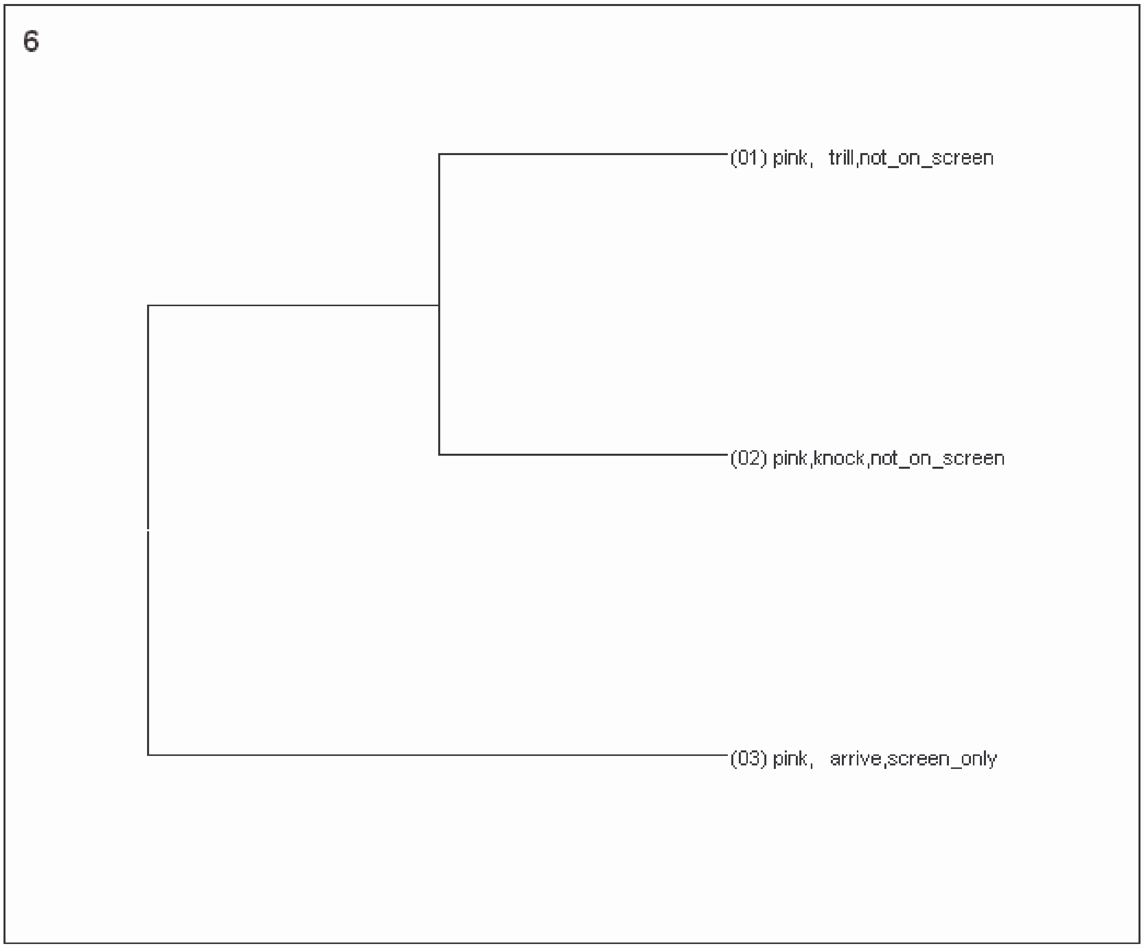

Figure 11. Tree diagram for pattern 6: Pink produces a single knock after a trill. The numbers in parentheses indicate the order of occurrence.

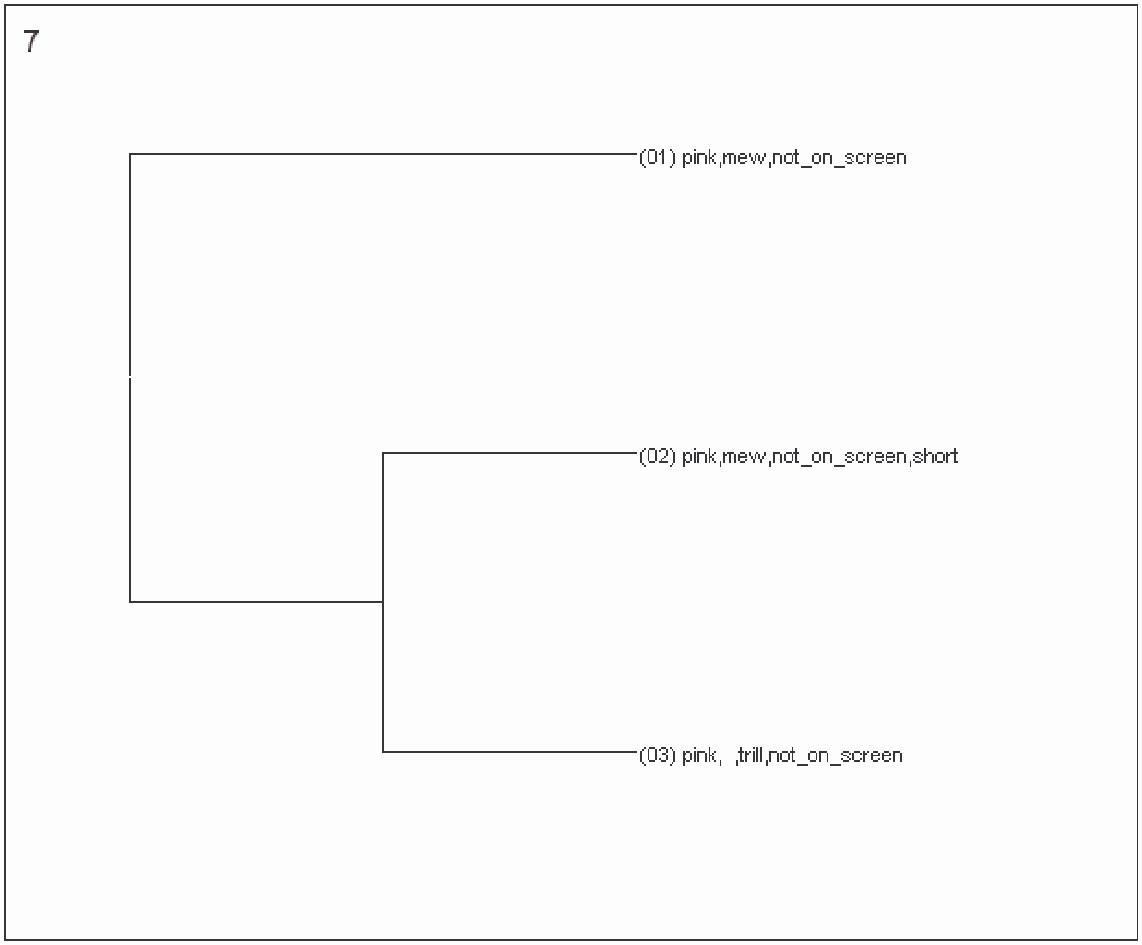

Figure 12. Tree diagram for pattern 7: Pink produces a mew or a combination of mews before a trill. The numbers in parentheses indicate the order of occurrence.

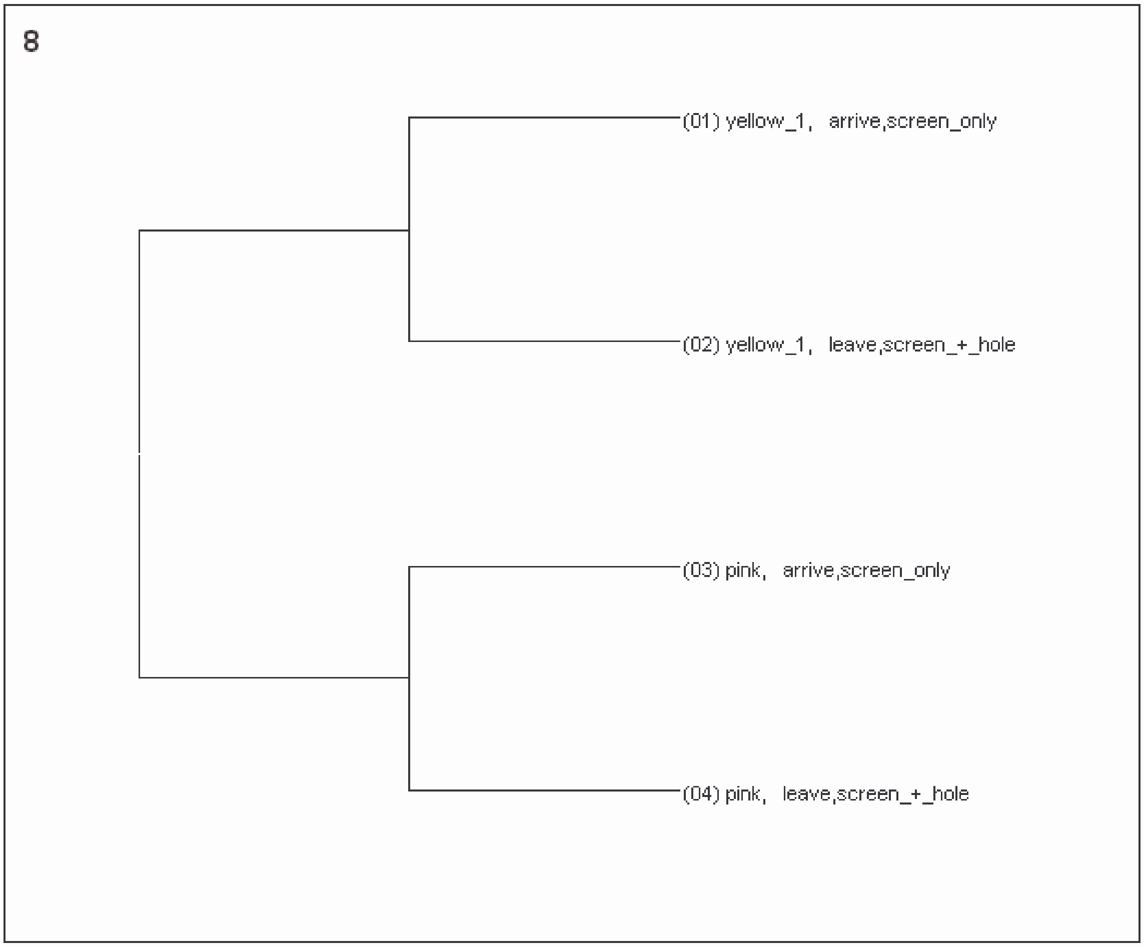

Figure 13. Tree diagram for pattern 8, detected within the “free-ranging female(s)” recordings: Pink arrives into the breathing hole after Yellow 1 left. The numbers in parentheses indicate the order of occurrence.

DISCUSSION AND CONCLUSIONS

A relatively simple system of classification was used to score Weddell seal calls in this study. This system included a limited number of vocalization types that were defined by a few simple characteristics because the acoustic properties of each call were not measured. The number and attributes of these vocalization types appeared to be sufficient to efficiently categorize Weddell seal calls as only a small percentage of the recorded vocalizations could not be identified according to this system. However, the degree of confidence in categorizing vocalizations could have been increased if the scoring had been performed by more than one observer.

Chirps were found to be the most common vocalization overall. Chirps are not sex-specific: they are produced by both male and female Weddell seals. Watkins and Schevill (1968) found that chirps were often produced by seals swimming from one breathing hole to another. They suggested that the function of chirps was related to inquiry and navigation. Findings from my study support Watkins and Schevill's hypothesis. With the exception of close-range interactions, chirps may be produced by Weddell seals on a constant basis simply to maintain contact between conspecifics, inform each other of their location, and could also be used as directional cues (Kooyman 1981).

Male and female Weddell seals appeared to use different vocal repertoires. Females produced primarily chirps and jaw claps, whereas mews, growls, knocks and trills were almost exclusively emitted by males. Only a small percentage of these latter vocalizations were attributed to females or unidentified seals. It is likely that if vocalizing seals could be identified with more certainty, mews, growls, knocks, and trills would have been attributed to males only. These observations are consistent with findings from previous research on Weddell seal underwater calls (Thomas & Kuechle 1982) and surface calls (Oetelaar et al. 2003).

Not surprisingly, the frequencies of several vocalization types emitted by the territorial male Pink were affected by the following social parameters: the sex of the conspecifics present in Pink's territory, and the presence of free-ranging females (versus Pink being alone), independently of their number. What was surprising, however, was how these social parameters affected the frequencies of Pink's vocalizations. First, Pink emitted chirps more often when a male was present in its territory. It has been suggested that chirps were submissive vocalizations (Thomas et al. 1983; Thomas 1991). However, this interpretation does not explain the results from this study. All encounters between Pink and the males that were released into the breathing hole resulted in violent fights, even though they did not last long. In every case, the released males ended up permanently leaving Pink's territory. Therefore, it is unlikely that Pink was acting and vocalizing submissively during, and immediately following these encounters. As mentioned earlier, chirps might be used by Weddell seals to maintain contact with each other and obtain directional cues. It is possible that the increase in chirp frequency emitted by Pink when another male was present in its territory conveyed a warning message instead, informing the intruder that the area they entered was an established territory, and that this territory was actively defended by its owner. Moreover, high-pitched calls have been found to be part of highly-aggressive displays in South American sea lions (Fernàndez-Juricic et al. 2003). In close-range aggressive interactions between Weddell seals, chirps, which are high-pitched vocalizations, might serve a similar function when emitted by territorial males.

Second, Pink produced growls, knocks, mews, trills, and whistles at a higher frequency when a female (versus a male) was present in its territory. Similarly, growls and mews from Pink were more frequent when one or more free-ranging females were present (versus Pink being alone). It is also important to remember that all these vocalizations were found to be almost exclusively produced by males. Owings and Morton (1998) developed an approach they called the assessment/ management approach. This approach states that individuals that can successfully assess reliable cues and manage the behaviors of conspecifics will have a greater reproductive success. It also predicts that roar- and growl-like vocalizations will be favored by sexual selection because they are indicators of the body size and resource-holding potential of the males emitting the vocalization (Schusterman & Van Parijs 2003). In the view of Morton and Owing's ideas, it is reasonable to suggest that male-specific vocalizations in Weddell seals, which are affected by social context, evolved because they provide cues for females to assess the fitness of the vocalizing males, and opportunities for males to influence mate choice by females. This approach would also explain some of the patterns that were detected by Theme, such as Pink emitting growls while a female leaves the breathing hole, Pink producing mews as Yellow 1 arrives into the hole, mews preceding Pink's trills, or single knocks following them. What the territorial male may try to do in such situations is to get the attention of females and provide them with reliable cues so that they can evaluate its quality. Combining these vocalizations would increase its chances of being chosen as a mate because it would provide females with even more reliable information. These vocalizations, or sequences of vocalizations, might advertise the good health of the male, as well as its superior status, maturity and learning skills (Rogers 2003). They might also give additional cues on the emotional state of the territorial male (Owings and Morton 1998).

The sequences of vocalizations and behaviors described previously are examples of ritualized displays because they include a limited number of components and some attention-getting components, and are repeated over time (Bradbury and Vehrencamp 1998b). Other ritualized patterns were detected by Theme, such as Pink announcing its arrival into or departure from the breathing hole by a trill, females leaving the hole after Pink produced a trill, or Yellow 1 and Pink taking turns to breathe in the hole. Similar patterns had been observed in a previous study in McMurdo Sound (Watkins & Schevill 1968). One needs to recall that breathing holes constitute an important resource for Weddell seals. Fighting with females for access to the breathing hole would likely reduce the mating success of the territorial male. However, giving up access to the breathing hole in favor of a female might decrease the chance of survival of the territorial male and the reproductive success of the female. Therefore, sexual selection would favor the evolution of stereotyped advertisement displays and behavioral patterns that would reduce the risk of conflict between a territorial male and a female over access to the breathing hole. Moreover, the artificial breathing hole used in our study was located a couple of hundred meters away from another breathing hole. Perhaps Pink was using that hole as an alternative place to breathe. Stereotypy was also observed when a given vocalization was produced in series. The mean number of chirps per series produced by Pink was not affected by the sex of the seal present in its territory, nor by the presence or number of free-ranging females. This result was expected in regards to previous research on stereotypy of vocalizations in Weddell seals. Moors and Terhune (2004) showed that, overall, Weddell seals mainly produce vocalizations of stable duration and stable rhythm patterns. They also suggested several functions for the regular repetition of elements in Weddell seal calls. Our findings tend to support the following hypothesis: the number of vocalizations per series produced by a given seal remains relatively constant because it helps in individual recognition, and would therefore not be affected by social context. However, the repetition rate might change depending on the level of background noise (Terhune et al. 1994). In male Australian fur seals, the production of series of barks was also found to provide information on the identity of the caller (Tripovich et al. 2005). Ritualized vocal and behavioral patterns, as well as stereotyped series of vocalizations, likely evolved to ensure that a given signal or pattern would not be confused with another signal (Rogers & Kaplan 2002:1-25), to provide reliable information (Owings & Morton 1998), and to limit conflicts (Schusterman & Van Parijs 2003).

Vocal repertoires greatly differed between male and female Weddell seals, and the frequencies of the vocalizations produced by the territorial male were affected by social context. On the other hand, frequencies of behavior types remained very similar between sexes and were largely unaffected by social context. Two hypotheses could explain these results. First, underwater behaviors of Weddell seals might be dictated by the physiological needs of the individuals, especially for breathing. Oxygen stores have been found to be directly proportional to the body mass of the individuals (Pabst et al. 1999). Therefore, it is assumed that a male and a female with the same body mass have similar oxygen stores. Second, Weddell seal vision can be limited in the underwater environment depending on the environmental conditions, such as the thickness of the ice cover (Kooyman 1981). This implies that underwater behaviors, unless they involve physical contact with a conspecific (e.g. fights and copulation), might not provide useful cues for females to assess male fitness. Therefore, behaviors might be less likely to affect reproductive success, which would limit the potential for evolution of sex-specific behaviors or sex-specific behavioral time-budgets. However, a couple of remarks need to be made here. It was found that Pink came and left the breathing hole more often when a female was present in its territory. It is possible that this change reflected an increase in "patrolling" frequency to defend the resource that the breathing hole represents. However, aggressive behaviors from Pink (e.g. biting) were rarely observed toward captured or free-ranging females that were present in the hole; whereas, Pink often bit and violently fought with the released males. It is more likely then that coming and leaving the hole more frequently when a female was present was a way for Pink to increase the probability of encounters with females. Finally, none of the free-ranging females were observed in the company of pups. Behavioral and vocal responses by females with pups should be expected to differ from what was observed in this study as

Kooyman (1981) reported aggressive advertisements from females with pups toward males or other females if they approached too closely.

Male and female Weddell seals observed during this study showed differences in the use of vocalization types. Social context, especially the sex of the conspecifics present in the territory, affected the frequencies of the vocalizations emitted by the territorial male, but not the frequencies of its behaviors. Finally, the stereotyped number of chirps per series produced by the focal male, and the patterns that were detected suggest that the vocalizations and behaviors used by Weddell seals during the reproductive season might be ritualized to some degree. Given the small sample sizes, the findings from this study should be considered with caution though, and cannot be generalized to the whole species. However, I hope these results, and the proposed interpretations, showed the benefits of using an evolutionary-based model of communication in studying the role of vocalizations in animals, such as the assessment/management approach developed by Owings and Morton (1998). I also hope these findings will be used a basis for further studies, such as playback experiments. Observing the responses of seals to played-back calls from territorial and nonterritorial males, from reproductive and non-reproductive females, would help in determining whether vocalizations are the only cues used by Weddell seals to assess and manage conspecifics during the breeding season. Moreover, genetic studies to evaluate the reproductive success of males could also be conducted. Identifying correlations between vocalization characteristics and reproductive success of male Weddell seals would strongly support the hypothesis that male-specific vocalizations provide information on male quality and are used by females to choose their mates, and are therefore favored by sexual selection.

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2002-2003	Undergraduate exchange student program (ISEP), Southwestern University, Georgetown, TX “Licence” in Biology of organisms, 3rd year undergraduate French degree, home institution: University of Rennes 1, France
2000-2002	“DEUG” in Life Sciences, 2nd year undergraduate French degree, options in Ecology, Ethology and Animal communication, University of Rennes 1, France

Research experience

Spring 2004	Research intern for the Marine Mammal Research Program, Texas A&M University, Galveston, TX. Influence of habitat and shrimping on feeding behavior of bottlenose dolphins (*Tursiops truncatus*) in the Galveston Bay Estuary, Texas - Paula Moreno’s Ph.D. project.
Spring 2003	Research in Biopsychology class, Southwestern University, Georgetown, TX. Social and vocal interactions in Weddell seals (*Leptonychotes weddellii*).
Fall 2002	Ecology class, Southwestern University, Georgetown, TX. Peaks of activity and synchrony in the Lesser snow goose (*Anser caerulescens caerulescens*).
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Honor societies

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