HUMPBACK WHALE (*MEGAPTERA NOVAEANGLIAE*) COMMUNICATION: THE CONTEXT AND POTENTIAL FUNCTIONS OF PEC-SLAPPING BEHAVIOR ON THE HAWAI'IAN WINTERING GROUNDS

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ABSTRACT

Humpback whales display a variety of percussive behaviors that may function as communication between conspecifics. Pectoral-fin slapping behavior is commonly observed in a variety of marine mammals including seals, dolphins, and humpback whales. Data from 5-years of behavioral observations of humpback whales on the Hawaiian wintering grounds were compiled and analyzed. Overall findings suggest pec-slapping behavior is dependent on the performer's age class, sex, and social role. Adult females appear to pec-slap in competition groups in efforts to encourage competition from surrounding males, indicating her readiness to mate. Adult males pec-slap while disaffiliating from other males, possibly in attempts to maintain a non-agonistic male association. Subadult pec slapping is likely a form of "play", an important characteristic in the development, coordination, and learning in young mammals. These discoveries can serve as tools to enhance the interpretation of humpback whale social behavior, and provide a model for understanding other percussive behaviors.

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LIST OF ABBREVIATIONS

Presumed Gender	Behavioral Role	Abreviation	Description
Female	Mother	**M**	An adult-sized whale remaining in closest proximity to a calf often making contact with it
	Nuclear Animal	**NA**	The lone adult-sized female in a group with more than 1 adult male; often identified by her proximity to the primary escort
Male	Single Escort	**E**	A lone adult-sized male accompanying a mother and her calf
	Primary Escort	**1E**	The male positioned closest to a mother often between her and one or more other adult males. The 1E often performs head lunges, linear bubble trails, and chasing (see Baker & Herman, 1984) while attempting to defend the position next to the female
	Secondary Escort	**2E**	A second adult male with a mother and calf who is not the primary escort
	Nuclear Primary Escort	**N1E**	The male positioned closest to the nuclear animal, often between her and and one or more other adult males. The N1E often performs head lunges, linear bubble trails, and chasing (see Baker & Herman, 1984) while attempting to defend the position next to the female
	Nuclear Secondary Escort	**N2E**	A second adult male with nuclear animal not occupying the primary escort position
	Singer	**S**	A whale producing song which appears to attenuate when surfacing
	Adult and Singer	**A/S**	A whale that was observed both singing and not singing
Either	Calf	**C**	A whale very small in size (4 - 5.5 m) usually accompanied by its mother
	Yearling	**Y**	A whale which appears too large to be a calf (8 - 10 m) but continues to behave like a calf towards its mother
	Juvenile	**J**	A whale too large to be a calf, small in size (10 - 12 m), and no longer accompanied by its mother
	Subadult	**SA**	Any whale classified as a C, Y, or J (is presumed to be sexually immature)
	Adult	**A**	A whale which appears to be full grown (greater than 12 m) but does not match any of the descriptions above (may or may not be sexually mature)
	Dyad Adult	**DA**	An adult-sized whale observed together with one other adult whale

LIST OF ABBREVIATIONS (Cont.)

Abbreviation	Description
MC	Mother and calf
MCE	Mother, calf, and a single escort
MCx**E**	Mother, calf, and more than one (x) escort competing with the primary escort
1A	Single adult
2A	A dyad (2 adults), usually male/female, occasionally both are male but rare
x**A**	More than 2 adults (x), usually a single female with competing males, occasionally all males but this is rare (Clapham et al., 1992; pers. obs)

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1 INTRODUCTION

1.1 Overview

Humpback whales (*Megaptera novaeangliae*) display a variety of behaviors on the wintering grounds that may function as communication between conspecifics. Some of these behaviors, termed “surface-active”, are visible from the water’s surface. Surface-active behaviors involve a portion of the whale’s body temporarily rising above the water before crashing back down onto its surface. Of all the baleen whales, humpbacks are considered one of the most surface-active and acrobatic (Leatherwood, Caldwell, & Winn, 1976), and are often seen performing a variety of these aerial behaviors. The contexts in which these behaviors are performed are numerous. However, the role they play in communication remains uncertain (Whitehead, 1985).

Humpback whale physiology is somewhat unique among the baleen whales in that humpbacks possess exceptionally long “pectoral fins” (Figure 1), sometimes referred to as “flippers”. These pectoral fins can extend more than 4-m (Tomilin, 1967; True, 1904) which can be up to a third of the whale’s adult body length. The pectoral fins provide humpbacks with exceptional underwater maneuverability (Edel & Winn, 1978; Nishiwaki, 1972; Tomilin, 1967) and may also assist with thermoregulation (Felts, 1966; Kanwisher & Sundnes, 1966; Scholander & Shevill, 1955). Humpbacks will use their pectoral fins to herd fish during feeding bouts (Howell, 1970). Also, mothers and their offspring may use their pectoral fins to establish physical contact during pair-bonding, and males in competition have been observed to wrap their pectoral fins around another male or female (Pack, Herman, Craig, Spitz, & Deakos, 2002; Pack et al., 1998). Principal escorts will often extend their pectoral fins out to the sides when in competition, causing them to brake suddenly and sink backwards into the water as they attempt to strike the whale behind them with their tail flukes (pers. obs.) Additionally, pectoral fins can also be used to manipulate and investigate objects in their surroundings (pers. obs.).

Most of these pectoral fin behaviors occur below the water's surface. However, the most recognizable use of the pectoral fins above the water is during percussive behavior when a whale extends its pectoral fin high into the air and then strikes down onto the surface of the water. This "pectoral-fin slapping" behavior or "pec-slapping" behavior as will be referred to in this paper, is not only impressive visually but is audible in air for at least several hundred meters around the whale. Although countless lay observers and researchers of humpbacks have observed them pec-slapping, the function of this behavior remains poorly understood (Clapham, 2000).

The aim of the current study was to develop a better understanding of pec- slapping behavior of humpback whales in their wintering grounds. It begins by reviewing some basics in communication while outlining the costs and benefits of various types of communication in a marine environment. The biology and social behavior of humpback whales on their wintering grounds is described followed by an examination of likely known methods of communication utilized by humpbacks given their physiology and social biology.

1.2 Communication

In the animal kingdom, communication with conspecifics occurs for a variety of reasons: to solicit food from parents, display threats between opponents during conflict, deter predators, warn others of danger, attract members of the opposite sex, etc. (Dugatkin & Reeve, 1998). Communication has been described as "an action by one organism that alters the behavior pattern of another organism in a fashion that is adaptive to either one or both of the participants" (Wilson, 1975). This occurs when a signal originating from a sender, either intentionally or unintentionally, is detected and processed by one or several receivers. The signal is generally a conspicuous and often stereotyped behavior that is noticeably different from other events and tends to communicate the internal state and possibly the intention of the sender (Pryor, 1986).

A communication signal can take many forms and can be influenced by several factors: the sender's intention, the type of environment through which the signal must traverse, and the physiological mechanisms available for producing and receiving the signal. For example, the sender may wish to target one specific receiver (private), or several receivers (group) at one time. The distance a signal must travel, how long it needs to persist in the environment in order to be detected, and the urgency of the message are all important variables that will shape a signal (Sebeok, 1977).

1.2.1 Communication in the Marine Environment

Signals that are best adapted to the environment in which the animal lives will be naturally selected. Signals produced in the ocean will transmit differently than those produced on land. Among marine mammals, adaptation to a strictly marine environment has favored a primary sensory modality based on sound production and reception (Wood, 1973). Other modalities, such as the sense of smell, are diminished or even absent (Caldwell & Caldwell, 1972a). The available sensory channels that are utilized by marine mammals today are acoustic, tactual, visual, and chemical (gustatory) (M. C. Caldwell & D. K. Caldwell, 1977; Winn & Schneider, 1977). Except for the bottlenose dolphin (*Tursiops truncatus*) (Herman, 1980) and California sea lion (*Zalophus californianus*) (Thomas, Kastelein, & Supin, 1992), few studies have examined in any detail, the sensory capabilities of most marine mammals.

1.2.1.1 Acoustic Signals

Sound travels about 3.6 times faster underwater (1,230 m/s) than in air (340 m/s). Sounds can be heard over great distances, especially if the signals are loud and produced at depth (Rogers & Kaplan, 2000). Large whales can efficiently use very low-pitched sounds to communicate over kilometers (Clark, 1990; Mobley, Herman, & Frankel, 1988). Sounds allow for rapid transmission of information, and have the potential for a large range of information by manipulating the frequency and amplitude of the signal. Sound signals are, however, usually of short duration and otherwise energetically expensive (Ryan & Wilczynski, 1988; Wells & Taigen, 1989). Sound signals are usually indiscrete allowing unintended receivers to pick up the signal, they can sometimes be hard to localize, and can be masked by surrounding noise.

Most marine mammals are known to produce sounds (Evans, 1967), but little is known about the types of information that are carried within these sounds. Whistles produced in bottlenose dolphins have been shown to carry information about the identity of individuals (Caldwell & Caldwell, 1965), as well as context-related information (Janik, Dehnhardt, & Todt, 1994). Among some species such as elephant seals (*Mirounga angustirostris*), females in estrous are known to produce a copulation call that incites aggressive competition between males (LeBoeuf, 1974). Acoustic signals can be produced vocally or by percussion.

1.2.1.2 Visual Signals

Visual signals have the advantage of being easily localizable, however, like acoustic signals, they may be subject to “eavesdroppers.” Under the sea, light conditions and visibility can vary considerably, restricting the visual sense to short distances in reliably clear environments. In bottlenose dolphins, it has been shown that vision both in air and underwater is highly developed (Herman, Peacock, Yunker, & Madsen, 1975). Visual signals in mammals generally consist of body coloration, body postures, and movements (Rogers & Kaplan, 2000). Many body postures are used as visual displays during competition and courtship (D. K. Caldwell & M. C. Caldwell, 1977).

1.2.1.3 Tactual Signals

Direct physical contact is an excellent modality for the immediate transfer of information to a recipient. The signal is discrete and easy to locate (Krebs & Davies, 1997). The type and location of a tactile signal can be quite variable and has the ability to carry much information. The signal is limited, however, to very short ranges and is not compatible with communicating to multiple recipients at once.

Dolphin skin has been shown to be richly innervated (Simpson & Gardner, 1972) suggesting touch is an important sensory modality. Touch seems to be an important component for reinforcing pair-bonding in both odontocetes (Evans & Bastian, 1969) and mysticetes (pers. obs.), but can also be used in aggressive contexts during fighting or disciplining conspecifics (D. K. Caldwell & M. C. Caldwell, 1977).

1.2.1.4 Chemical Signals

Chemical signals are believed to be one of the oldest types of signals among animal species. The use of pheromones in water, if the water is still, will spread by diffusion over short distances. Currents can also carry pheromones over very long distances, enabling communication with multiple recipients. The different volatilities of the chemical components in the signal may also provide information on the age of the signal (Kennedy & Marsh, 1974). The propagation direction of the chemical signal, however, is limited to the direction of the current (Rogers & Kaplan, 2000). Additionally, localization can be difficult (Gerhardt, 1983). Chemical signals that degrade quickly through dilution in a marine environment are less suited for long distance communication. They may, however, be effective in communicating to nearby neighbors. Chemical signals are limited in repertoire since they tend to be rather stereotyped.

In marine mammals, chemical sources such as urine and feces can carry tremendous information about the immediate hormonal condition and physiological state of an animal, and possibly assist in individual recognition (Caldwell & Caldwell, 1967; Kuznetsov, 1978; Norris & Dohl, 1980).

1.2.1.5 Percussive Signals

Percussive signals are unique because they carry a visual, acoustic, and possibly a tactile component to the signal. These signals are commonly produced by a body part while making forceful contact with a surface. These types of signals are common among terrestrial species, including certain mammals. Banner-tail kangaroo rats (*Dipodomys spectabilis*) will foot-drum to communicate ones' identity to neighbors (Randall & Stevens, 1987); and male gorillas will engage in chest-beating during threat displays towards other males (Schaller, 1963).

In marine mammals, these signals can occur through "slap sounds". At the surface of the water, slap sounds are produced by aerial displays; below the water, they are the result of two surfaces being struck against each other. These behaviors are believed to serve a communicatory function (Clark, 1983; Nachtigall, Au, Pawloski, Andrews, & Oliver, 2000; Silber, 1986; Thompson, Cummings, & Ha, 1986; Tyack & Whitehead, 1983; Wahlberg, Lunneryd, & Westerberg, 2002) .

The acoustic component of these signals is typically broadband, intense, and of short duration (Clark, 1983; Thompson et al., 1986). Some researchers attribute these displays as partially due to “aggression” or “disturbance” (D. K. Caldwell & M. C. Caldwell, 1977).

Striking a part of the body onto the water’s surface can also produce air-borne and seismic vibrations. These vibrations may create movements of water very close to the signaler, which may be effective for short-range signals (Krebs & Davies, 1997). However, these signals appear to be energetically expensive and would suffer extreme attenuation.

1.3 Humpback Whale Biology and Behavior

Humpback whales are a cosmopolitan species. They are found in high latitudes during the spring, summer, and autumn months where they feed (Chittleborough, 1958, 1965; Dawbin, 1966). In winter, they migrate to low latitude waters where mating and calving activities take place, and where feeding is rare or absent (Chittleborough, 1965; Dawbin, 1966; Lockyer, 1981).

The Hawaiian islands are the major wintering grounds for North Pacific humpback whales, where as many as 5,000 to 6,000 whales aggregate each year (Calambokidis et al., 2000). Whales depart the feeding grounds in late autumn and begin to arrive in Hawaiian waters in early December. Lactating females are the first to arrive, followed by immature whales, mature males, resting females (whose ovaries and mammary glands showed no evidence of recent activity), and lastly by pregnant females (Chittleborough, 1965; Dawbin, 1966; Nishiwaki, 1959, 1966). On the return migration to the feeding grounds, the newly pregnant females depart first, while females rearing a calf depart last.

The length of stay for individual whales while on the Hawaiian wintering grounds will vary according to gender, age, and reproductive state (Craig, 1995; Craig, 2001). Juveniles and females without calf arrive in Hawaii and depart earlier than males and females with calf. Of the whales that were observed more than once during a season, the majority had a resighting interval of two weeks or less. The longest interval between first and last resight (76 days) was by a male. Humpbacks can travel great distances during their limited stay on the wintering grounds. Mate (1998) tracked one whale who traveled 850 km and visited 5 islands in only 10 days; and a mother with her calf who traveled at an average speed of 150 km per day for 4.5 days. These data support the notion that strict territoriality on the wintering grounds does not exist (Tyack, 1981). However, residency to specific areas, at least in females, may be affected by reproductive status (Craig & Herman, 2000).

Pregnant females have a gestation period somewhere between 10.5 and 12 months (Chittleborough, 1958, 1965; Mathews, 1937; Nishiwaki, 1959), presumably come to the wintering grounds to give birth and nurse their calf. Although females occasionally calve in consecutive years (Clapham & Mayo, 1990; Glockner-Ferrari & Ferrari, 1990; Weinrich, Bove, & Miller, 1993), most females will on average calve every 2 to 3 years (Baker, Perry, & Herman, 1987; Clapham & Mayo, 1990; Craig & Herman, 2000). Actual mating and calving has yet to be reliably documented in this species.

During their stay on the wintering grounds, males compete with other males for mating opportunities. They may compete by singing song (Clapham & Mattila, 1990; McSweeney, Chu, Dolphin, & Guinee, 1989; Payne & McVay, 1971; Winn & Winn, 1978) or by direct physical competition (Baker & Herman, 1984; Darling, 1983; Tyack & Whitehead, 1983). Humpback whale mating strategies have been described as male dominance polygyny (Clapham, 1996). This is a common strategy among males who are unable to defend resource territories or multiple females, who do not assist in parental care, who exhibit communal display behavior, and who physically compete with other males for mating access to estrus females (Emlen & Oring, 1977). Herman and Tavolga (, 1980 #1049) have described the mating system for humpback whales as comparable to a lek system, a definition further modified to incorporate the movement of displaying males and termed a ‘floating lek’ system (Clapham, 1996).

A humpback whale competitive group consists of a single adult female and two or more escorting males. The male attempting to maintain the position next to the female is termed the “principal escort” while the other males in the group are termed “secondary escorts” (Tyack & Whitehead, 1983). Agonistic behavior between males may escalate as they compete for proximity closest to the female (Baker & Herman, 1984; Clapham, Palsboll, Mattila, & Vasquez, 1992; Tyack & Whitehead, 1983). Initial dominance sorting between competing males may be resolved by the exhibition of threat displays. If these displays are not sufficient in sorting out dominance between two males, they may resort to attempts at physical injury or physical displacement of the opponent.

Generally, the seriousness of male-male competition is likely to reflect their lifetime reproductive opportunities. Humpback whales potentially have reproductive opportunities spanning over 40 years. Therefore, fighting to the death would be rare (Enquist & Leimar, 1990; Pack et al., 1998).

Immature or "subadult" whales are also found on the wintering grounds. In fact, whales of immature size were found to occupy 39.1% of whales which were measured in Maui waters between 1997 and 1999 (Spitz, 1999). Little is known about why subadult males and females undertake the long migration to the wintering grounds since food is absent and they are not reproductively active. Immature sized males occupied 50.0% of male partner roles, 44.3% of secondary escorts roles, 37.1% of single escort roles, and only 5.6% of principal escort roles. The majority of immature sized females occupied 75% of female partner roles. The determining factor of immature size were mean lengths reported by (Nishiwaki, 1959) of North Pacific humpback whale sexual maturity (11.56 m for males and 11.89 m for females). Therefore, a proportion of the individuals measured in Spitz (1999) could have been small sized sexually mature individuals that were classified as immature.

With the exception of a mother and her calf, associations between humpbacks on the wintering grounds tend to be fluid, brief, and may last only a few hours (Baker & Herman, 1984; Mobley & Herman, 1985; Tyack, 1981). Adult females actively avoid each other on the wintering grounds (Herman & Antinoja, 1977; Herman, Forestell, & Antinoja, 1980) and are rarely observed alone (Gabriele, 1992).

Because of the extensive movements over great distances on their wintering grounds in search of mates and other individuals of interest, adult humpback whales must have mechanisms in place for locating, assessing, and communicating to one another. Some of these mechanisms are beginning to be understood (described below), while others are still unknown.

1.4 Humpback Whale Communication on the Wintering Grounds

1.4.1 Acoustic Signals

1.4.1.1 Song

Humpback whales are known to sing while on the wintering grounds (Payne & McVay, 1971; Winn & Winn, 1978). Underwater observation of the genital region have indicated that singers are male (Glockner, 1983). The song is complex and consists of a set of 5 to 7 themes that are repeated in sequence. The structure of the song will change gradually throughout the season with almost all individuals making the same changes (Guinee, Chu, & Dorsey, 1983; Payne & Payne, 1985; Payne, Tyack, & Payne, 1983).

Several hypotheses have been put forth about the function of song, but its true function remains speculative. The most commonly proposed function of song is a sexual display by males (Glockner, 1983; Winn, Bischoff, & Taruski, 1973) used to attract females (Tyack, 1981; Winn & Winn, 1978). However, little support for this theory exists. Other functions include song as a beacon to attract distant females to an area (Herman & Tavolga, 1980), a method to synchronize estrus in females (Baker & Herman, 1984), a display of male fitness (Chu & Harcourt, 1986; Chu, 1988; Darling & Berube, 2001), and a method of echolocation by males in search of suitable mates (Mercado, 1998). Frankel et al. (1995) found supporting evidence that at least one function of song is to serve as a spacing mechanism among singers.

Interestingly, song playback experiments (Mobley et al., 1988; Tyack, 1983; Tyack & Whitehead, 1983) and extended observations of singers (Darling & Berube, 2001; Tyack, 1981), showed no evidence of females approaching the song source, except for a few rare exceptions (Medrano et al., 1994; Tyack, 1981). On the contrary, Darling and Berube (2001) observed only males approaching singers and engaging in brief, non-agonistic encounters, potentially a process of males assessing other males.

Most singers tend to be solitary and stationary, but are occasionally observed escorting a female (Baker & Herman, 1984; Darling, 1983; Herman & Tavolga, 1980; Tyack, 1983).

“Communal displaying” is commonly seen in many species and often serves more than a single function (McComb, 1987; McElligott & Hayden, 1999; Wolff, 1998). Therefore, each of the hypothesized functions of humpback whale song is not necessarily mutually exclusive from one another; song very likely serves several of the proposed functions.

1.4.1.2 Social Sounds

Social sounds differ from song in that they do not exhibit a consistent rhythmic and continuous pattern (Silber, 1986). On the wintering grounds, social sounds have been associated with competitive groups (Tyack & Whitehead, 1983). Silber (1986) found that social vocalizations in the Hawaiian humpback whale occurred almost exclusively in groups of three or more whales and was clearly related to group size and surface activity. When a new whale enters the group, the rate of vocalizations increases dramatically. Silber (1986) speculated that males are responsible for the majority of social sounds while they compete for temporary social dominance and proximity next to the female. He thought this might be due to a temporary upset in the current established dominance hierarchy among the males.

Vocal threats require minimal energy to produce and are often coupled with visual threat displays to convey levels of aggression (Silber, 1986). These vocal threats may travel across distances of 9 km or more to attract other whales (Tyack & Whitehead, 1983).

1.4.2 Visual Signals

In many species, dominant males attempt to discourage subordinate males through a variety of physical behaviors that are visually perceivable. These behaviors can be a way of signaling superiority over the addressee by communicating “I am stronger than you” but without intentions to fight (Walther, 1984).

In humpback whales, dominance displays between escorting whales follows a progression from simple interception and broadside displays, to head lunging, charge-strikes, and possible displacement of the principal escort (Baker & Herman, 1984). Initial broadside displays involve the principal escort moving horizontally across the path of a challenging male who begins moving towards the female. This behavior is commonly seen in competing male ungulates (Walther, 1984). If challenging persists, this leads to more aggressive displays. These include head lunging in which the male’s rostrum erupts through the surface of the water in a forward lunge or the underwater release of air which takes the form of linear bubble trails, underwater blows, and occasionally release of air from the mouth (Baker & Herman, 1984). It is believed that the bubbles may cause visual disorientation to an intruding whale (Baker & Herman, 1984). Explosive respirations at the surface producing a brief trumpeting noise sometimes referred to as a “tonal blow” may be equivalent to “snorts” in dolphins which are produced in association with disturbances (M. C. Caldwell & D. K. Caldwell, 1977). S-shape postures are also occasionally seen by the principal escort (Helweg, Bauer, & Herman, 1993) a common aggressive display observed in dolphins (Caldwell & Caldwell, 1972; Puente & Dewsbury, 1976; Tavolga, 1966).

Erect displays or “piloerection”, which give the appearance that an animal is larger than it really is, are also very common in competing animals (Darwin, 1872) and can be performed in conjunction with other displays. Humpback whales achieve this by engorging their ventral pleats with air or water through their mouths or possibly from their lungs (Yablokov, Bel'kovich, & Borisov, 1972) during a head lunge, creating a visual appearance of being physically larger in size (Baker & Herman, 1984). These open-mouth head lunges sometimes result in a jaw clap where the whale’s jaw closes abruptly while out of the water, a behavior regarded as a threat signal in dolphins (McBride & Hebb, 1948).

If nothing is resolved through dominance displays, competitors may switch to threat displays which state “I am going to fight you” indicating an immediate readiness to fight (Walther, 1984). In humpback whales these displays usually involve chases or charges between the principal escort and challenging males (Baker & Herman, 1984).

1.4.3 Tactual Signals

Although little documentation exists about tactile behavior in humpbacks, body contact appears to play an important role in mother-calf pair-bonding and nursing (Glockner-Ferrari & Ferrari, 1985). Orphaned humpback calves can be heavily scarred from continuous attempts to rub against other whales and boats (pers. obs.). However, between adults, little contact is observed, except when engaged in competitive behavior. Between competing males, if aggressive visual displays are not sufficient to deter an opponent, the contest may elevate to the level of charge-strikes. This may be an attempt to displace an opponent by physically moving his body to the side, or an attempt to injure the opponent by striking him with his rostrum or tail flukes (Baker & Herman, 1984). Barnacles which are often attached to the whale's rostrum and the edges of the tail fluke could enhance the level of injury caused to the opponent (Baker & Herman, 1985).

1.4.4 Chemical Signals

As has been reported in other marine mammals (Caldwell & Caldwell, 1967; Kuznetsov, 1978; Norris & Dohl, 1980), urine and feces are likely to be important sources of information about the hormonal and physiological condition of an individual. Although humpbacks are fasting while on the wintering grounds, they are frequently observed urinating and occasionally defecating (pers. obs.).

Escorting males are most often trailing behind the female. In some instances, the escort will position his rostrum very close to her genital region (Pack et al., 2002), possibly in attempts to monitor her hormonal state by detecting pheromones released into the water.

1.4.5 Percussive Signals

Humpback whales are well known for their acrobatic and exuberant surface-active behaviors. These behaviors may have both a visual, acoustic, and tactile component to them.

Some hypothesize that leaps and aerial actions of some species of dolphins may serve as visual displays with a communicative function (Pryor, 1990) possibly related to specific internal states (Defran & Pryor, 1980). Against the dark surface of the ocean, spray produced by surface activity heightens the visibility of many sorts of aerial behaviors, and may increase the utility of these actions for visual communication (Pryor, 1990). Leaping above the surface of the water could be a method for dolphins to gather long distance visual information about prey availability (Wursig & Wursig, 1979).

However, most aerial displays are not very visible to conspecifics since they are likely to be under the water most of the time and unable to see through the water surface except directly overhead. Therefore, any social information in leaps or other surface activity is probably contained in the splashing or slapping noises accompanying the activity (Pryor, 1990). The sound of a small dusky dolphin breach has been described to travel up to 1-km (Wursig & Wursig, 1979).

Surface active displays performed by mysticetes can produce underwater sound that may carry for several kilometers (Gilmore, 1961; Payne, 1978; Payne & McVay, 1971; Saayman, Taylor, & Bower, 1973; Scammon, 1874). The loudness of slap sounds resulting form aerial displays can be quite variable depending on the orientation of the whale as it strikes the surface (Dahleim, Fisher, & Schempp, 1984; Watkins, 1981; Wursig et al., 1984).

Many of these surface-active behaviors performed by humpbacks on the wintering grounds have been proposed as threat displays during male-male competition (Baker & Herman, 1984; Herman & Tavolga, 1980; Whitehead, 1985). These behaviors are also frequently observed outside the context of competition such as when whales come together or split apart (Baker & Herman, 1985).

Breaching, head slapping, peduncle slapping, tail slapping, and pec slapping (Figure 2), are all surface-active behaviors performed by humpback whales. These behaviors can produce slap sounds while creating a very large splash and substantial bubbles at the water's surface.

1.4.5.1 Breaching

Many species ranging from large whales to the smallest dolphins have been known to breach (Pryor, 1986). Gray whale breaching has been described as the release of excess exuberance, a display of strength and agility by a male towards a competitive male, or as a challenge towards another whale or even a boat, in defense of interests, or of territory (Gilmore, 1961). Gilmore (1961) also suggested that breaching by mothers and calves occur during play. Breaching has been described as a spacing mechanism between whales or a mechanism for humpback whales to remain in acoustic contact (Herman, 1980) and has been observed by an affiliating whale just prior to joining a competitive group (Baker & Herman, 1984). Frankel (1995) observed a whale breach that was immediately followed by cessation of singing by two nearby animals suggesting the sound of this aerial behavior can intentionally or unintentionally convey information to other whales. However, considering the high energy demands required during multiple breaches, it is unlikely that this behavior evolved principally for acoustic communication

(Herman, 1980). Whitehead (1985) concluded that breaching often serves to accentuate other visual or acoustic communication during social encounters.

1.4.5.2 Head Slapping

Head slaps are similar to breaches in that the whale thrusts its front end out of the water but does not twist its body before hitting the water's surface. Instead, the whale slaps down against the surface of the water with its chin. This behavior is not well documented. Whitehead (1985) observed that humpbacks in the North Atlantic perform full breaches about 80% of the time, and head slaps about 20% of the time. Coleman (1994), using a shore-based observation platform, investigated the possible functions of humpback whale aerial displays in the Hawaiian wintering grounds. He found that head slapping increased in frequency with increasing pod size and attributed this to a change in motivational state.

1.4.5.3 Peduncle Slapping

Peduncle slapping is another commonly observed display in which the whale throws its tail stock to one side above the surface of the water creating a large splash. This behavior is also not well documented. Coleman (1994) proposed that males may perform the behavior as a threat display and that females may use it for mate avoidance. Two males traveling together were observed to immediately turn towards, approach, and affiliate with a mother immediately after she peduncle slapped about 800 m away (pers. obs.).

One of the affiliating males then displaced the current escort for the principal escort position.

1.4.5.4 Tail slapping

Tail slapping is a behavior commonly seen in both odontocetes and mysticetes. Much like a beaver may slap its tail on the water's surface to warn conspecifics of danger (Hodgdon & Lancia, 1983), a dolphin tail slapping has been described as an alarm call which causes the whole school to dive (Pryor, 1986). Defran and Pryor (1980) suggest tail slaps as an indication of fear or stress. Shane (1990) interpreted tail slaps in bottlenose dolphins during feeding as a greeting when two separate groups meet. Some researchers speculate tail-slaps are conveying threats or accompanying "frustration" in addition to establishing contact (M. C. Caldwell & D. K. Caldwell, 1977).

On the feeding grounds, humpback whales have been observed using their tails to assist in surface feeding (Weinrich, Schilling, & Belt, 1992). On the wintering grounds, Herman and Forestell (1977) observed a humpback whale emerging from below a vigorously tail-slapping whale and rapidly swimming away as if chased. Tail slapping has also been observed by competing males just prior to disaffiliating from the group (Baker & Herman, 1984), and occasionally by the nuclear animal within a competitive group. The resulting extensive underwater and aerial sounds that are produced can likely be localized by other whales, and the properties of the sound may possibly have an acoustic advantage over vocally produced sounds (Herman et al., 1980).

1.4.5.5 Pec Slapping

Pec-slapping behavior is commonly observed in a variety of marine mammals including seals (Wahlberg et al., 2002), dolphins (D. K. Caldwell & M. C. Caldwell, 1977) and whales (Clark, 1990). During a pec slap, the animal will roll to one side or onto its back while lifting the pectoral fin above the water before striking it back down onto the surface.

In humpback whales, the lead animal among competitive groups has been observed to perform pec-slapping behavior around competing males, often while inverted at the surface (Baker & Herman, 1984). Coleman (1994) suggested the behavior is a response of the female to the aggression and advances of competing males in her vicinity. The inverted posture may be a way for the female to avoid copulation from males by restricting genital access, a behavior commonly seen in female right whales (Mandojana, 1981). However, unlike right whales, since competing males rarely make direct physical contact with the female (Pack et al., 2002), such avoidance behavior seems unnecessary.

Coleman (1994), investigated 166 observations of pec slapping over 98 hours of observation during a single season. He found that pec slapping was exhibited most often in 3 adult groups and in partner groups (dyads) when compared to all other groups. Pec slapping was least observed in calf pods or singletons. Calf pods containing escorts pec slapped more often than those without escorts. He also found that pec slapping increased with increasing pod size except when a calf was present, implying the presence of the calf inhibited pec-slapping behavior. He proposed that pec-slapping behavior may be performed by defending males as a threat display to dissuade challenging males, or by a female in order to dissuade mating attempts.

Coleman, (1994) concluded that the social context could be a reliable predictor of the likelihood of exhibition of aerial behavior. However, the motivation driving individuals within a group to perform these behaviors are likely to differ based on the individual's age class, sex, and behavioral role. Since adult males, adult females, and sexually immature whales have different incentives for visiting the wintering grounds, they each in turn would perform pec-slapping behavior in ways that meet their own social and communicatory objectives.

Formal studies attempting to understand the function of pec-slapping behavior are lacking. Although several hypotheses have been put forth, only speculation exists about its function. To date, no one has attempted to examine the performance of pec-slapping behavior at the level of the individual.

For the present study, data from 5-years of behavioral observations of humpback whales on the Hawaiian wintering grounds were compiled and analyzed. These data were used to examine: (1) in which **group types** pec slapping occurred, (2) which **individuals** were performing pec-slapping behavior, and (3) what **function** pec-slapping behavior might serve. Information on the age class, sex, and social role of the performer as well as social contexts in which the behavior occurs are discussed. Existing hypotheses on function are investigated and new hypotheses are proposed.

2 METHODS

2.1 Study Area

Research was conducted in waters of the Auau channel located between the four-island-region of Maui, Lanai, Molokai, and Kahoolawe (Figure 3). This area is highly concentrated with humpback whales during the winter season (Herman & Antinoja, 1977; Mobley, Bauer, & Herman, 1999).

2.2 Data Collection

2.2.1 Permits

All research was carried out under federal and State of Hawaii research permits enabling research vessels and/or divers to approach the whales up to one whale's length distance.

2.2.2 Boat based research

Boat based research was conducted almost daily as weather permitted. Whales were approached and observed opportunistically between January and April of each year from 1997 through 2001. Research vessels used for the surveys ranged in size between 6 and 9-m. Generally only one research vessel was used but on several occasions two research vessels operated independently to increase observation encounters. The most frequently used vessels were a 5.2-m Boston Whaler equipped with an 88-hp Johnson outboard motor, and a 5.6-m Seaswirl equipped with a 150-hp Johnson outboard motor.

Observers on the boat sighted whales using relatively subtle cues such as the vapor of a blow or the temporarily exposed back of a whale at the surface, to dramatic ones such as breaches or tail slaps. After confirming the sighting, the research vessel carefully approached the whale(s) so as not to disturb their natural behavior. Whether there was one or several whales could usually be confirmed on approach. A group of whales was defined as two or more whales usually within 50-m of one another that either remained stationary together or traveled together in the same direction. The group composition was assigned based on the individual behavioral roles in the group (see list of abbreviations for descriptions). All whale groups and individuals were approached at random.

Surface behavioral observations, performed by experienced observers, were manually recorded for the duration of the observations. Each behavioral occurrence was marked with the time of day. The total "observation period" lasted anywhere between 1 min to over 9 hrs with an average observation period of about 1 hr. The first group of the day that was tracked was labeled as group #1 and each subsequent group was sequentially numbered thereafter. If a whale disaffiliated from the group or a new whale joined, the group was treated as a new observation period. When the group composition changed but the group still contained at least one individual whale of the previous group, the assigned group number remained the same but a letter was affixed each time the group composition changed (e.g. a, b, c, etc.).

Whales within a group could very often be uniquely identified by the shape of the dorsal fin and/or by the unique pigmentation pattern on the ventral surface of the tail flukes. When possible, behavioral roles and gender were assigned to the performer of a behavior.

The unique underside of each whale's tail fluke (Katona et al., 1979; Katona & Whitehead, 1981) was photographed for identification purposes using Canon EOS cameras equipped with Canon 100-300 mm EOS lenses and Kodak TMAX 400 speed black-and-white film.

A Trimble Navigation Ensign Global Positioning System (GPS) was used to acquire accurate satellite data location readings at 10-20 min intervals while tracking the groups. These readings could be analyzed at a later time to report the distance, direction, and average speed of travel.

2.2.3 Underwater Observations

An underwater videographer equipped with a snorkel, mask, and fins took underwater observations opportunistically. When whales were stationary or slow moving, the diver could approach the whales quietly at the surface, observe underwater behavior, and obtain gender identifications. Genders were confirmed by the presence of a hemispheric lobe just posterior to the genital slit in females, and the absence of the lobe in males (Glockner, 1983; True, 1904).

A Sony TRV-7 digital video camera placed inside a Jaymar underwater housing in combination with a high-frequency (200 kHz) Depthmate hand-held sonar device was used by the diver for collecting body size measurements of the whales using an underwater videogrammetric technique (Spitz, 1999; Spitz, Herman, & Pack, 2000).

2.2.4 Research Personnel

A typical vessel crew consisted of two co-investigators and 3 research assistants. One co-investigator acted as the boat driver and maneuvered the boat carefully around the whales while narrating surfacings, dives, travel directions and speed, as well as a detailed account of all behaviors being performed together with the identity and behavioral role of the whale or whales performing the behaviors. The second co-investigator entered the water opportunistically to document and record underwater behavior, identify genders, and obtain length measurements of individual whales. Research assistants included a data recorder who inscribed behavioral narrations and frame numbers of photographs taken, together with the exact time the information was given. The data recorder also inscribed GPS coordinates that were obtained every 20 min by the second research assistant. The third research assistant attempted to obtain black-and-white fluke photo-identifications for each individual whale in the group.

2.3 Data Analysis

The data collected during all 5 years were compiled in a customized database developed using Filemaker Pro 5 software. A number of variables from the database were then imported into Microsoft Excel 2001 for analysis. See Table 1 for a description of the variables used in the database.

A group was considered to contain a pec slapper if one or more whales were observed pec slapping anytime during the observation period. An individual was considered to be pec slapping if the individual was observed pec slapping anytime during the observation period. Pec slapping percentages were calculated by dividing the total number of pec slapping observations (i.e. successes) by the total number of all observations (i.e. successes and failures). Regardless of how often an animal pec slapped during a single observation, or how long the period of observation, if pec slapping occurred anytime during the observation period, that particular observation period was scored as a success. If at anytime the composition of the group changed (whales affiliated or disaffiliated), the change was noted and a new observation period began.

The percentage of successes to total observation periods was calculated for different group types, and for different behavioral roles. Some of these percentages were compared against one another and tested for statistical differences. Pec-slapping percentages for groups and for individuals were analyzed independently.

2.3.1 Percentage of Group Types Observed Pec Slapping

The percentage of groups observed pec slapping within a group type was calculated by dividing the number of groups of that type that contained pec slapping by the total number of groups of that type observed (both pec slapping and non-pec slapping) and multiplying by 100.

i. i)

ii. $$\frac{Total\,Number of Groups of this Type Observed Pec\,Slapping}{Total\,Number of Groups of this Type Observed} \times 100$$

2.3.2 Percentage of Behavioral Roles Observed Pec Slapping

The percentage of individual whales observed pec slapping within a behavioral role was calculated by dividing the number of pec-slapping whales observed in that behavioral role by the total number of individual whales observed (pec slapping and non pec slapping) in that behavioral role and multiplying by 100.

iii. ii)

$$\frac{Total Number of Individuals Occupying this Behavioral Role Observed Pec Slapping}{Total Number of Individuals Occupying this Behavioral Role} \times 100$$

2.3.3 Percentage of Affiliations and Disaffiliations Surrounding Pec Slaps

The percentages of affiliations and disaffiliations preceding and following the performance of pec-slapping behavior by each adult behavioral role were calculated. In order to associate the group composition change with the pec-slapping performer, only individuals for whom they were the only pec slapper in the group were used.

iv. iii)

$$\frac{\textit{Number of AFFILIATIONS occurring PRIOR to a pec slapping performance}}{\begin{gathered}\textit{Total number of group composition changes (affiliations/disaffiliations/no change)}\\ \textit{occurring PRIOR to a pec slapping performance}\end{gathered}} \times 100$$

v. iv)

$$\frac{\textit{Number of AFFILIATIONS occurring AFTER a pec slapping performance}}{\begin{gathered}\textit{Total number of group composition changes (affiliations/disaffiliations/no change)}\\ \textit{occurring AFTER a pec slapping performance}\end{gathered}} \times 100$$

vi. v)

$$\frac{\textit{Number of DISAFILIATIONS occurring PRIOR to a pec slapping performance}}{\begin{gathered}\textit{Total number of group composition changes (affiliations/disaffiliations/no change)}\\ \textit{occurring PRIOR to a pec slapping performance}\end{gathered}} \times 100$$

vii. vi)

$$\frac{\textit{Number of DISAFFILIATIONS occurring AFTER a pec slapping performance}}{\begin{gathered}\textit{Total number of group composition changes (affiliations/disaffiliations/no change)}\\ \textit{occurring AFTER a pec slapping performance}\end{gathered}} \times 100$$

2.3.4 Statistics

Three types of statistical analyses were used: student's t-test for unequal variances, chi-square, and regression.

Calculated percentages of observed pec slapping were only reliable to the extent that the mean observation period for the numerator did not differ significantly from the mean observation period for the denominator. Therefore, a student's t-test for unequal variances was used to compare the differences between mean observation periods on pec-slapping and non-pec-slapping individuals.

Chi-square analysis was used to compare pec-slapping percentages either across observation periods, between different group types, or between different behavioral roles. Chi –square analysis was also used to compare the percentage of affiliations and disaffiliations surrounding pec-slapping behavior and changes in group compositions.

Regression analysis was used to investigate the percentages of pec slapping being performed in relation to group size.

3 RESULTS

Altogether, 3164 groups and 8824 individual whales were observed over 5 years between 1997 and 2001 for a total of 2,222 hours of observation (Table 2). Overall, 17% (537 of 2627) of the groups and 7% (591 of 8233) of the individuals were observed pec slapping. The mean observation period for groups in which no pec slapping was observed was 38.78 min with a standard deviation of 32.85 min. For groups in which pec slapping was observed, the mean observation period was 58.47 min with a standard deviation of 44.58 min.

Pec-slapping groups were observed on average 13.89 min longer than non-pec-slapping groups, a significant difference ($t(660, N = 3164) = -9.71$, $P < 0.05$). The mean observation period for individuals who were not observed pec slapping was 47.13 min with a standard deviation of 44.02 min. For pec slapping individuals, the mean observation period was 58.85 min with a standard deviation of 43.82 min. This difference of 11.72 min was also significantly different ($t(678, N = 8824) = -5.97$, $P < 0.05$).

Both significant findings indicate that pec-slapping groups and individuals were observed for longer periods of time on average than non-pec-slapping individuals. These differences in mean observation periods can be interpreted in two ways; either once pec slapping was observed, the tendency was to observe the whales for longer periods or, the whales that were observed longer were more likely to be seen pec slapping. In either case, pec-slapping percentages are proportional to the amount of observation time given to those individuals.

3.1 Data Controls

3.1.1 Observation Periods

The groups and individual whales represented in Table 2 are intended to be a representative sample of humpback whales on the Hawaiian breeding grounds and are intended to portray an accurate distribution of pec-slapping percentages among the various groups and individual behavioral roles.

In order to control for the number of individuals in a group, each individual observed was treated as an independent observation. Ideally, each observation would have a fixed observation period so that all observations get equal observation time and can be directly compared. Unfortunately, circumstances in the field often don't allow for such control and other means must be implemented to standardize the observation periods.

All individuals observed were divided according to 9 observation intervals of increasing observation duration. The percentage of individuals observed pec slapping was calculated for each interval. The effect of observation time on the probability of observing a pec-slapping individual was examined. These data are shown in Table 3 and Figure 4.

Shortest observations lasted only a few seconds (these were opportunistic observations of nearby whales while working with a different group of whales). The longest observation of an individual was 9 hrs and 14 min. The majority of observations (94%) were between 1 and 120 min. Approximately 2% of the observations were less than 1 min and 4% were greater than 120 min.

If pec slapping were equally likely to be observed during an observation period regardless of duration, the percentage of pec slappers observed for each observation period should fall somewhere near the overall mean of 7%. This is not the case. As the observation interval increases, the percentage of pec slapping per individual observed also increases for observation intervals up to about 100 min. The increase is about 1 to 2% for each increase in observation time of 20 min. Beyond 100-120 min of observation, pec-slapping percentages vary considerably. This is likely attributable to small sample sizes and a substantial increase in the percentage of competitive groups in which pec slapping is commonly observed. Competition accounted for 45% of the individuals observed for observation intervals less than 120 min, but accounted for 72% of the individuals observed greater than 120 min (Figure 4).

In order to standardize the observation period, a subset of data was selected for which the mean observation period for pec slappers was not significantly different from the mean observation period for non pec slappers. The data subset was also selected based on the criteria that the percentage of pec slapping did not change significantly within the boundaries of the observation interval chosen.

All observations between 60 and 120 min met these criteria (Figure 4). No significant differences were found between the mean observation duration for pec-slapping and non pec-slapping groups (t (580, N = 582) = -0.83, $P > 0.05$), or for pec-slapping and non pec-slapping individuals (t (202, N = 1964) = 0.60, $P > 0.05$) (Table 4). Additionally, no significant differences were found between individual pec-slapping percentages (X^2 (2, N = 1964) = 1.30, $P > 0.05$) for each 20 min observation increment between 60 and 120 min (Table 5). This new subset of data represented 18% (582 of 3164) of the overall groups observed, and 22% (1964 of 8824) of all individuals observed. This data subset accounts for 777 observation hours on different groups of whales, and 2,710 observation hours on individual whales. Competition accounted for 37% of the groups and 60% of the individuals observed, an increase from 28% of groups and 47% of individuals calculated in the original dataset. Competitive groups contain more animals and therefore longer observation times are generally needed to obtain all necessary information from the group.

3.1.2 Visibility

Another concern was that pec-slapping individuals could be more easily seen from a distance than an individual that was not pec slapping and therefore a bias would exist in locating pec-slapping individuals more often than non pec-slapping individuals. This potential bias could also inflate pec-slapping percentages within the population. Since less than 9% of the pec slappers in this dataset were initially observed from a distance, (15 out of the 171 pec slappers observed), the visibility confound can be treated as negligible.

3.2 Who is pec slapping?

3.2.1 Group Characteristics

Individuals were divided and compared according to 9 group characteristics. These were, in each case, the presence or absence of a mother, calf, yearling, juvenile, singer, male, competition, dolphin, and partner. Theses variables were assessed for their significance in affecting the percentage of pec-slapping behavior observed by a group of whales.

The subset of data comprising individual observations between 60 min and 120 min were used. Chi-square analysis was used to test the significance of each characteristic's influence on the percentage of pec slapping observed. The results are listed in Table 6 and are shown graphically in Figure 5. The only variables that showed a significant effect on the percentage of pec slapping observed by a group were the presence of a juvenile ($X^2(1, N = 1964) = 4.17, p < 0.05$) and the presence of a singer ($X^2(1, N = 1964) = 7.75, p < 0.05$). Individuals in groups containing a juvenile were observed with significantly higher percentages of pec slapping than individuals in groups without, and individuals in groups containing a singer were found with significantly lower percentages of pec slapping than individuals in groups without.

3.2.1.1 Age Class and Gender

Subadults were observed pec slapping twice as often (12%) than all adults combined (6%) (X^2 (1, N = 1964) = 9.42, $P < 0.05$) (Table 7). Among the adults, females (13%) were observed pec slapping more than 3 times as often as males (4%) (X^2 (1, N = 1746) = 52.26, $p < 0.05$) (Table 7). These data are shown graphically in Figure 6.

3.2.2 Behavioral Roles

Further analyses at the level of the individual's behavioral role were performed.

Overall, the mean pec-slapping percentage for an individual whale observed between 60 and 120 min was 9% (171 of 1964) (Table 6). Behavioral roles were grouped according to a gender that could be inferred. Inferred female roles included mothers (M) and nuclear animals (NA) (Baker & Herman, 1984; Clapham et al., 1992; Tyack & Whitehead, 1983). Inferred male behavioral roles included single escorts (E), primary escorts (1E), secondary escorts (2E), nuclear primary escorts (N1E), nuclear secondary escorts (N2E), and singers (S) (Baker & Herman, 1984; Clapham et al., 1992; Glockner, 1983; Glockner-Ferrari & Ferrari, 1985; Herman & Antinoja, 1977; Mobley & Herman, 1985; Tyack & Whitehead, 1983). Behavioral roles for which genders could not be inferred included calves (C), juveniles (J), yearlings (Y), lone singletons (1A), and dyad adults (2A). The percentage of pec slapping observed for each behavioral role is presented in Table 8 and shown graphically in Figure 7.

If each individual were equally likely to be observed pec slapping then we would expect to find the percentage of pec slapping around the mean of 9%. Behavioral roles that were observed pec slapping more than the mean were NAs (20%), Cs (11%), Ys (15%), Js (25%), 1As (14%) and 2As (12%). All adult male behavioral role percentages fell well below the mean with percentages ranging between 1 and 4%. It should be noted that 2Es had significantly shorter observation times on pec-slapping individuals than non-pec-slapping individuals and therefore the pec-slapping percentage (4%) may be somewhat underestimated. Mothers (8%) were the only other behavioral role that had a pec slapping percentage below the mean.

3.2.2.1 Adult Females

Between the two adult female behavioral roles, NAs had a significantly greater percentage of pec slapping (20%) than all Ms combined (8%) (X^2 (1, N = 370) = 9.38, $P < 0.05$) (Table 8).

All adult females in competitive groups were observed pec slapping in significantly higher percentages (19%) than adult females in non-competitive groups (8%) (X^2 (1, N = 494) = 10.70, $P < 0.05$) (Table 9) suggesting competition may influence pec-slapping behavior among adult females. It should be noted that adult females pec slapping in non-competitive groups were observed significantly longer than those in competitive groups possibly inflating the percentage of pec slapping observed for this group (8%).

The adult female category for individuals in non-competitive groups included half of the dyad group individuals. This was justified since the majority of dyad pairs have been found to be male-female partners (Brown & Corkeron, 1995; Spitz, 1999, pers.obs.), and among dyads, pec slapping is observed almost equally as often in both genders (see Figure 10).

When comparing adult females in competitive and non-competitive groups, but removing all groups in which a C is present, adult females in competitive groups pec slap almost twice as often (20%) as adult females not in competitive groups (11%). This difference however is not statistically significant (X^2 (1, N = 287) = 3.05, P > 0.05). The trend adds support that competition can increase the percentage of pec slapping in adult females but the statistical result suggests that the presence of a C can inhibit adult female pec slapping behavior.

Although Ms in competitive groups (16%) are observed pec slapping almost 3 times as often as mothers not in competitive groups (6%), this difference is not significant (X^2 (1, N = 207) = 2.96, P < 0.05). The lack of significance is likely due to a small sample size issue among Ms in competitive groups.

Although Ms pec slap significantly less than NAs, if we only compare Ms that are in competitive groups (16%) with NAs (20%), the difference is no longer significant (X^2 (1, N = 45) = 0.16, P > 0.05) (Table 9) adding additional support that competition can elevate pec slapping behavior in adult females beyond the inhibition of pec slapping that might be caused by the presence of a calf.

When all adult females with C (Ms) (8%) were compared with all adult females without C (NAs and 2As)(16%), we observe significantly more pec slapping by females without C (X^2 (1, N = 909) = 5.91, $P < 0.05$) (Table 9) adding support that the presence of a calf may inhibit pec slapping in adult females.

These results are shown graphically in Figure 8.

The following are summaries of the descriptions for pec-slapping NA and M observations. Specific anecdotes can be found in Appendix C.

3.2.2.1.1 Nuclear Animals

95 Observations – NA's accounted for 52% (95 of 181) of all pec slapping adult females in the full dataset. For most scenarios in which the NA performs pec slapping, the group appears to be quite active. The N1E is generally performing linear bubble trails, head lunges, and often chasing away challengers. The aggression often escalates to the point of charge-strikes between males. Occasionally, the NA is seen performing tail slaps, breaches, and tonal blows. However, pec-slapping behavior in this context is the predominant surface-active behavior by the NA. Males are often joining and leaving the group and pec slapping by the NA seems to occur intermittently throughout. In competitive groups that begin as a male-female pair, pec slapping by the female may

begin once whales are observed approaching from a distance or in close proximity to the pair. Affiliate males eventually join the male-female pair and pec slapping by the NA persists until the group eventually returns to a dyad status. On a few occasions, as a disaffiliate male began to move away from the NA, the NA clearly changed direction of travel towards the male causing the male to rejoin the group. Pec slapping by the female can continue even shortly after all the challenging males have left. On one occasion this resulted in more males joining the pair. But most often, once the disaffiliated males are no longer visible in the area for a period of time, pec slapping subsides and the remaining male-female dyad may become stationary with long dive times. The behavior by the NA is consistent even when a challenger displaces the N1E. This occurred in 5 of the 95 observations.

3.2.2.1.2 Mother in Competitive Group

15 observations – Mothers in competitive groups accounted for 8% (15 of 181) of all adult female pec slappers. In competitive groups with the M pec slapping, the C also tends to be surface active. Occasionally we see other behaviors performed by the M, but not frequently. For example, of the 15 encounters, a breach was observed 4 times, tail slapping 3 times, a peduncle slap once, and a tonal blow once. On 7 occasions we saw a disaffiliation by a challenger. It seems that the MCE group may initially be quiet. However, approaching challenging males detected by the M apparently cause her to pec slap and perform other surface-active behaviors. Once the challenging males disaffiliate,

whether or not displacement of the 1E occurred or not, pec slapping by the M subsides. This behavior is thus very similar to pec slapping in NAs.

3.2.2.1.3 Mother With Calf

5 Observations – Mothers with calf only accounted for 3% (5 of 181) adult female pec slappers. During 4 of the 5 observations, both whales were surface active and pec slapping occurred. Breaching and head slapping by the M occurred on 3 occasions, tail slapping in 4, peduncle slapping in 3, and head slapping in 2. The C also performed tail slaps, breaches, head slaps, and pec slaps. There was no indication of whales in the immediate vicinity and no change in group composition occurred. Surface activity from both whales seems to erupt suddenly and subsided equally as fast. If the calf was attempting to mimic the mother, it was not apparent.

3.2.2.1.4 Mother With Yearling

1 Observation - Only a single case of a pec-slapping M with her Y was ever observed and accounted for 1% (1 of 181) of all adult female pec slappers. Similarly to a lone M and C, both Y and M were surface active together. In addition to pec slapping, peduncle slaps, and tail slaps, the M performed head slaps and a breach. The Y performed pec slaps and breaches. The composition of the group remained the same throughout.

3.2.2.1.5 Mother with Calf and Single Escort

9 Observations – Occurrences of a pec slapping M with her C and an accompanying E accounted for 5% (9 of 181) of all adult female pec slappers. Out of 9 M, C, and E observations where the M was observed pec slapping, a change in group composition was observed only once. An E disaffiliated, leaving behind the M and C. Breaching was the predominant other behavior performed by the M and occurred on 4 of the 9 observations. The C was also surface active on at least 7 of the 9 occasions and initiated surface activity at least twice. The E was also surface active on at least 5 of the 9 occurrences. These groups can appear to erupt into surface-active behavior suddenly with no apparent reason, but can also erupt when being joined by other whales. Behavior often resides back to normal shortly thereafter.

3.2.2.2 Adult Males

Among adult male behavioral roles, all percentages of pec slapping observed fell below the overall mean of 9% (Table 8 and Figure 7). Highest percentages at 4% were observed by Es, 1Es, and 2Es, followed by Ss at 3%, N2Es at 2%, and N1Es with the lowest percentages at 1%. Overall, differences in pec-slapping percentages among these adult male behavioral roles were not significantly different from one another (X^2 (5, N = 1109) = 6.00, P > 0.05).

When males in competitive groups are compared with males in non-competitive groups (including half of the males in male-female dyads), we find pec slapping occurs significantly more often by males who are not in competitive groups than males who are (X^2 (1, N = 1262) = 18.53, P < 0.05) (Table 10). Statistically, adult males as a whole are equally likely to pec slap whether or not a C is present in the group (X^2 (1, N = 1262) = 0.11, P > 0.05) (Table 10).

These results are shown graphically in Figure 9.

The following are summaries of pec-slapping descriptions of adult male behavioral roles. See Appendix 3 for specific anecdotal descriptions.

3.2.2.2.1 Single Escorts to a Mother and Calf Pair

23 Observations – Single escorts represent 16% (23 of 145) adult male pec slappers. In only two observations did the MCE gain an affiliate. When this occurred, the quiet MCE group erupted with surface-active behaviors. The original E became surface active and pec slapping became a part of his behavioral repertoire. The M and C also became surface active. The second more predominant context is independent of affiliating whales. Among these 19 observations, the E initiated surface activity 15 times, the C initiated during 4 observations, and M only once. The M was surface active during 4 of the 23 observations and the C was surface active during 10 of the observations. The E occasionally corals the M by frequently moving out in front of her, approaching very close to her, or circling her, causing her to change her direction of travel. On one occasion the E disaffiliated and joined another nearby MC pod.

3.2.2.2.2 Primary Escorts to a Mother and Calf Pair

9 Observations – Pec slapping 1E’s account for 6% (9 of 145) of all pec slapping adult males. The context here is generally associated with an affiliating whale. Of 9 observations, M was surface active during 3 observations as well as the C. The number of pec slaps performed by the 1E is generally low (less than 5) and in combination with several other surface active behaviors such as breaches, head slaps, head lunges, peduncles slaps, and underwater blows.

3.2.2.2.3 Nuclear Primary Escorts

3 Observations – N1E’s accounted for 2% (3 of 145) of all pec-slapping adult males. The numbers of pec slaps performed by the N1E were limited to 1 or 2. The NA was also pec slapping in all 3 cases. One case describes a single female joining a pair of males. Lone females are rarely observed unless they are subadults. The second case was an N1E who was displaced and pec slapped just before disaffiliating. The third case involved an active group of 5 adults where at least 3 whales were pec slapping simultaneously

3.2.2.2.4 Secondary Escorts to a Mother and Calf Pair

11 observations – 2E’s accounted for 8% (11 of 145) of all pec slapping adult males. The trend here seems to be that pec slapping occurs in highly competitive groups with the pec slapping whale often disaffiliating. Of 11 observations, 8 contained a 2E disaffiliating.

Six of these disaffiliates were confirmed to be the pec slapping 2E. Five of the six 2E's disaffiliated together with 1 or 2 other whales. The other 2E disaffiliated alone. On only 1 occasion was pec slapping observed in the distance by a disaffiliate which was the 2E who disaffiliated alone. All other pec-slapping observations occurred prior to disaffiliation while the 2Es were still in the main group.

3.2.2.2.5 Nuclear Secondary Escorts

37 Observations – N2E's accounted for 26% (37 of 145) of all pec-slapping adult males. Of these 37 cases, only 1 affiliation was observed and 8 disaffiliations. Of the 8 disaffiliations, 7 were known to be the pec-slapping N2E, the other was unidentified. Of the 8 disaffiliating N2E pec slappers, 4 of them left the group alone, while the other 4 left together with 2 or 3 other whales. Three of the 4 lone disaffiliates were observed pec slapping as they moved away from the main group. The other 4 disaffiliates that left the group with other whales were not observed pec slapping as they moved away from the group. One group of 3 N2E disaffiliates was observed pec slapping far off in the distance long after leaving the group. It is unsure if this whale was still together with the other two whales.

3.2.2.2.6 Singers

5 Observations – S's accounted for 3% (5 of 145) of all adult pec slappers. Most of the pec slapping was observed from a distance, which may have involved other whales in the group at the time of the pec slapping. It is possible that a disaffiliation had just occurred.

Two exceptions should be noted. The first is one in which the S traveled together with a small whale before affiliating with a MCE. The second is when the S affiliated with a dyad and became the challenger.

3.2.2.3 Neutral Adult Roles

Among lone adults, rarely do we observe a female by herself. Therefore, most lone adults are likely to be males. Nine lone adults were observed pec slapping. Two were confirmed as males but the gender of the other 7 were not confirmed (Figure 10).

Among dyads, almost equal numbers of confirmed females (12) and confirmed males (10) were observed pec slapping (Figure 10). The sexes of the remaining 36 pec-slappers in dyads were unidentified.

When the percentage of pec slapping observed in lone adults (16%) was compared to the percentage of pec slapping observed in dyads (13%), no significant difference was found (X^2 (1, N = 276) = 0.00, P > 0.05) (Table 8).

The following are summaries of pec-slapping descriptions of neutral adult male behavioral roles. See Appendix 3 for specific anecdotal descriptions.

3.2.2.3.1 Lone Singletons

42 Observations - Occasionally, pec slapping in singletons was observed immediately following the disaffiliation of a whale between a dyad. But, most often, pec slapping

occurred when a second animal was in the immediate area of the singleton, or just prior to the affiliation with another whale. Since single adult females are rare, most likely the other whale was a male. Single whales that are small in size (immature) appear to pec slap independently of other whales in the vicinity.

3.2.2.3.2 Dyads (34 total observations)

3.2.2.3.2.1 Male-Male Dyads

17 Observations – Male pec slappers that partnered with another male accounted for 50% (17 of 34) of all pec-slapping dyads. Three male-male dyad contexts were encountered. Both males either disaffiliated from one another (9 observations), or left a competitive group together (2 observations), or joined a competitive group together (5 observations). The last observation was a pair of males that left a group together then rejoined a different group together.

Of the 9 observations when both males disaffiliated, all but once was only one of the two males pec slapping as they moved apart. Five of these pairs resulted from a male joining a singer. Singing may or may not stop. The interaction between the two males is generally brief and usually results in a disaffiliation shortly after (within 5 to 20 minutes). Of these 5 pairs, the singer was pec slapping on 3 occasions and the affiliate on 2 occasions either just prior to or during the disaffiliation. Surface-active behaviors often involve pec slapping and occasionally tail slapping as both whales move apart. The behavior may persist even when the whales are over 100 yards apart. The interaction appears to be non-agonistic.

Sometimes the pair will remain together and affiliate with a competitive group or join members of another group to create a competitive situation (6 observations). When this occurs, most often the affiliating pair remains on the periphery as 2Es. On one occasion, one of the affiliates displaced the primary in a MCE group, and the other male partner left the group with the displaced primary.

Lastly, two males may leave a competitive group together (2 observations). In this instance, many surface-active behaviors including pec slapping are observed between the two males (tail swish, tonal blows, peduncle slaps, tail slaps, and tail extensions). Normal agonistic/competitive behaviors such as head lunging and linear bubble trails are not observed.

3.2.2.3.2.2 Male-Female Dyads

13 observations - The context in which we observe a male-female dyad pec-slapping group appears much different than a competitive group that is reduced to a male-female partner. The male in the current dyad context does not usually exhibit competitive behavior such as head lunges and linear bubble trails. These whales also behave differently from a male-male dyad in which pec slapping is almost exclusively the behavior performed. Many behaviors are performed in the context of a female-male dyad including tonal blows, tail swishing, tail slapping, head slapping, and peduncle slapping

by the female and tail slapping, peduncle slapping, tonal blowing, and breaching by the male. The repertoire of surface-active behaviors included with the pec slaps is large, similar to what we see in subadult whales. Also, the interaction between the male and female in the dyad appears to be non-agonistic. This type of active group can rapidly return to quiet, stationary behavior with long dive times (typical dyad behavior). On a few occasions, the group experiences an affiliation of one or more males, and on only one occasion did the original male leave the female. This last observation provides some evidence for the female attempting to rid herself of the current male or attract other males in order to have him displaced.

3.2.2.3.2.3 Male-Female Dyads Resulting from Competition

2 Observations – Under this context, all challenging males disaffiliate leaving only the male and female dyad. The female, who was pec slapping prior to the disaffiliation of the challenging males, continues to pec slap even though no challenging males are present. This results in the affiliation of another male. The new affiliate immediately displaces the defending male. Although the female continues to pec slap, she is occasionally observed swimming inverted below him. The female appears to be soliciting the new primary by exposing her genital region to him, a behavior seemingly incompatible with a female wishing to rid herself of the primary. Along with this apparent solicitation behavior, she continues to pec slap.

3.2.2.4 Subadults

Subadults were observed pec slapping significantly more often (12%) than all adults combined (6%) (X^2 (1, N = 1964) = 9.42, P < 0.05) (Table 7 and Figure 6). Although subadult pec slapping percentages appear to increase with increasing age class (C=11%, Y=15%, J=25%) (Table 8 and Figure 7), statistically, these differences are not significant (X^2 (2, N = 222) = 2.43, P > 0.05). This maybe due to small sample sizes for both Y (N = 13) and J (N = 12) categories. Additionally, weaned Ys (no longer with M) can often be mistaken as Js since they are difficult to categorize in the field simply based on size estimation by eye. Therefore, the J category may be contaminated with mislabeled Ys.

The sex of pec slapping subadults was fairly evenly split among males and females for all 3 subadult behavioral roles (Figure 11). Sixteen male calves and 11 female calves were observed pec slapping, while 25 others were not sexed. Both a male and a female yearling were observed pec slapping and a third yearling that was not sexed. Lastly, 2 male and 3 female juveniles were also observed pec slapping, and 3 others were not sexed.

The numbers of cases for subadult behavioral role categories are too few to perform meaningful statistical comparisons.

The following are summaries of pec-slapping descriptions of subadult behavioral roles. See Appendix 3 for specific anecdotal descriptions.

3.2.2.4.1 Calves

82 Observations – Calves accounted for 74% (82 of 111) of all subadult pec slappers. It is not uncommon to observe a C surface active regardless of the activity of other whales in the group. C energy levels can escalate rapidly as they begin rolling more frequently at the surface, occasionally performing a number of surface active behaviors including breaches, head slaps, tail slaps, and occasionally pec slaps.

3.2.2.4.2 Yearlings

10 Observations – Y's accounted for 9% (10 of 111) of all subadult pec slappers observed. Of the 10 Ys, only 3 were weaned. Ys, still with their Ms, behave very similarly to calves. However, weaned Ys, once on their own, begin to behave similarly to Js. One very distinct weaned Y, reportedly seen 2 weeks earlier with her mother, performed over 100 pec slaps. These behaviors may be associated with having recently been weaned. Weaned Ys seem to have a greater repertoire of surface-active behaviors compared with calves, swim directions can become much more variable and non-linear, and affiliations with or by other whales are uncommonly seen. Since M and Ys could often be mistaken for a dyad group, and weaned Ys may often be classified as Js, Ys are most likely under-represented in the data. Interpretation of such small sample sizes should be treated with caution.

3.2.2.4.3 Juveniles

19 Observations – Of all pec-slapping subadults, Js accounted for 17% (19 of 111) of observations. Of these, Js were observed doing peduncle slaps on 8 occasions, peduncle lifts on 6, breaching on 9, head slaps on 1, tonal blows on 10, tail slaps on 8, underwater blows on 6, tail swishes on 2, tail extensions on 5, and head rises on 6 of the 19 observations. Of the 19 observations, no change in group composition occurred in 12, and affiliations and disaffiliations occurred in 3. For some of these groups, this behavior also accompanied approaches to boats, manipulation of objects suspended in the water, surfing wave swells, and pursuing dolphins.

One specific observation is worth noting here. This involved a rare occasion of a S together with a J. During this observation, the majority of surface activity was performed by the J and coincided with the time the two whales began moving apart and eventually disaffiliating from one another.

3.3 When are they pec slapping?

3.3.1 Affiliations and Disaffiliations

In order to provide potential information relevant to function, the number of affiliations and disaffiliations were examined surrounding pec-slapping and non pec-slapping individuals. If the number of whales present during an observation changed at any time during the observation period (gained or lost individuals), a new observation period was initiated. The number of affiliations and disaffiliations that occurred before an observation period was initiated and after an observation period was terminated for both observations that contained and did not contain a pec-slapping individual were noted. Most observation periods never encountered a change in the number of whales present and were therefore scored as if no affiliations or disaffiliations occurred prior to or following the observation period.

Only observation periods in which a single pec-slapping individual was observed were counted in order to assess the influence of only a single behavioral role. And only observation periods with no pec-slapping individuals observed were counted in order to eliminate any influence on composition change that may be caused by other pec-slapping whales in the group.

The objective was to look at the direction of change in group composition (gained individuals or lost individuals) and determine whether the act of pec slapping occurred more often following a particular change in group composition (associated with an animal beginning to pec slap) or prior to a change in group composition (pec slapping was followed by a change in group composition). As a control, these changes were contrasted against changes that occurred independently of pec-slapping behavior. These data are listed in Table 11.

Percentages were not calculated for N1E, and S behavioral roles since they have only a single recorded pec-slapping observation. Affiliation and disaffiliation percentages for adult female behavioral roles prior to pec slapping are plotted in Figure 12, and following pec slapping in Figure 13. Affiliation and disaffiliation percentages for adult male behavioral roles prior to pec slapping are plotted in Figure 14, and following pec slapping in Figure 15. Caution must be taken when interpreting certain percentages due to very small sample sizes used in the calculations.

A subset of male and female behavioral role percentages and combinations of percentages were selected and compared statistically (Table 12).

Among adult females, affiliations and disaffiliations are common both before and after pec slapping by the female. For adult males, the same is true, but affiliations and disaffiliations occur less frequently. The exception occurs following an adult male pec slapper, we find a higher percentage of disaffiliations (37%) compared with the percentage of disaffiliations following an adult female pec slapper (26%). Statistically, percentages of affiliations or disaffiliations both prior to and following pec slapping do not differ significantly if the pec slapper is an adult male or an adult female (X^2 (1, N = 74) = 0.12, 0.01, 1.22, 0.61, $P > 0.05$).

When adult female pec slappers were compared with non pec-slapping adult females, significantly more affiliations (X^2 (1, N = 517) = 4.10, $P < 0.05$) and disaffiliations (X^2 (1, N = 517) = 8.71, $P > 0.05$) occurred following pec slapping than when no pec slapping was performed.

When adult male pec slappers were compared with non pec-slapping adult males, the only significant finding was more disaffiliations occurred following pec slapping by an adult male (X^2 (1, N = 1088) = 4.48, $P < 0.05$) than when pec slapping was absent.

Among NAs, any change in group composition did not have a significant effect on her pec-slapping behavior; and pec slapping made no significant impact on changing the group composition (X^2 (1, N = 190) = 0.01, 0.07, 1.91, 0.01, $P > 0.05$).

N2Es had significantly more disaffiliations after they were observed pec slapping than when not observed pec slapping (X^2 (1, N = 534) = 5.79, $P > 0.05$). These disaffiliates, for the most part, were the pec-slapping N2E.

3.3.2 Group Size

Figure 16 shows the percentage of pec slapping observed within a competitive group by 2 adult female (NA and M) and 2 adult male (N2E and 2E) behavioral roles as a function of the group size (number of secondary escort males present). The data were fitted to a regression line and tested for significance (Table 13). None of the competitive group behavioral roles showed any significant linear trend in the percentage of pec slapping as a function of group size (r^2 = 0.11(NA), 0.71(M), 0.01 (N2E), 0.07 (2E), $P > 0.05$).

3.4 Acoustical Properties

The spectrogram in (Figure 17) demonstrates the sound properties created by a pec slap on the surface of the water. The signal produced is broadband ranging from 50 Hz up to

17 kHz, and is followed by an echo that is most likely a reflection of the signal against the ocean floor.

Using the elapsed time between the pec slap and the echo, the approximate water depth at which the pec slap occurred was calculated. Using the speed of sound calculated in coastal waters off the island of Hawaii at 1532.5 m/sec (Frankel, Clark, & Gabriele, 1996) and a delay of 73 msec (110 msec - 37 msec) as the time between the pec slap signal and the echo, the depth at the location of the pec slap should be 0.073 sec X 1,532.5 m /sec divided by 2 which is equal to 55.94 m. The depth obtained from a nautical chart for the exact GPS coordinate where this pec slapper was observed is approximately 60 m.

Thompson et al. (1986) measured the source level of the surface impact caused by a pec slap from a humpback whale. Their source level (defined as the acoustic intensity 1 m away from the sound source) of the pec slap ranged from 162-171 dB, re 1 uPa, 1 m. However, a critical component in estimating source levels is knowing the exact distance from the animal to the receiver (Urick, 1983), a component lacking in the study by Thompson et al. (1986) who only used visual cues to estimate the whale-to-hydrophone distance. Nonetheless, these values can be used to calculate a very crude estimate of the propagation range of a pec slap impact signal.

Mercado (1999) developed a model for determining sound transmission loss in shallow waters around Hawaii. Transmission loss (TL) can be measured as “a log r” where “a” is a fixed constant dependent on water depth, source depth, and optimum frequency. Using a mean depth of 100 m, a source depth of 5 m, and optimal frequency of 4000+ Hz, the minimum constant for “a” is 15.7 (see Table 2 in Mercado & Frazer, 1999). The range “r” in meters can be calculated as the maximum distance at which the pec-slap signal could travel before enough transmission loss would burry the signal into ambient noise.

Au et al. (2000) measured ambient noise levels in Hawaiian waters during high (119 db re 1 uPa) and low (103 dB re 1 uPa) densities of chorusing humpback whale singers. When singer density is high, a 171 dB pec-slap signal would be reduced to ambient noise levels at a distance of 2 km. When singer density is low, a 171 dB pec-slap signal would be reduced to ambient noise levels at a distance of 21 km. This assumes a peak signal frequency of 315 Hz. Upper frequency portions of the pec-slap signal will attenuate much more quickly and therefore will have a much shorter range.

4 DISCUSSION

The overall results indicate that the percentage of pec-slapping behavior observed by an individual humpback whale will differ based on the performer's age class, sex, behavioral role, and on particular characteristics of the group. In the following sections, these relations are discussed more fully and various interpretations considered.

4.1 Pec Slap Acoustical Properties

The acoustical properties of the pec slap are an interesting component and can provide insight into its communicatory capabilities. A 171 dB (re 1 uPa, 1 m) pec slap signal (Thompson et al., 1986) can potentially be received by another whale from 2 to 21 km in the distance depending on the amount of whale chorusing at the time of the signal. Pec slapping can therefore be a mechanism to communicate not only to whales in the immediate vicinity or group, but also to whales in the surrounding area.

Recently, Wahlberg et al. (2002) measured pec slap source levels in wild harbor seals of 186-199 dB re 1 uPa, pp, suggesting that possibly a motivated humpback whale may have the ability to create a pec slap signal capable of traveling much beyond a 21 km radius. The broadband properties of a pec slap signal also make the signal easier to localize.

4.2 Adult Female Pec Slapping and its Implications for Communication

Among adult females, those in competitive groups are more than four times as likely to pec slap than those who are not in competitive groups. Even when Cs are present, which tend to inhibit pec slapping by their mothers, the impact is minimal in contrast to competition. The presence of competing males is a significant factor related to increased percentages of pec slapping by adult females.

Nuclear animals and Ms in competitive groups often begin to pec slap after one or more challenging males are observed in the nearby area. These males later join and form a competitive group at which time the group may gain and lose challenging males frequently. Pec slapping by the adult female will occur intermittently throughout.

These findings can be used to assess the various proposed hypotheses for adult female pec slapping.

4.2.1 Adult Females Pec-Slap to Repel Unwanted Males

If pec slapping were an effective means to drive away unwanted males, we should expect to observe some males disaffiliating after the female has pec slapped. The results show a significant increase in male disaffiliates when the female pec slaps compared to when she doesn’t pec slap, however there is also a significant increase in the number of affiliates.

If pec-slapping adult females were attempting to drive males away from the group, we would expect to find adult females pec slapping more often in larger pods when more males were present. Coleman (1994) found a positive correlation in pec-slapping rates by NAs with increasing group size. Although this study did not look specifically at pec-slapping rates, pec-slapping percentages of individual NAs or Ms did not increase with increasing group size. Coleman's results may be confounded by the inability to confirm the identity of the pec slapper in the groups being observed from shore. With increasing numbers of males in a group, there is an increasing probability that a male will eventually pec slap, possibly giving the impression that a female is pec slapping more often. Unless the identity of the pec slapper can be confirmed, conclusions about individual pec-slapping rates can be inaccurate.

Ms calve on average every 2 or 3 years, and therefore most Ms will not mate during a season they have a calf. Ms should therefore be less interested in potential mates than NAs. If pec slapping were an attempt to repel males away, we would expect Ms to be more likely to pec slap in competition groups than NAs. This study found the opposite. NA's were just as likely or more likely to pec slap in competitive groups than M.

The presence of a C had a significant reduction in the percentage of pec slapping observed by adult females. If Ms restricted their pec-slapping activity due to the potential danger of injuring their C with their pectoral fin, this could explain why Ms pec slap less frequently than nuclear animals. However, since Ms are observed pec slapping next to their calves even when no adult males are known to be in the area, it appears that she has enough awareness and control to avoid injury to her C.

When an E is present with the M, the sudden eruption of M pec-slapping activity generally corresponds with one or more affiliate males joining the pod. Once the new joiners disaffiliate, pec-slapping behavior subsides. This indicates a reaction to the potential for competition around the female. This may be interpreted in two ways; she may be reacting to entice competition among the new challengers or, she may be attempting to discourage the males from affiliating.

Occasionally, displacement of the defending male by a challenger will occur and the new primary remains with the female after all other males have left the group. If her motivation for pec slapping initially was to repel the incoming males, then pec-slapping behavior should continue in efforts to expel this unwanted male. We observe the contrary; regardless of which male remains with her in the end, pec slapping always subsides when challengers are no longer in the immediate area.

The need to drive males away from the group seems unnecessary since females almost never experience agonistic behavior from males in competitive groups. NAs will frequently go completely stationary while males compete closely around her (pers. obs.). Ms and their calves also seem undisturbed by the surrounding competition. However, Ms will almost never allow her C to surface alone within a competitive group, perhaps an indication of some concern for her C’s safety.

These results provide little supporting evidence towards the hypothesis that adult females pec slap in attempts to repel males away from the group.

4.2.2 Adult Females Pec Slap to Attract Males

If pec slapping by the NA were a mechanism to attract males to affiliate and compete, we would expect to find significantly more affiliations taking place following pec-slapping behavior by the NA. Results showed that both affiliations and disaffiliations occurred equally as often following pec slapping by the NA. We would also expect to observe initial pec slapping by the female prior to any challenging males joining the group. These observations are also rare. Most pec slapping by females begins once males have already joined the group or once males are in the immediate vicinity. Females without calf, which are more likely to seek out mating opportunities, should pec slap more often than females with calf. The data support this expectation. However, no significant differences exist when only competitive groups are analyzed unless the complete dataset are used in the analysis.

Some supporting evidence exists for the hypothesis that pec-slapping adult females are attempting to attract males. However, the support is weak suggesting that this may only be a partial explanation.

4.2.3 Adult Females Pec Slap to Entice Male Competition

If adult female pec slapping were performed to entice male competition, we may expect to observe more frequent displacement of the primary escort in groups where the female is pec slapping. Out of 27 displacements observed, 22-33% followed pec slapping by the adult female, and 41% followed pec slapping or tail slapping by the adult female.

Adult female pec-slapping behavior can begin when males are near, then can be performed intermittently after the males have joined the group, and may persist for short periods after the males disaffiliate. This supports the idea that she continues to entice the males to compete until the challenging males have determined a successor, and disaffiliate from the group. Once the males are out of range, she ceases to pec slap. Since aggressive acts directed towards the female are very rarely witnessed, it would be to her advantage to invite male challengers to compete so that she can make an assessment about the fitness of her escort.

Although the properties of the sound of a pec slap are not well suited for long-range communication, pec-slapping acoustics may be directed at animals nearby or already in the pod. This may explain why pec slapping by females appears to begin when males are nearby.

Since one primary objective of adult females while on the breeding grounds is to seek out potential mates, reviewing potential female reproductive strategies may provide insight into the motivating factors that are driving adult females to pec slap.

4.2.3.1 Female choice

Whenever reproductive success is at stake for either gender, both sexes should be discriminatory in choosing mates (Fisher, 1958). In species such as humpback whales, males play no part in parenting their offspring. The male's only contribution to the offspring is his genes. Females have a much greater investment in their offspring and therefore have more at risk when selecting a partner. In such cases, the female is more likely to be selective of mates which have some fitness-promoting quality (Arak, 1983; Clutton-Brock, Guniess, & Albon, 1982; Darwin, 1871; Trivers, 1972).

When a female begins to ovulate, she may not necessarily mate with her current escort. In some species such as in ungulates, male "escorting" behavior is referred to as "tending" behavior. Adult female ungulates often attempt to replace an unwanted "tender" with a more fit, higher-ranking male (Hogg, 1984; Mathews & Adler, 1978; Mathews & Adler, 1979; Wolff, 1998). For example, American bison (*Bison bison*) cows show preference for higher ranking bulls and seek to replace their lower ranking tending bull by running away from him, or by approaching higher ranking males (Wolff, 1998). Tending male bighorn sheep (*Ovis canadensis*) must defend against other competing males and often mount the female and complete copulation as she runs (Hogg, 1984). These "female recruitment runs" will often solicit challengers that refused to challenge prior to the run, and can result in as many as 11 bulls in a single run (Wolff, 1998).

Humpback whale competition groups behave similarly to these female driven recruitment runs seen in some ungulates. Female humpbacks have been observed in competitive groups as large as 19 individuals (Baker & Herman, 1984; Clapham et al., 1992; Tyack & Whitehead, 1983).

Female African elephants are known to solicit guarding behavior from high-ranking males but rarely from low-ranking males (Poole, 1989). They facilitate mating with large musth males (characterized by an increased level of testosterone, increased aggression, and a temporary rise in dominance, (Schulte, 1999 #184)), by standing still. In contrast, they attempt to outrun younger non-musth males (Moss & Poole, 1983; Poole, 1982). Female elephants are also known to give a loud pulsated roar in the presence of a younger low-ranking male in attempts to attract the attention of nearby higher ranking males and prevent lower ranking males from mating with them (Poole, 1989).

Female humpback whales may be using similar strategies in attempts to mate with a higher-ranked or more-fit male. Glockner-Ferrari and Ferrari (1985), reported attempts by females in competitive groups to influence the choice of an escort, and Clapham et al. (1992), reported one instance of a female acting agonistically towards another male when the male was known to be a subadult. Size, endurance, and fighting ability would seem to be important male characteristics used for selection by females and physical competition between males could allow females to assess the fitness of a potential mate.

4.2.3.2 Estrus

The most advantageous time for males to exert energy in competition should be when the female nears ovulation. Although it is known that the sexual peak for female humpbacks occurs during the winter (Chittleborough, 1958, 1965; Mackintosh, 1942; Mathews, 1937), the actual duration of estrus for females of any mysticete is unknown (Clapham, 1996). Some humpback whales are known to be polyestrus in that if they do not conceive during their first ovulation, they may go into estrus a second time. Chittleborough (1954) calculated that 72% of females ovulated only once during a season but others ovulated 2 or 3 times.

The duration of estrus in many ungulate species that practice female escorting and engage in male-male competition is relatively short, only a matter of days. For example, in African elephants a female may have a single estrus period lasting 5 days every 4 years (Garstang, Larom, Raspet, & Lindeque, 1995; Moss & Poole, 1983). Estrus in American bison may last only 1-2 days (Asdell, 1964; Kirkpatrick, Kincy, Bancroft, Shideler, & Lasley, 1991) and as little as a few hours in Red Deer (Clutton-Brock et al., 1982). Some observations of female humpback whales observed in competitive groups over a period of 3 days (Clapham, 1996), would suggest a similar estrus duration.

4.2.3.3 Female Advertisement

In species where females have a relatively short estrus period, it is critical that they be able to advertise their state of receptivity quickly to as many males as possible. The advertising signal will vary according to the distance of the intended receiver(s).

For a female elephant that experiences a 2-6 day estrous period every 5 years, it is critical that she be able to attract distant mates quickly. They do this by producing low-pitched sounds often below the range of human hearing which can travel over great distances of at least 4 km away (Langbauer, Payne, Charif, Rapaport, & Osborn, 1991; Payne, Langbauer, & Thomas, 1986; Poole, Payne, Langbauer, & Moss, 1988), and potentially up to 10 km away (Larom, Garstang, Payne, Raspet, & Lindeque, 1997), to attract distant high-ranking males. The high-pressure acoustic properties of an estrous rumble (up to 117 dB SPL at 1 m) make it well suited as a location beacon (Langbauer, 2000). The fluctuating high and low frequency sweeps, and the richness of the harmonic can help the listener to localize the call and determine how distant the caller is (Langbauer, 2000).

How female humpbacks advertise estrus is unknown but considering the acoustical transmission properties of water, the most energetically efficient method to solicit distant males would be through vocalizations. Whether or not females produce low frequency or even subsonic vocalizations remains to be studied.

Chemical signals can also be an effective method of advertising estrus. Sex pheromones are chemicals secreted by one sex that cause behavioral reactions that facilitate mating in the opposite sex (Shorey, 1976). Some male ungulates (Lindsay, 1965) and potentially dolphins (Norris & Dohl, 1980) are known to be able to recognize a females state of receptivity from excreted sex pheromones. Most escorts position themselves slightly behind the female when escorting, one possible reason being the ability to monitor her hormonal state through her excretions.

In addition to long-range acoustic signals, short-range visual signals can also be effective. Elephant cows will perform a very distinctive "estrous walk" which involves walking around the outside of her family group, often looking back over her shoulder (Poole & Moss, 1981). When she is joined and guarded by a bull, she will often continue to walk slowly in circles while looking back to keep the bull in sight (Poole & Moss, 1981). This display is more suited for targeting nearby individuals.

Similarly to female elephants who attract the attention of nearby higher ranking males and prevent lower ranking males from mating with them (Poole, 1989), female humpback pec-slapping may indicate a discontent with her current principal escort. Pec slapping could entice more competition among the males, allowing the female to more effectively evaluate male fitness. It is also to her advantage to communicate to these males that she is in estrus. With little risk to herself within a competitive group, she maximizes her chances of a mating opportunity with the most fit male.

4.2.4 Mother and Calf Communication

While on the breeding grounds, the strongest bond that exists between two whales is that of a M and her C. During the C's early development, this M and C bond is likely strengthened through frequent tactile interactions. The M's visual contact of her C is apparent as she immediately moves towards her C when the C begins to approach an escort, a boat, or a diver. These retrievals by the M can accompany vocalizations by the M, C, or both (pers. obs).

Other methods of communication may take the form of surface-active behaviors. Ms are observed pec slapping in situations that appear to be independent of males. Ms alone with their C will sometimes erupt suddenly with surface activity. Unlike in competitive situations, the behavior performed is not necessarily exclusively pec slapping. A variety of behaviors are observed including breaching, head slapping, tail slapping, and peduncle slapping. This eruption of activity by the M tends to coincide with the C being surface active as well and both whales begin to exchange surface-active behaviors.

Humpback whales (Weinrich et al., 1992) and other cetaceans (Norris, 2002; Pace, 2000) have been known to learn through imitation. It is possible that humpback Ms and Cs are doing the same. The C may learn through observation of her M and by attempting to mimic her behavior. Investigating the sequence of behaviors between Ms and their C could provide insight into this hypothesis.

These signals may also carry with them information about the displayer's energy or emotional state. Pec slapping and other coinciding surface-active behaviors may be an attempt by the mother to discipline her C. Since the C may also be surface active while M is stationary below the surface, the C may perform the behavior in frustration towards the M who may be restricting the C from nursing (Coleman, 1994), or from pursuing other interests. When an E is not present, the group composition remains stable, suggesting the behaviors are likely intended for one another.

4.3 Adult Male Pec Slapping and its Implications for Communication

The reproductive success of male humpback whales is partially limited by access to a limited supply of females in estrous. Male humpbacks appear to move about in search of receptive females either by singing, traveling alone, or while escorting another female. Any associations between males appear to be fluid, unstable, and very short lived (Baker & Herman, 1984; Herman & Antinoja, 1977; Mobley & Herman, 1985; Tyack, 1983). Since competition rather than cooperation seems to exist between males on the wintering grounds, males should have little need for communication unless it's directly related to male-male dominance and reproduction. However, the idea of male-male cooperation on the wintering grounds (Brown & Corkeron, 1995), or the formation of coalitions (Clapham, 1996; Clapham et al., 1992) has not been discounted.

Several hypotheses have been proposed for adult male pec slapping and are discussed below.

4.3.1 Adult Male Pec Slaps are Aggressive Displays

If pec slapping were used as a display of aggression among competing males, we would expect to observe competing males pec slapping more often than non-competing males. Results of this study indicate that the reverse is true; non-competing males are observed pec slapping twice as often as competing males. We would also expect to find the largest and most dominant competing males (N1Es) (Spitz, 1999; Spitz, Herman, Pack, & Deakos, 2003) displaying pec slaps more often than subordinate N2Es. NIEs showed the lowest percentage of pec slapping among all male behavioral roles.

These data do not support the function of pec slapping by adult males as an aggressive display towards other males.

4.3.2 Adult Males Pec Slap to Repel Other Males

Significantly more disaffiliations occurred following pec slapping by adult males than when no pec slapping occurred. However, among pec slapping N2Es, the pec slapper was almost unequivocally the disaffiliating whale. Since attempting to repel males away is an agonistic behavior, pec slapping by males should accompany other aggressive displays. This is not the case, pec slapping by males rarely accompanied aggressive displays by the pec-slapping male.

When a lone male is joined by another male, the majority of the time the affiliation is brief and non-agonistic (Darling & Berube, 2001). One of the whales is often a singer whose song gets interrupted by the intruder. This second male may remain in close proximity to the singer for over an hour before actually affiliating (pers. obs.), possibly assessing or attempting to learn from the singer. The affiliation tends to be short (less than 20 min), and as the whales move apart, one may begin to pec slap. The pec slapper is sometimes the singer and sometimes the affiliate. Similar observations have been reported by Spitz (1999, p. 74). If pec slapping were a repellant, we would expect the behavior to occur only prior to the whales moving apart.

One or both whales have been observed pec slapping prior to an affiliation. If pec slapping prior to the affiliation were attempts to drive the partner whale away, there would be no need for both whales to pec slap since they could simply go their own separate ways.

One member of the pair often appears smaller in size, possibly a subadult. This younger whale may be learning from association with an active or passive partner. Further studies looking at the body size of male partners is needed to understand if age class is playing a role in these brief associations between males.

These data do not support male pec slapping as a repellant display to drive away other whales.

4.3.3 Males Pec Slap to Maintain Associations with Other Males

N2Es and 2Es will often pec slap immediately prior to or during their disaffiliation from a competitive group. In this context, pec slapping as a repellant behavior does not make sense since the pec slapper is clearly the individual disaffiliating. Pec slapping simply to indicate to others that you are about to leave the group seems energetically wasteful unless there is some potential benefit to the displayer. The female is unlikely to ever leave her more dominant principal escort in order to join a lower ranking secondary who was too unfit to displace the principal male. Therefore a display towards the female would most likely be ineffective.

What is observed quite frequently is the affiliation and disaffiliation of two or more males together. These whales generally behave in a non-agonistic way towards one another , possibly acting as a type of coalition (Clapham et al., 1992). Males prior to disaffiliating from the competitive group were observed pec slapping, but rarely when more than one whale was moving away form the main group. On the contrary, disaffiliating secondary escorts that were alone were much more likely to pec slap as the whale was moving away from the main group. This may be an attempt by the disaffiliating male to communicate to one or more males within the group to join him in the disaffiliation. Perhaps the signal is directed towards a whale that was already paired with the disaffiliating male within the competitive group.

Affiliate male pairs do not seam to cooperate with one another in attempts to displace principal escorts (pers. obs.). In fact, after one such displacement had taken place following the affiliation of a male pair together, the partner male then disaffiliated together with the displaced principal escort. Since male-male associations do not appear to be cooperative strategies to displace a principal escort, the purpose of this association is not clear. The association may simply be an act of learning to assist with social development.

If pec slapping by disaffiliating 2Es were a successful mechanism to invite other males within the group to join with him in the disaffiliation, we should expect to find pec slapping disaffiliates regain one or more male partners more often than non-pec slapping disaffiliates. This requires further investigation.

When both males in a dyad are observed pec slapping, the reciprocating pec slapper may signify a consensus to maintain the association and explains why in this context, both whales remain together. When only a single male is pec slapping in a dyad, the continuation of the behavior as the whales move farther and farther away seems to support the idea that pec slapping is an attempt to maintain the affiliation. In some cases pec slapping does not begin until the whales have already begun moving some distance apart.

Escorts in groups with C had higher percentages of pec slapping among adult male behavioral roles, however the difference was not statistically significant. Spitz (1999) found that 37.1% of single escorts were of sexually immature size but only 5.6% of principle escorts were of immature size. Many of these escorts in C groups may be subadult males. Subadults were observed pec slapping twice as often as adults. If these escorts in C groups represent smaller and younger males, higher percentages of pec slapping among these males may result from subadult tendencies.

What is commonly seen in a MCE groups with a pec-slapping E outside of the context of affiliating males, is seemingly antagonistic behavior by the E towards the M. Generally escorts remain quite passive, almost always trailing behind the mothers. In the context of a pec-slapping E, they are frequently observed moving out in front of the M, cutting off her direction of travel, and causing her to change her direction. This behavior appears to be antagonistic. Why the E would resort to antagonistic behavior towards the M is unclear. Pec slapping does not appear to be a threat display so this would be incompatible with aggression towards the M. Perhaps the antagonism is a response to the females disinterest in him (see Glockner-Ferrari and Ferrari (, 1985 #28), Clapham et al. (1992)), and the pec slapping is communicating his interest to maintain the affiliation. This non-typical behavior by Es directed towards Ms may be attributable to their young age and subadult tendencies.

These data provide supporting evidence that pec slapping may be communicating an intention by one male to maintain an affiliation with another male.

4.4 Subadult Pec Slapping and its Implications for Communication

4.4.1 Practice and Play

Growth and development for calves on their wintering grounds is a critical element necessary for survival and preparation for the return migration to the feedings grounds. To assist in development, calves may perform a variety of behaviors for the sole purpose of developing muscle and muscle coordination. These types of behaviors, considered "play", are common in young mammals (Fagen, 1981). By performing a mixture of behaviors, different muscles are developed and body coordination can improve.

The M may encourage the learning and development of certain behaviors by performing the behavior initially and having her calf mimic. Practice or play can involve the performance of a variety of behaviors at one time since the performer is not intentionally communicating. This could explain why C surface-active behaviors generally involve performing many different behaviors at one time. Pec slapping, a behavior that requires more coordination than a head slap or a breach, is not observed as frequently by calves as other behaviors. More sophisticated behaviors such as pec slapping may not be as necessary communicatively for a calf until much later in development. The M must find a balance between energy conservation of her limited resources while facilitating and encouraging physiological development of her C. She may do this by regulating bouts of activity, by initiating or terminating them, causing the C to respond in turn by also becoming surface active or by ceasing activity.

While on the breeding grounds, subadults (including Ys no longer with their Ms), have much different objectives than adults or calves. Since feeding is absent and they are not yet mature enough to participate in sexual activity, the seemingly barren breeding grounds appear to have little to offer them. However, an important aspect of immature development may involve learning through practice and observation of others.

Ys no longer with their Ms begin to behave more similarly to Js. More sophisticated behaviors such as pec slapping, tail slapping, and peduncle slapping are performed more frequently along with other surface active behaviors such as head slaps, breaches, tail swishes, tail extensions, underwater blows, and head rises.

Among lone Js, rarely do surface-active individuals seem to be directing their behaviors to nearby whales, and rarely do these behaviors involve other whales joining or leaving. The contexts surrounding these lone J pec slappers included: close approaches to boats, manipulation of debris in the water such as a piece of mesh or rope, the pursuit of dolphins, or even surfing wave swells. These are all contexts in which the active attempt by the performer to communicate to another whale seems absent. This is quite different from adult performers who’s pec-slapping behavior seems more directed at some type of endpoint, usually involving male competition, male associations, group composition changes, or simply M-C interactions.

Compared with Cs, the behavioral repertoire of surface-active behaviors increases in Ys and furthermore in Js. The Y appears to switch from one behavior to the next haphazardly. Pec slapping among J whales appears to be undirected towards a specific end goal and may also be a form of practice or play, aiding in the continued development of musculature and coordination. Practice or play should not be gender specific, which is also supported by these data. As Js mature, social interactions with other whales may become important. Pec slapping may act as a signal to nearby animals about an interest to create or maintain an affiliation.

4.5 Summary

1. Pec slap sounds can travel up to 7 km or more.
2. Subadults pec slap more than adults.
3. Females pec slap more than males.
4. Competitive females pec slap more than non-competitive females.
5. Competitive female pec slappers are likely soliciting competition between males when pec slapping and unlikely attempting to drive males away.
6. Non-competitive males pec slap more than competitive males.
7. Pec slapping is not an aggressive or dominance display between adult males.
8. Adult male pec slapping appears to be an attempt to initiate or maintain an affiliation with one or more other males.

9. Subadults perform an array of other surface-active behaviors in combination with pec slapping, possibly as a form of practice or play.

10. Calves are potentially learning complex behaviors by imitation of their mother.

11. Pec slapping is not correlated with pod size.

4.6 Conclusions

As is the case for many behaviors in the animal kingdom, pec slapping appears to be used by different individuals under different contexts. This can make attributing function very difficult since the same behavior by the same animal may carry a different function within a different context. In general, the percentage of pec slapping behavior performed by an individual has been shown to be dependent on the individual's age class, sex, and social role.

Overall these data seem to support pec-slapping behavior in adults as a mechanism for drawing attention to the performer of one or several nearby whales. In the context of competition, adult males and females use the behavior differently based on their social objectives.

Adult females perform the behavior within competitive groups, most likely to draw attention from nearby surrounding males, encouraging competition, indicating her readiness to mate, and possibly advertising her discontent with the current principal escort. Ms may pec slap in attempts to solicit surface activity from their calves through mimicry in order to encourage muscle development and coordination, and also to strengthen M-C social bonds.

Among adult males, pec slapping seems less integrated with competition and is observed more in non-agonistic male-male associations. Its lack of performance by dominant males in competition does not support its use as a threat or dominance display. Pec slapping is more often performed by males while disaffiliating from a partner or a group of whales, possibly in efforts to encourage one or more whales to remain with him.

Young whales perform pec-slapping behavior in almost every context. Pec-slapping by subadults rarely seems to correspond to outside stimuli unlike in adults, where the behavior seems more directed and specific to particular contexts. These surface-active-behavior episodes are likely a form of “play”, an important characteristic in the development, coordination, and learning in young mammals.

This improved understanding of who is performing pec-slapping behavior and the proposed theories of why it is being performed can serve as tools in helping researchers better interpret humpback whale social interactions and behavior in the field.

Follow up studies should expect to find principal escorts in groups with a pec-slapping NA or M to be smaller in size, and have a higher frequency of displacement than competitive groups in which the NA or M is not pec slapping. The pec slapper in a male-male dyad should be the smaller of the two males as he is more likely to attempt to maintain an association. A pec-slapping NA or M should be more likely to have a C the following season than a non-pec-slapping adult female. An N2E or 2E who pec slaps during his disaffiliation should gain an affiliate partner more often than one who doesn't pec slap, and male disaffiliations in groups should have lower percentages of pec slapping than lone-male disaffiliates. Lastly, pec-slapping Es and pec-slapping males in male-female dyads should be smaller in size than non-pec-slapping males found in these behavioral role.

APPENDIX A. TABLES

Table 1. Description of the different variables used in the database.

Variable	Description
Date	The date the group was observed
Group Number	The number sequencing the group observed that day starting with 1
Group Composition	A description of the number of whales in the group and each of their behavioral roles
Affiliation/Disaffiliation Before	This was a flag if an affiliation or a disaffiliation was observed just previous to this group
Affiliation/Disaffiliation After	This was a flag if an affiliation or disaffiliation was observed during our observation of this group
Number of Whales	Total number of whales in the group
Narration	A descriptive summary of the group observations
Underwater Narration	Descriptive summaries of all underwater observation for that group
Behavioral Role of Pec Slapper	Social role assigned to the pec slapper (see below)
Overall Behaviors Performed	A summary of all behaviors observed
Gender of Pec Slapper	Sex of the pec slapper confirmed from underwater observation
Total Number of Pec Slaps Observed	Total count of pec slaps by an individual
Starting Time	The time of day we began observing the group
Ending Time	The time of day we terminated observation of the group or the time a group changes composition
Total Time Observed	Time elapsed between the starting time and ending time

Table 2. Summary of the total number of humpback whale groups and individuals observed between 1997 and 2001 in Maui waters, their mean observation times, pec slapping percentages, and percentages in competitive groups.

	Non-Pec Slapping	Pec Slapping	Total	Percentage Observed Pec Slapping	Percentage in Competitive Groups
Whale Groups	2627	537	3164	17%	28%
Individual Whales	8233	591	8824	7%	47%
#Mean Observation Period per Group (min)	38.78	58.47	2,222 hrs		
Standard Deviation (min)	32.85	44.58			
*Mean Observation Period per Whale (min)	47.13	58.85	7,126 hrs		
Standard Deviation (min)	44.02	43.82			

Difference is significant ($t(660, N = 3164) = -9.71$, $P < 0.05$)

* Difference is significant ($t(678, N = 8824) = -5.97$, $P < 0.05$)

Table 3. The distribution and percentage of individual observations, their mean observation times, and percentage observed pec slapping according to the length of time the individual was observed.

Observation Period (min)	Number of Individual Observations	Percentage of All Individual Observations	Non pec slapping individuals	Mean Observation Time (h:m:S)	Pec slapping individuals	Mean Observation Period (h:m:s)	Percentage of All individuals Pec Slapping
< = 1	155	2%	153	0:00:15	2	0:00:17	1%
1-20	1902	22%	1818	0:12:09	84	0:12:12	4%
20-40	2638	30%	2487	0:30:08	151	0:31:10	6%
40-60	1762	20%	1633	0:49:23	129	0:49:32	7%
60-80	1002	11%	912	1:09:01	90	1:08:35	9%
80-100	590	7%	536	1:29:43	54	1:30:14	9%
100-120	374	4%	347	1:48:16	27	1:50:10	7%
120-140	159	2%	130	2:07:43	29	2:07:43	18%
>140	242	3%	217	3:49:52	25	3:17:37	10%
Overall	8824	100%	8233	0:47:43	591	0:58:51	7%

Table 4. Summary of the total number of groups and individual whales observed between a 60 and 120 min observation period, as well as the percentage of the original dataset, the percentage pec slapping, and the percentage in competitive groups.

	Non-Pec Slapping	Pec Slapping	Total	Percentage of Original Data	Percentage Observed Pec Slapping	Percentage in Competitive Groups
Groups	422	160	582	18%	27%	37%
Individual Whales	1793	171	1964	22%	9%	60%
#Mean Observation Period per Group (min)	80.41	81.65	777 hrs			
Standard Deviation (min)	15.51	16.67				
*Mean Observation Period per Whale (min)	82.78	81.98	2,710 hrs			
Standard Deviation (min)	16.35	16.67				

Difference is not significant (t (580, N = 582) = -0.83, P > 0.05)

* Difference is not signficant (t (202, N = 1964) = 0.60, P > 0.05)

Table 5. Distribution of individuals observed pec slapping and non-pec slapping and their percentages observed pec slapping according to their observation period between 60 and 120 min.

Observation Period (min)	Non pec slapping individuals	Pec slapping individuals	Percentage of individuals Pec Slapping	X^2 (2,1964)
60-80	911	90	9%	
80-100	535	54	9%	1.30*
100-120	347	27	7%	

*Difference is not significant ($P > 0.05$)

Table 6. Individual pec slapping percentages contrasted over 9 group characteristics and tested for significance.

Group Characteristic	Mean Non Pec-Slapping Obs. Period (h:m:s)	Mean Pec-Slapping Obs. Period (h:m:s)	Student T-test	df	*N*	Probability	Total Non-Pec-Slapping Individuals	Total Pec-Slapping Individuals	Percentage Pec Slapping	X^2 (1,1964)
All individuals	1:22:47	1:21:59	0.60	202	1964	0.55	1793	171	9%	
No Mother	1:23:46	1:22:06	1.01	139	1261	0.31	1145	116	9%	1.38
With Mother	1:21:04	1:21:24	-0.14	60	703	0.89	650	53	8%	
No Calf	1:24:07	1:22:31	0.98	142	1299	0.33	1180	119	9%	1.31
With Calf	1:20:13	1:20:22	-0.07	57	665	0.94	615	50	8%	
No Yearling	1:22:30	1:21:32	0.73	195	1919	0.47	1754	165	9%	0.04
With Yearling	1:34:33	1:36:20	-0.16	3	45	0.88	41	4	9%	
No Juvenile	1:22:51	1:21:46	0.79	194	1949	0.43	1784	165	8%	4.17*
With Juvenile	1:11:51	1:26:09	-2.44	6	15	0.05	11	4	27%	
No Male	1:16:49	1:16:05	0.11	193	86	0.91	78	8	9%	0.00
With Male	1:23:03	1:22:16	0.58	6	1878	0.57	1715	163	9%	
No Singer	1:22:41	1:21:55	0.56	8	1887	0.57	1724	163	9%	7.75*
With Singer	1:25:04	1:20:43	0.51	193	77	0.63	71	6	8%	
No Competition	1:19:13	1:21:37	-1.27	90	784	0.21	708	76	10%	1.74
With Competition	1:25:07	1:22:05	1.60	107	1180	0.11	1087	93	8%	
No Dolphins	1:22:44	1:21:54	0.61	197	1943	0.54	1776	167	9%	0.06
With Dolphins	1:27:48	1:20:25	1.77	7	21	0.12	19	2	10%	
Single Adults	1:16:32	1:25:49	-0.91	4	29	0.41	25	4	14%	0.00#
Dyad Adults	1:19:06	1:21:04	-0.66	34	247	0.51	218	29	12%	

X^2 (1, 276)

*Difference is significant ($P < 0.05$)

Table 7. List of mean observation effort and pec-slapping percentages for whales based on age class and gender. Statistical results of percentage comparisons are presented.

Behavioral Role	Mean Non Pec-Slapping Period (h:m:s)	Mean Pec-Slapping Period (h:m:s)	Student T-test for Proportion Effort	df	*N*	P	Total Non-Pec-Slapping Individuals	Total Pec-Slapping Individuals	Percentage Pec Slapping	X^2 (1,N)	*N*
Subadults	1:19:35	1:20:01	-0.13	31	222	0.90	192	26	12%	9.42*	1964
Adults	1:23:01	1:21:59	0.60	119	1746	0.55	1639	107	6%		
Adult Females	1:20:59	1:22:20	-0.59	77	494	0.56	426	63	13%	52.26*	1746
Adult Males	1:23:44	1:21:29	0.86	46	1262	0.40	1213	44	4%		

*Difference is significant (P < 0.05)

Note: Half the dyads were included as adult females (assuming 50% female, see Figure 13)

Table 8. List of mean observation efforts and pec-slapping percentages for each behavioral role. Statistical results for behavioral role comparisons are presented.

Behavioral Role	Mean Non Pec-Slapping Period (h:m:s)	Mean Pec-Slapping Period (h:m:s)	Student T-test for Proportion Effort	df	*N*	P	Total Non-Pec-Slapping Individuals	Total Pec-Slapping Individuals	Percentage Pec Slapping	X^2 (df,N)	df	*N*
Mother	1:19:23	1:24:01	-1.11	18	207	0.28	190	17	8%	9.38*	1	370
Nuclear Animal	1:25:30	1:19:51	1.60	44	163	0.12	131	32	20%			
Single Escort	1:18:54	1:15:35	0.41	3	109	0.71	115	5	4%	6.00	5	1109
Primary Escort	1:22:46	1:39:40	-3.43	2	46	0.08	44	2	4%			
Secondary Escort	1:25:27	1:14:52	2.65	6	165	0.04*	159	6	4%			
Nuclear Primary	1:24:18	1:16:26	n/a#	n/a	163	n/a	162	1	1%			
Nuclear Secondary	1:25:20	1:26:17	-0.15	11	586	0.88	574	12	2%			
Singer	1:21:44	1:03:00	n/a#	n/a	29	n/a	28	1	3%			
Calf	1:19:16	1:18:48	0.12	34	197	0.12	176	21	11%	2.43	2	222
Yearling	1:30:39	1:30:43	0.00	1	13	0.99	11	2	15%			
Juvenile	1:12:12	1:21:22	-2.23	9	12	0.05	9	3	25%			
Lone Adult	1:16:32	1:25:49	-0.91	4	29	0.41	25	4	14%	0.00	1	276
Dyad Partner	1:19:06	1:21:04	-0.66	34	247	0.51	218	29	12%			

#t-test unvailable due to insufficient sample size

*Difference is significant ($P < 0.05$)

Table 9. List of mean observation efforts and pec-slapping percentages for adult female behavioral roles. Statistical results of adult female behavioral role comparisons are presented.

Behavioral Role	Mean Non Pec-Slapping Period (h:m:s)	Mean Pec-Slapping Period (h:m:s)	Student T-test for Proportion Effort	df	*N*	P	Total Non-Pec-Slapping Individuals	Total Pec-Slapping Individuals	Percentage Pec Slapping	X^2 (1,N)	*N*
<u>Females</u>											
Non-Comp. Groups (2A+M)	1:18:23	1:25:49	-2.32	27	286	0.03*	262	24	8%	10.70*	494
Comp. Groups (NA+M)	1:25:03	1:20:12	1.52	53	208	0.13	169	39	19%		
Non-comp., No C (2A)	1:18:24	1:25:59	-1.70	16	124	0.11	110	14	11%	3.05	287
Comp., No C (NA)	1:25:30	1:19:51	1.60	44	163	0.12	131	32	20%		
Non-comp., With C (M)	1:18:22	1:25:37	-1.51	10	162	0.16	152	10	6%	2.96	207
Comp., With C (M)	1:23:29	1:21:45	0.22	7	45	0.83	38	7	16%		
Comp., No C (NA)	1:25:30	1:19:51	1.60	44	163	0.12	131	32	20%	0.16	539
Comp., With C (M)	1:23:29	1:21:45	0.22	7	45	0.83	38	7	16%		
No C (NA+2A)	1:22:15	1:21:43	0.19	59	287	0.85	241	46	16%	5.91*	207
With C (M)	1:19:23	1:24:01	-1.11	18	207	0.28	190	17	8%		

*Difference is significant ($P < 0.05$)

Note: Half the dyads were included as adult females (assuming 50% female, see Figure 10)

Table 10. List of mean observation efforts and pec-slapping percentages for adult male behavioral roles. Statistical results of adult male behavioral role comparisons are presented.

Behavioral Role	Mean Non Pec-Slapping Period (h:m:s)	Mean Pec-Slapping Period (h:m:s)	Student T-test for Proportion Effort	df	*N*	P	Total Non-Pec Slapping Individuals	Total Pec-Slapping Individuals	Percentage Pec Slapping	X^2 (1,N)	*N*
<u>Males</u>											
Non-Comp. Groups	1:19:15	1:19:21	-0.03	25	302	0.98	279	23	8%	18.53*	1262
Comp. Groups	1:25:03	1:23:50	0.31	21	960	0.76	939	21	2%		
Without Calf	1:24:04	1:21:30	0.79	32	931	0.43	900	31	4%	0.11	1262
With Calf	1:22:46	1:21:27	0.29	13	331	0.77	318	13	3%		

*Difference is significant (P < 0.05)

Note: Half the dyads were included as adult males (assuming 50% male, see Figure 10)

Table 11. The number of affiliations and disaffiliations that were observed before and after pec slapping was performed by a single whale.

		Preceeding a New Observation Period				Following a New Observation Period			
	Behavioral Role	No Affiliations	Affiliations	No Disaffiliations	Disaffili-ations	No Affiliations	Affiliations	No Disaffiliations	Disaffili-ations
Intermediate Pec Slapper	M	11	2	11	2	13	0	10	3
	M(Comp)	7	0	4	3	7	0	4	3
	NA	28	6	29	5	27	7	25	9
	All Adult Females	39	8	40	7	40	7	35	12
	E	6	0	6	0	6	0	6	0
	E/S	1	0	1	0	1	0	1	0
	1E	3	0	3	0	3	0	3	0
	2E	3	1	4	0	4	0	2	2
	N1E	0	1	1	0	1	0	0	1
	N2E	10	1	8	3	11	0	4	7
	S	1	0	1	0	0	1	1	0
	All Adult Males	24	3	24	3	26	1	17	10
No Intermediate Pec Slapper	M	301	13	294	20	302	12	304	10
	M(Comp)	32	10	37	5	37	4	34	7
	NA	130	26	133	23	140	16	119	37
	All Adult Females	431	39	427	43	442	28	423	47
	E	180	3	174	9	182	1	181	2
	E/S	13	0	10	3	9	4	12	1
	1E	32	10	37	5	38	4	35	7
	2E	47	25	67	5	67	5	57	15
	N1E	130	26	133	23	140	16	119	37
	N2E	407	116	466	57	480	43	385	138
	S	71	1	65	7	67	5	72	0
	All Adult Males	881	181	953	109	983	78	861	200

Table 12. Percentage of affiliations and disaffiliations occurring both before and after pec-slapping behavior was observed and contrasted with specific behavioral roles.

	Prior to New Observation Period		Following New Observation Period	
Comparison	Affiliation	Disaffiliation	Affiliation	Disaffiliation
Adult Females Pec Slapping	17%	15%	15%	26%
Adult Males Pec Slapping	11%	11%	4%	37%
X^2 (1, N = 74)	***0.12***	***0.01***	***1.22***	***0.61***
Adult Females Not Pec Slapping	8%	9%	6%	10%
Adult Females Pec Slapping	17%	15%	15%	26%
X^2(1, N = 517)	***2.95***	***1.02***	***4.10****	***8.71****
Adult Males Not Pec Slapping	17%	10%	7%	19%
Adult Males Pec Slapping	11%	11%	4%	37%
X^2(1, N = 1088)	***0.31***	***0.03***	***0.12***	***4.48****
NA Not Pec Slapping	17%	15%	10%	24%
NA Pec Slapping	18%	15%	21%	26%
X^2(1, N = 190)	***0.01***	***0.07***	***1.91***	***0.01***
N2E Not Pec Slapping	22%	11%	8%	26%
N2E Pec Slapping	9%	27%	0%	64%
X^2(1, N = 534)	***0.45***	***1.49***	***0.19***	***5.79****

*Difference is significant (P < 0.05)

Table 13. Regression of the percentage of pec slapping observed according to behavioral role against the number of secondary or nuclear secondary escorts in the pod.

Behavioral Role	R Square	Probability
Nuclear Animals	0.11	0.59
Mothers	0.71	0.16
Nuclear Secondary Escorts	0.01	0.89
Secondary Escorts	0.07	0.74

APPENDIX B. FIGURES

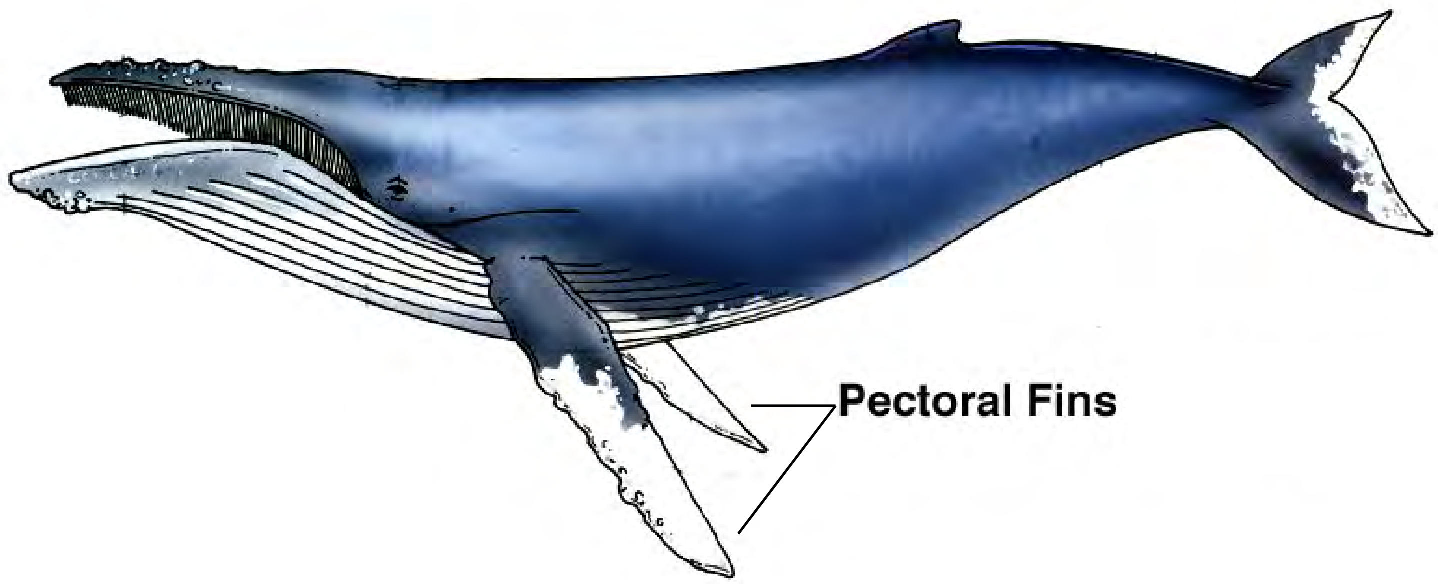
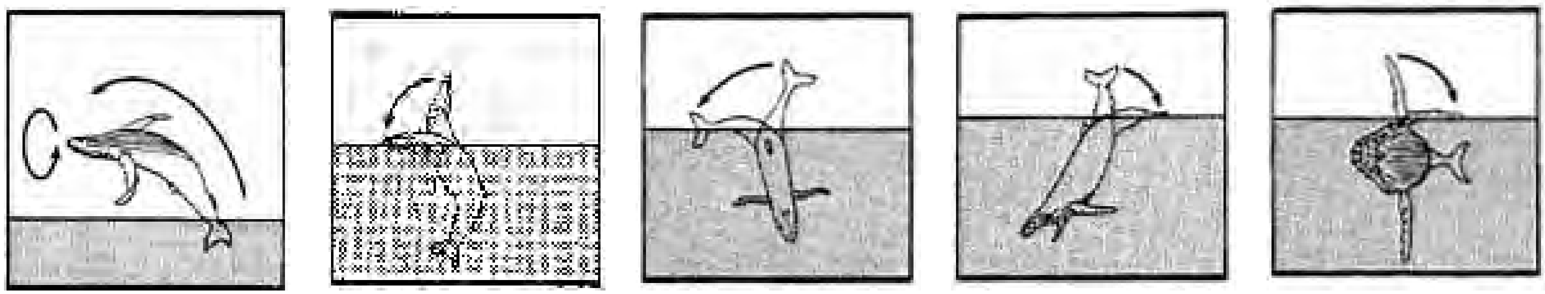


Figure 1. Illustration of humpback whale pectoral fins.



Breach. **Head Slap.** **Peduncle Slap** **Tail Slap** **Pec Slap**

Figure 2. Illustrations of common humpback whale surface-active behaviors.

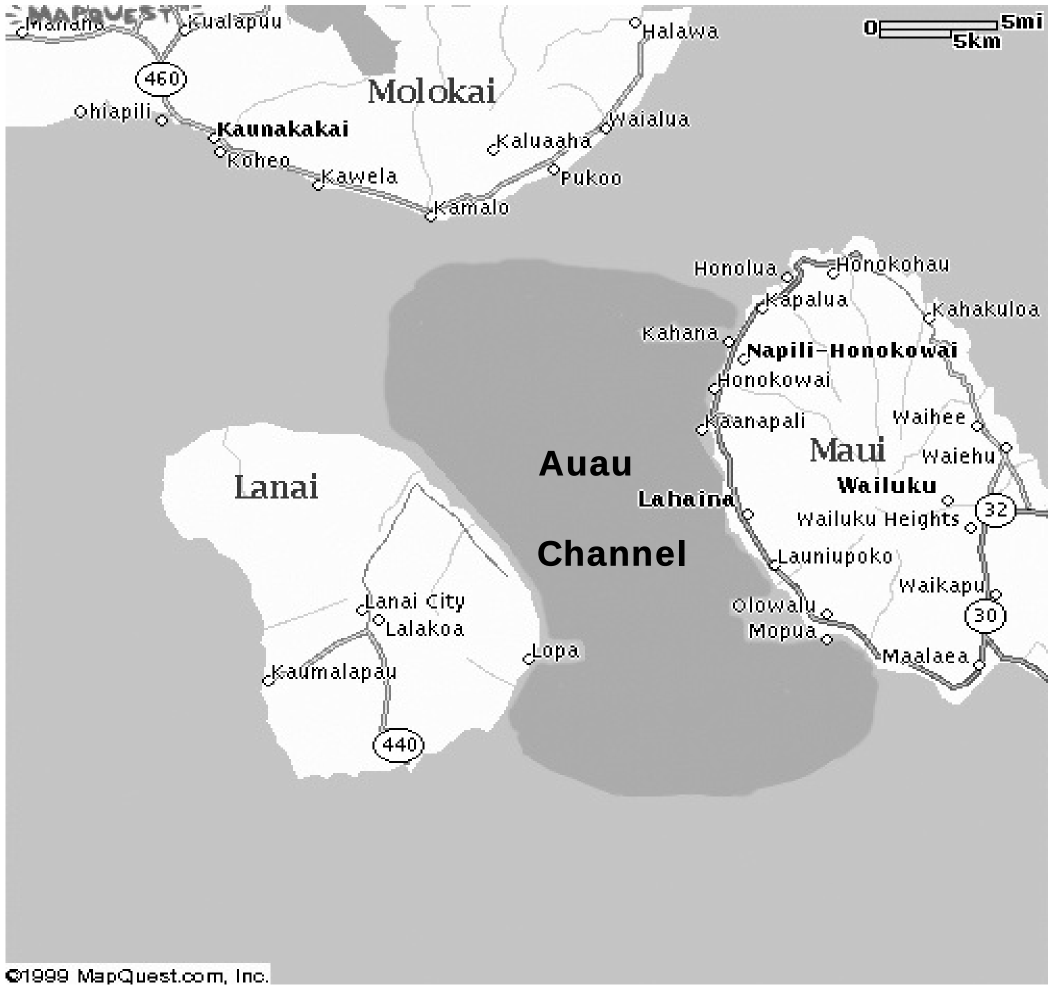


Figure 3. Maui study area. Most surveys were conducted within the dark gray highlighted region.

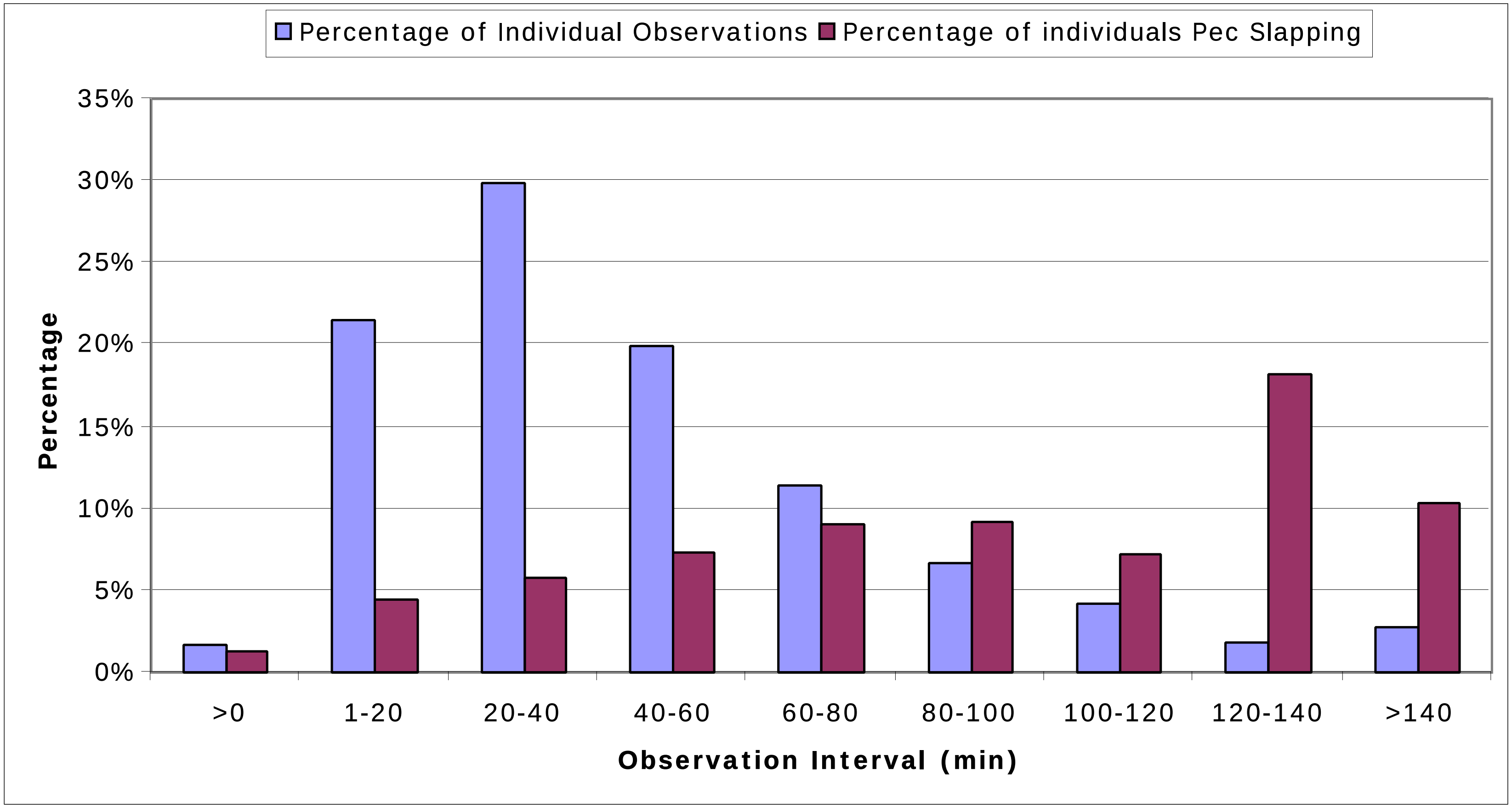


Figure 4. Comparison between the percentage of all observations and the percentage of pec slapping for each observation interval. The circle indicates the subset of data selected for analysis.

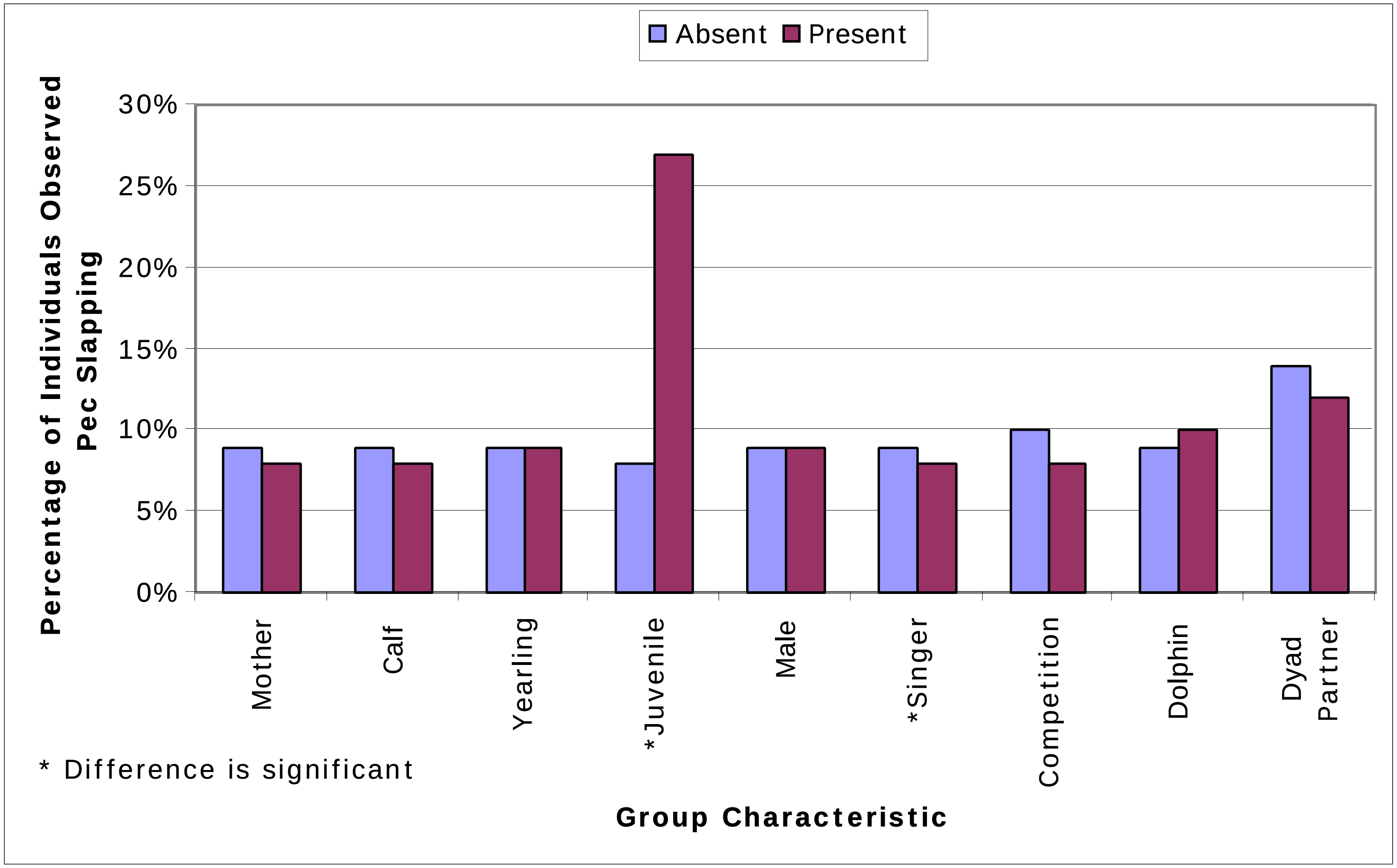


Figure 5. Percentage of individuals observed pec slapping contrasted over the presence or absence of 9 different group characteristics.

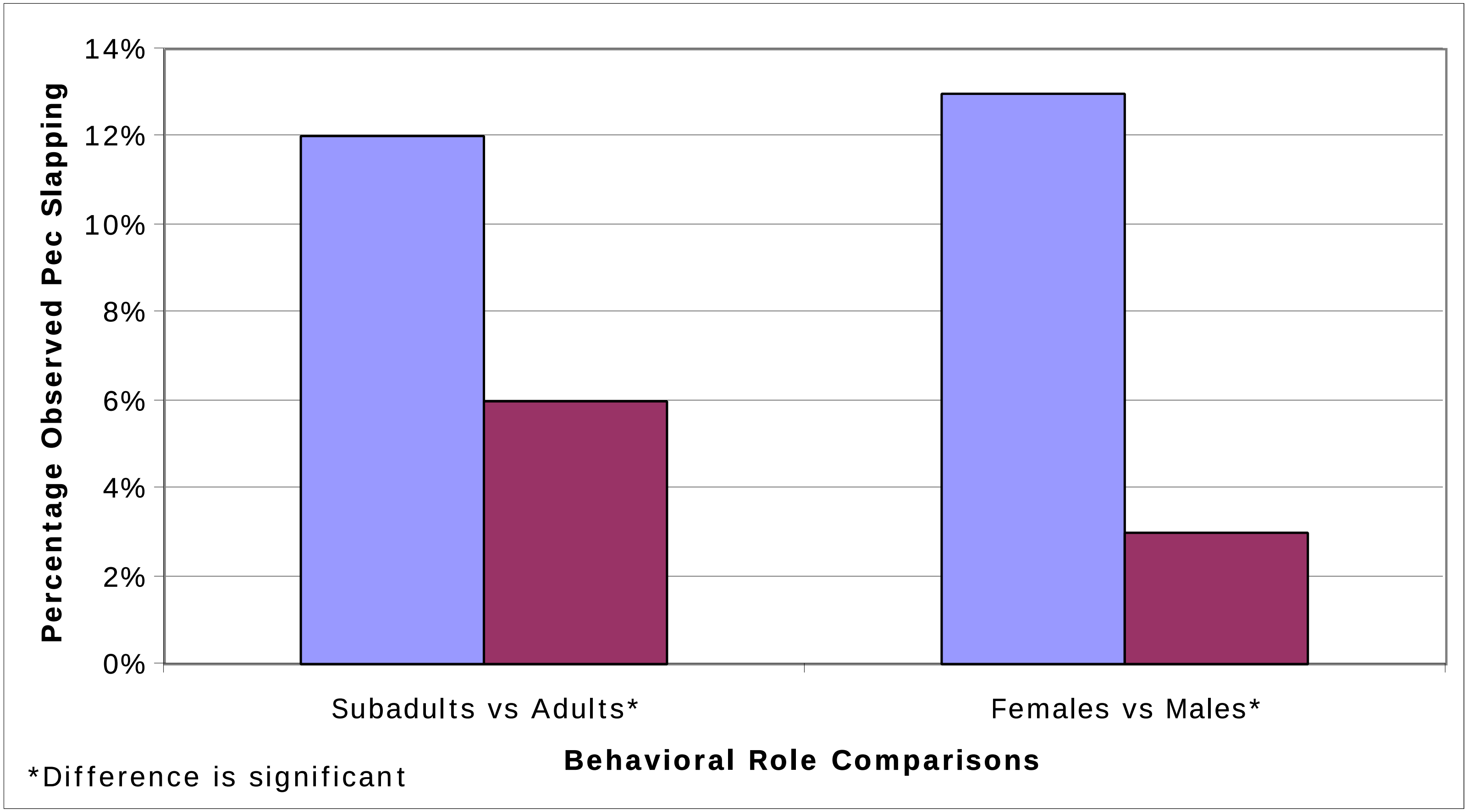


Figure 6. Pec slapping percentages compared for age class and gender.

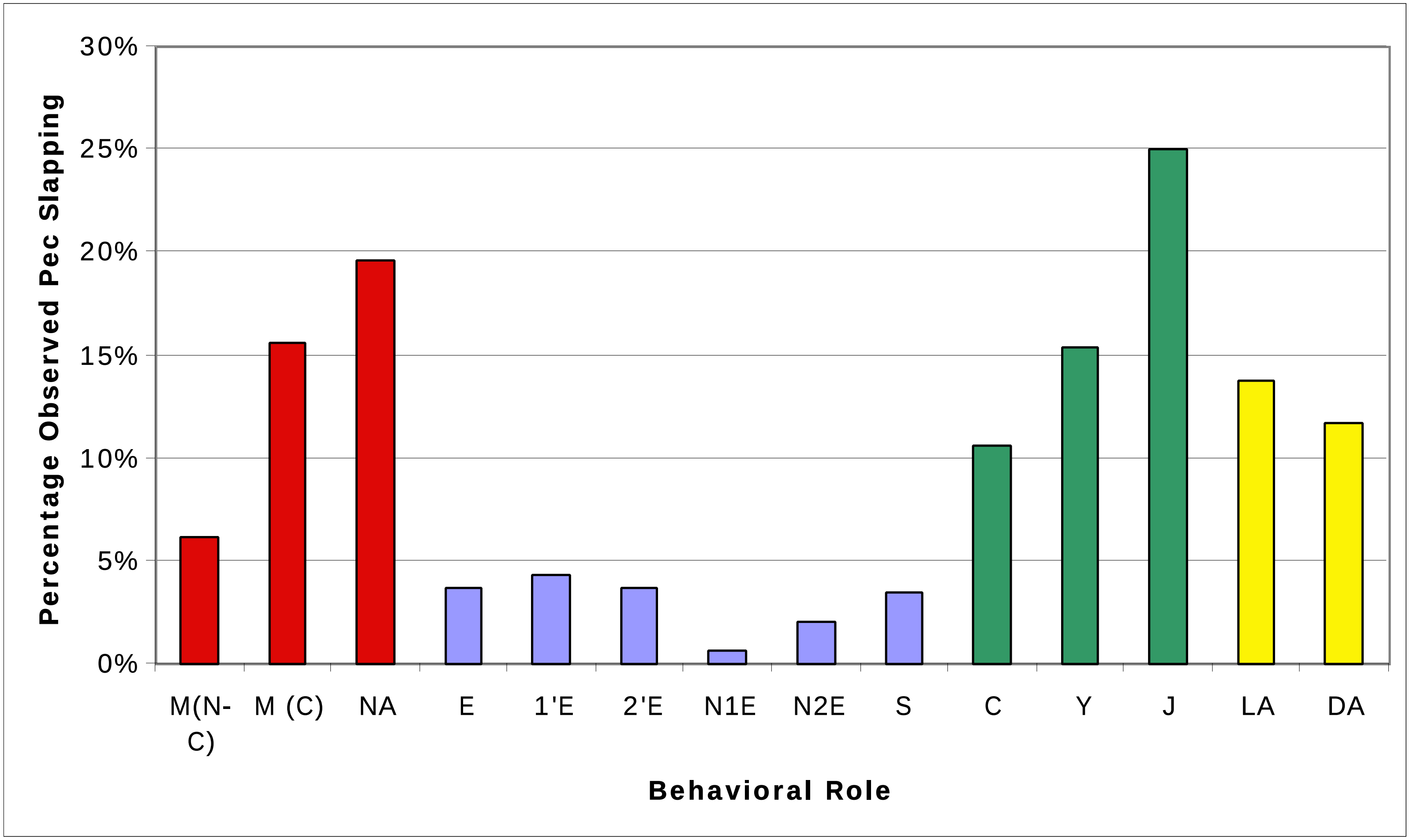


Figure 7. Percentage of pec slapping observed according to male, female, and neutral behavioral roles.

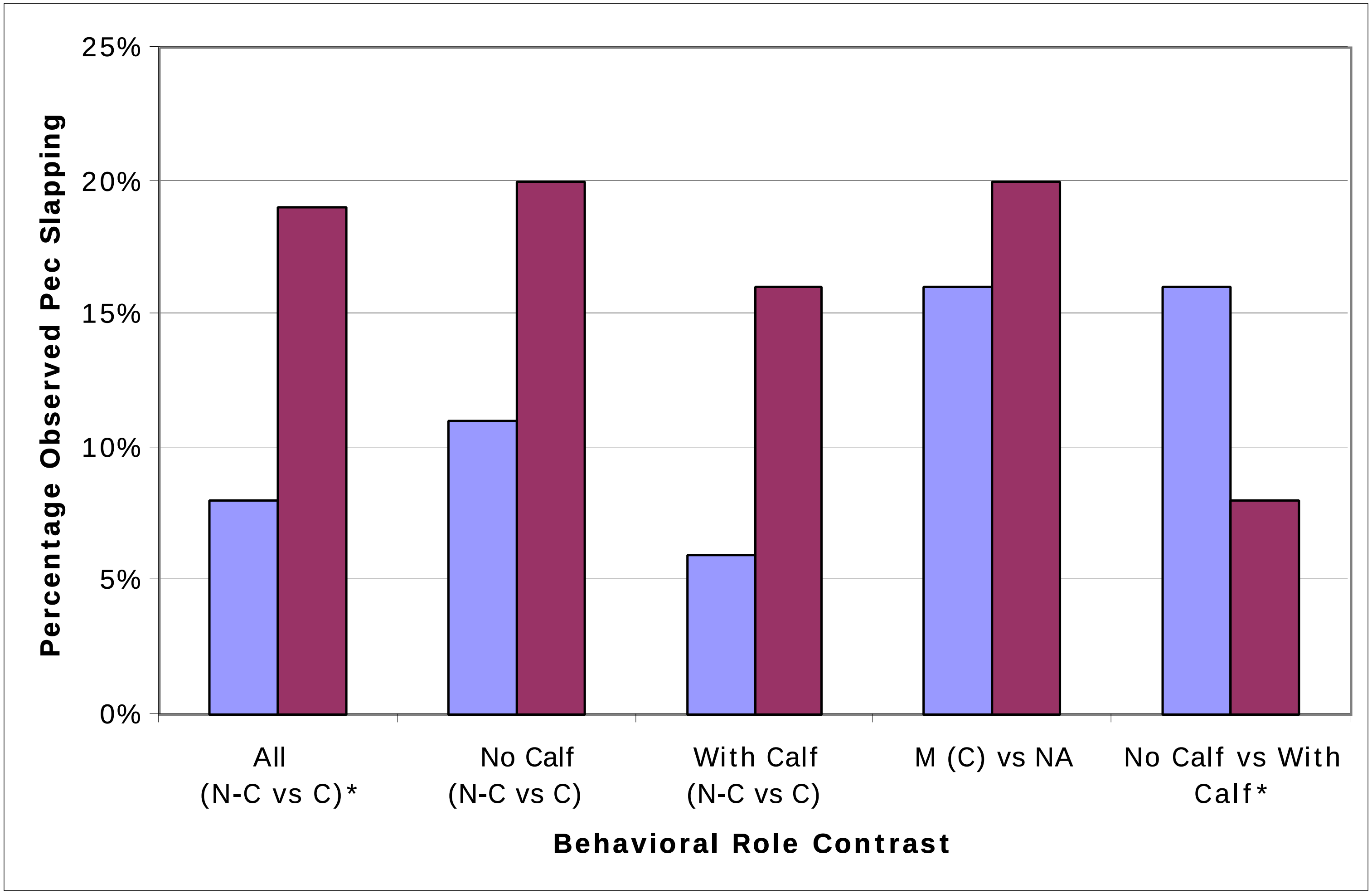


Figure 8. Five adult female behavioral role contrasts comparing the percentages of pec slapping and their significance.

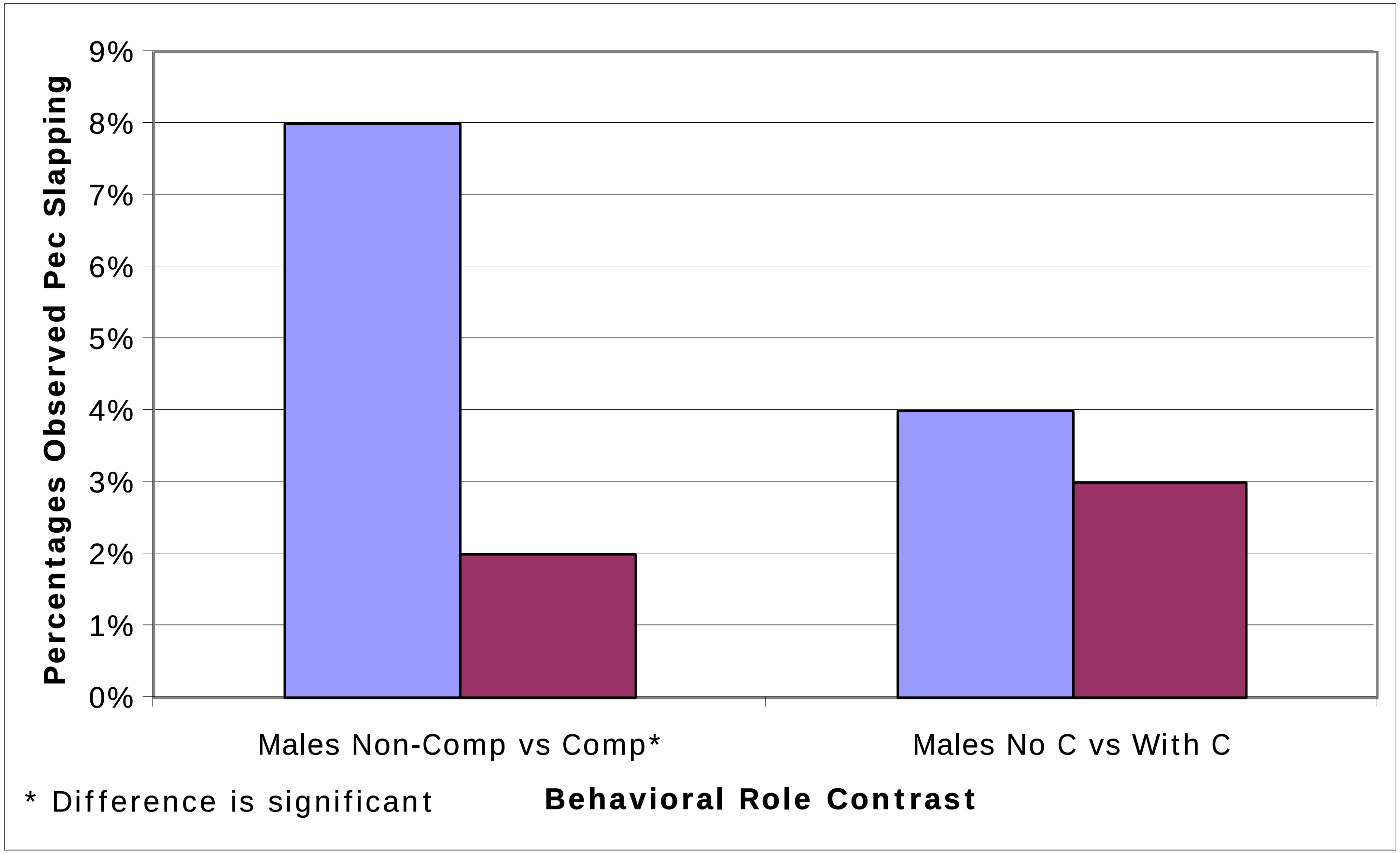


Figure 9. Two adult male behavioral role contrasts comparing the percentages of pec slapping and their significance.

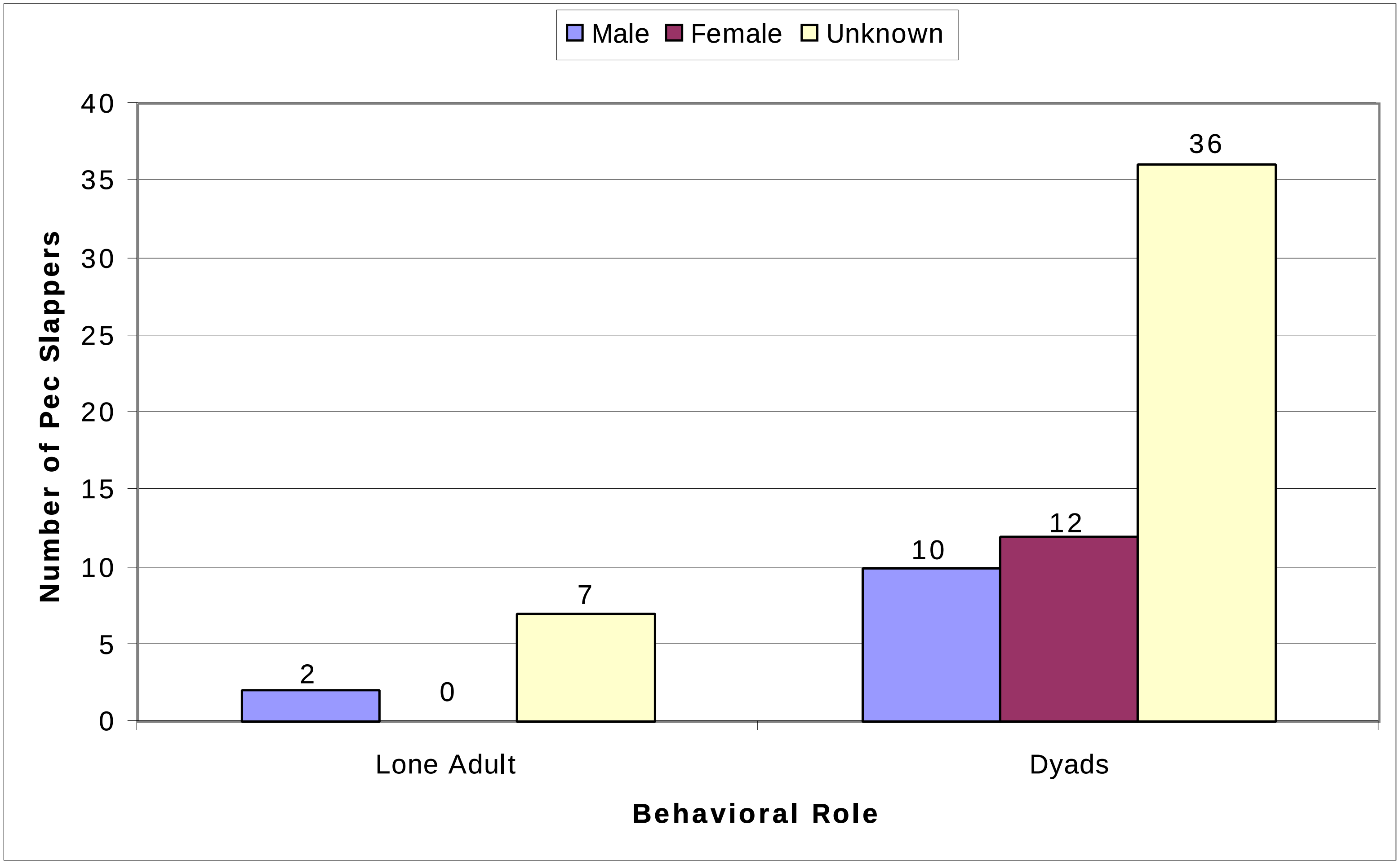


Figure 10. Distribution of individual pec slapper genders among lone adults and dyad groups.

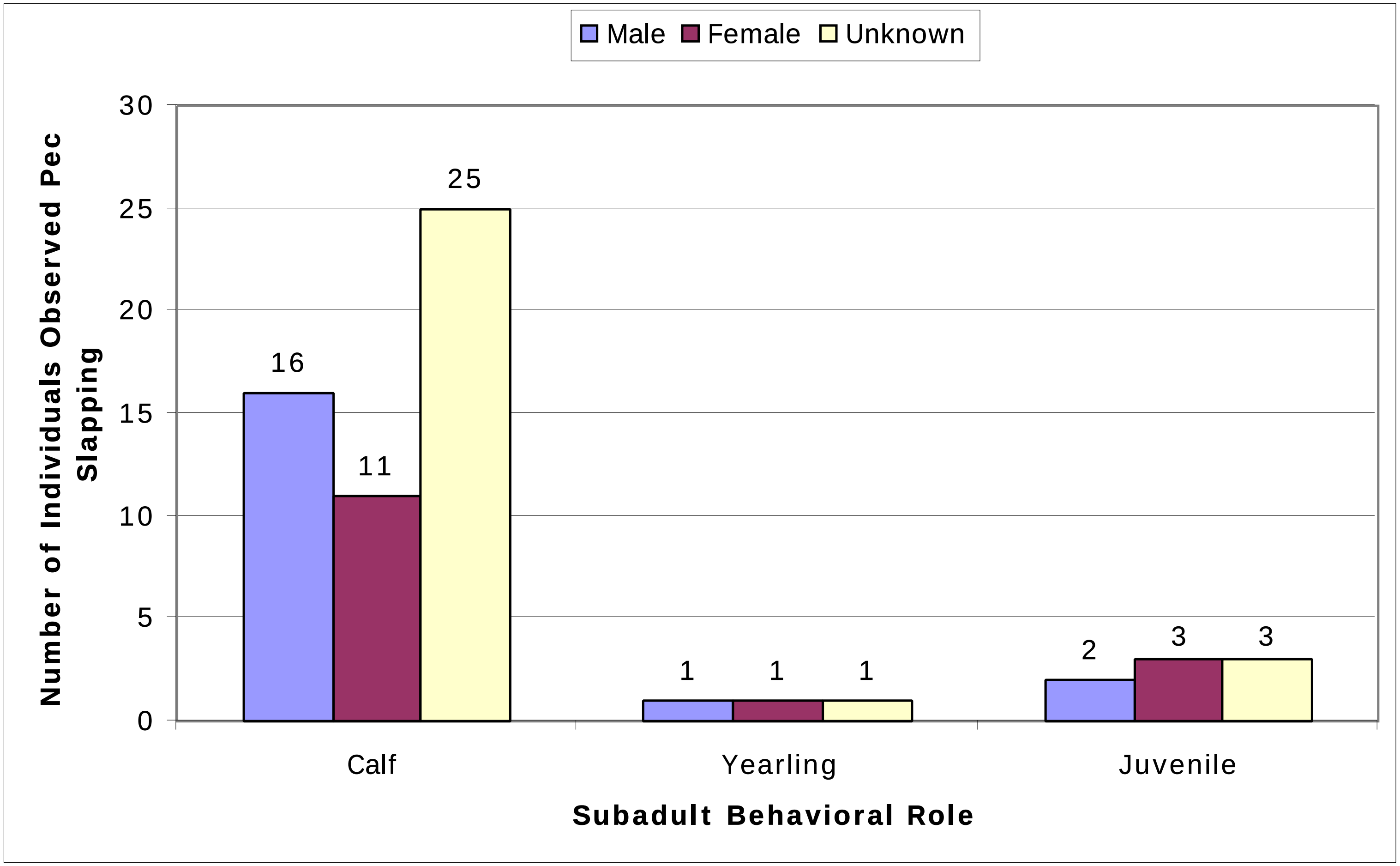


Figure 11. Distribution of pec slappers according to subadult behavioral role.

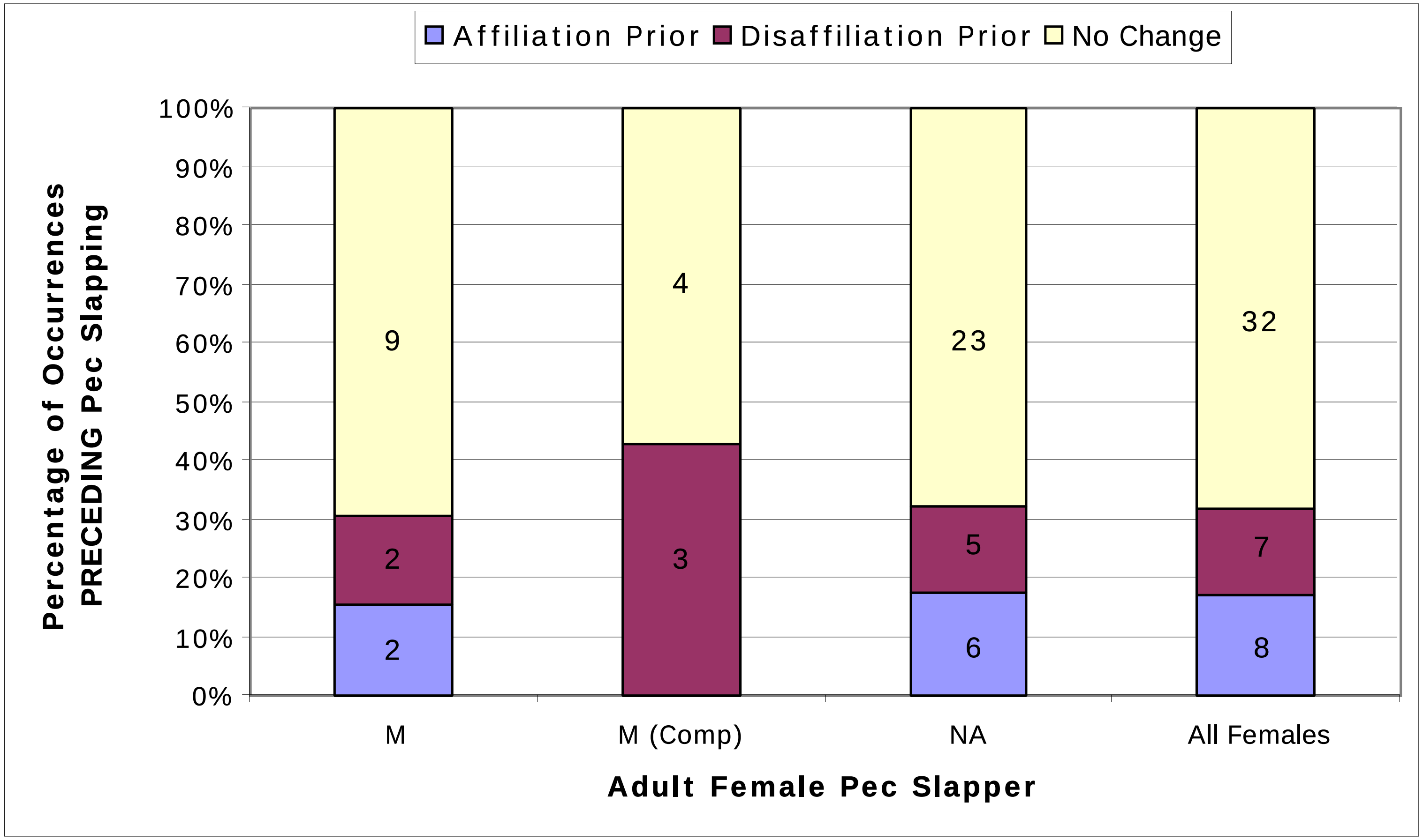


Figure 12. The percentages of affiliations, disaffiliations, and unchanged group compositions PRIOR to observing pec slapping by adult females.

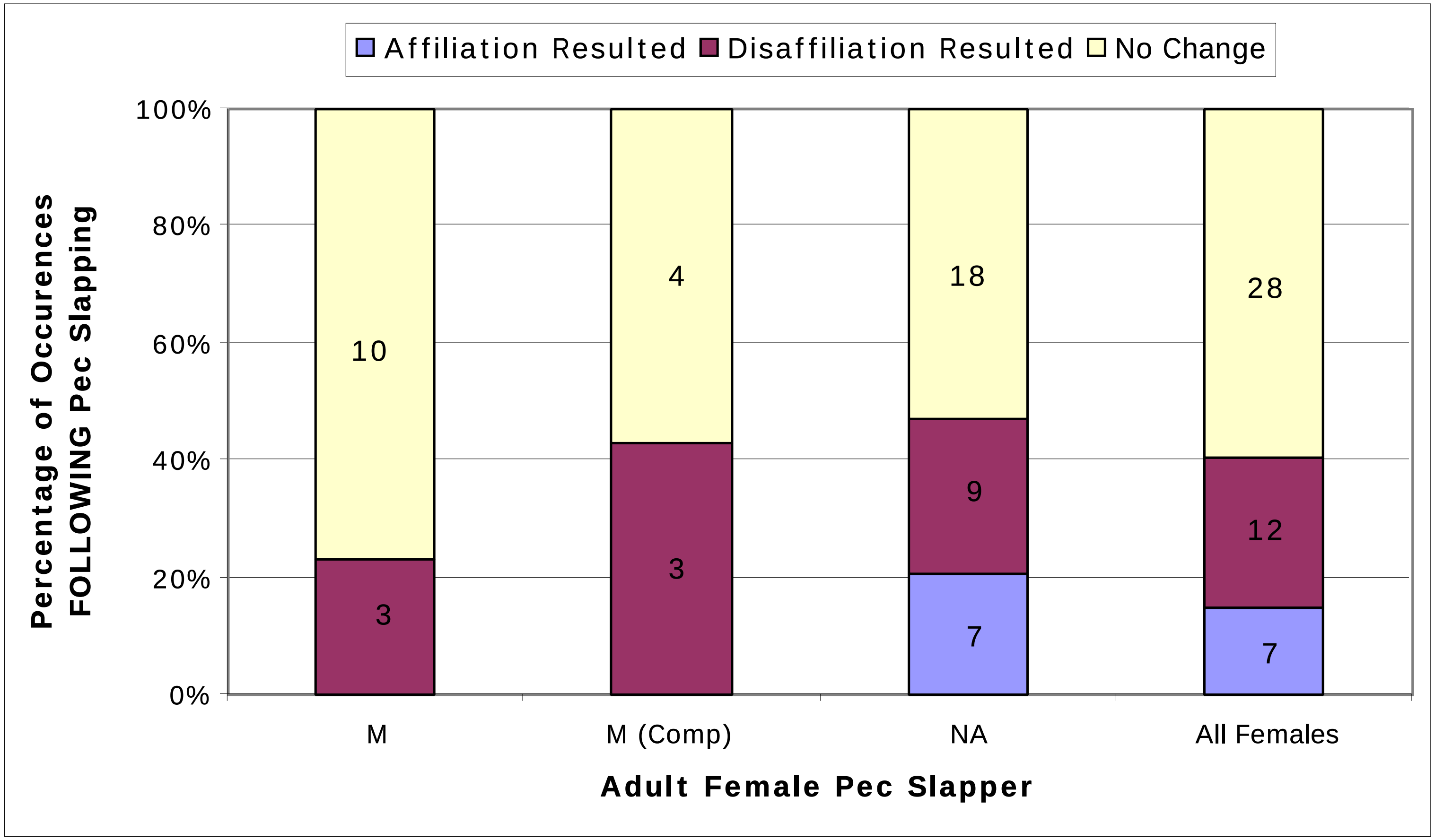


Figure 13. The percentages of affiliations, disaffiliations, and unchanged group compositions FOLLOWING the observation of pec slapping by adult females.

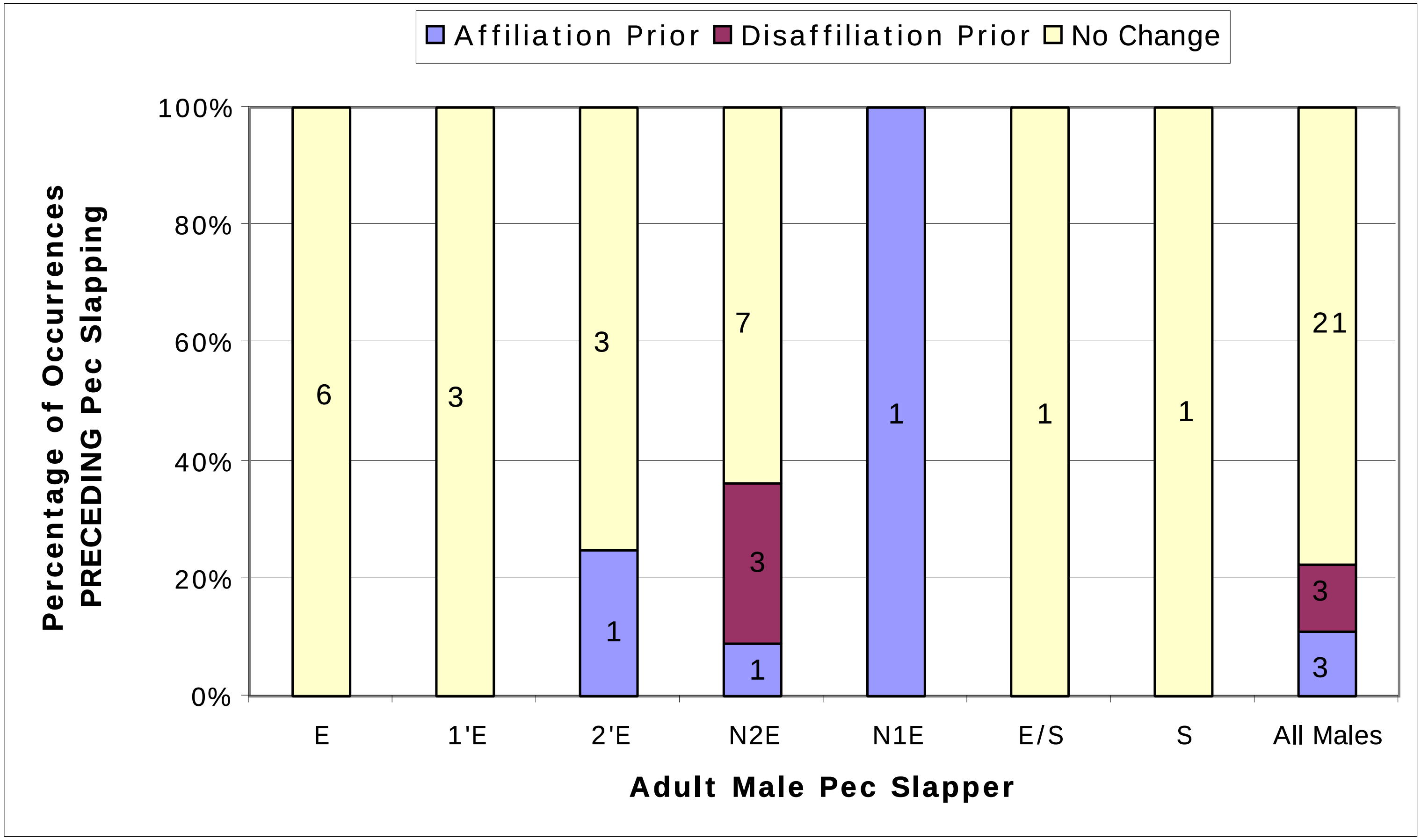


Figure 14. The percentages of affiliations, disaffiliations, and unchanged group compositions PRIOR to observing pec slapping by adult males.

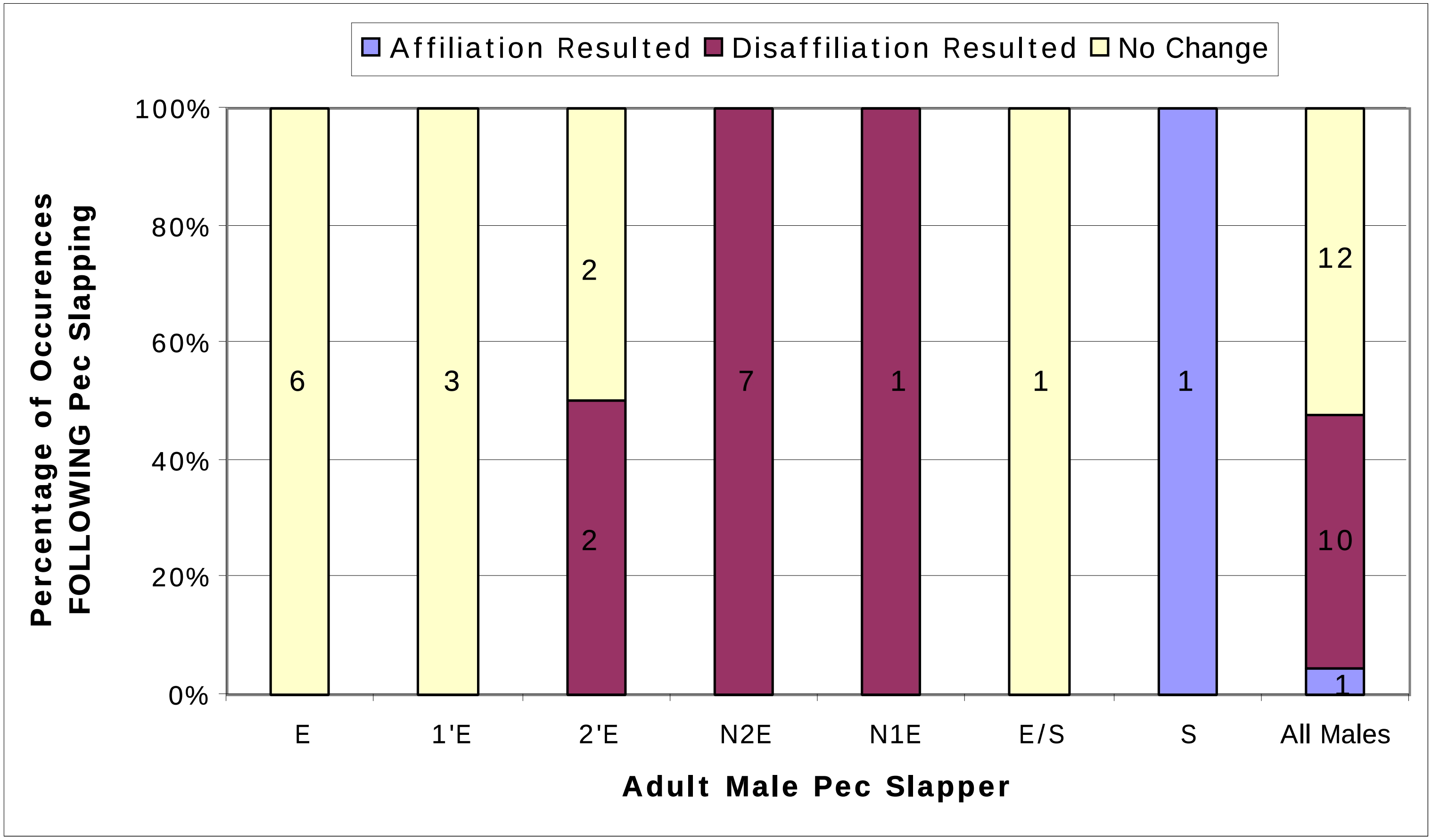


Figure 15. The percentages of affiliations, disaffiliations, and unchanged group compositions FOLLOWING the observation of pec slapping by adult males.

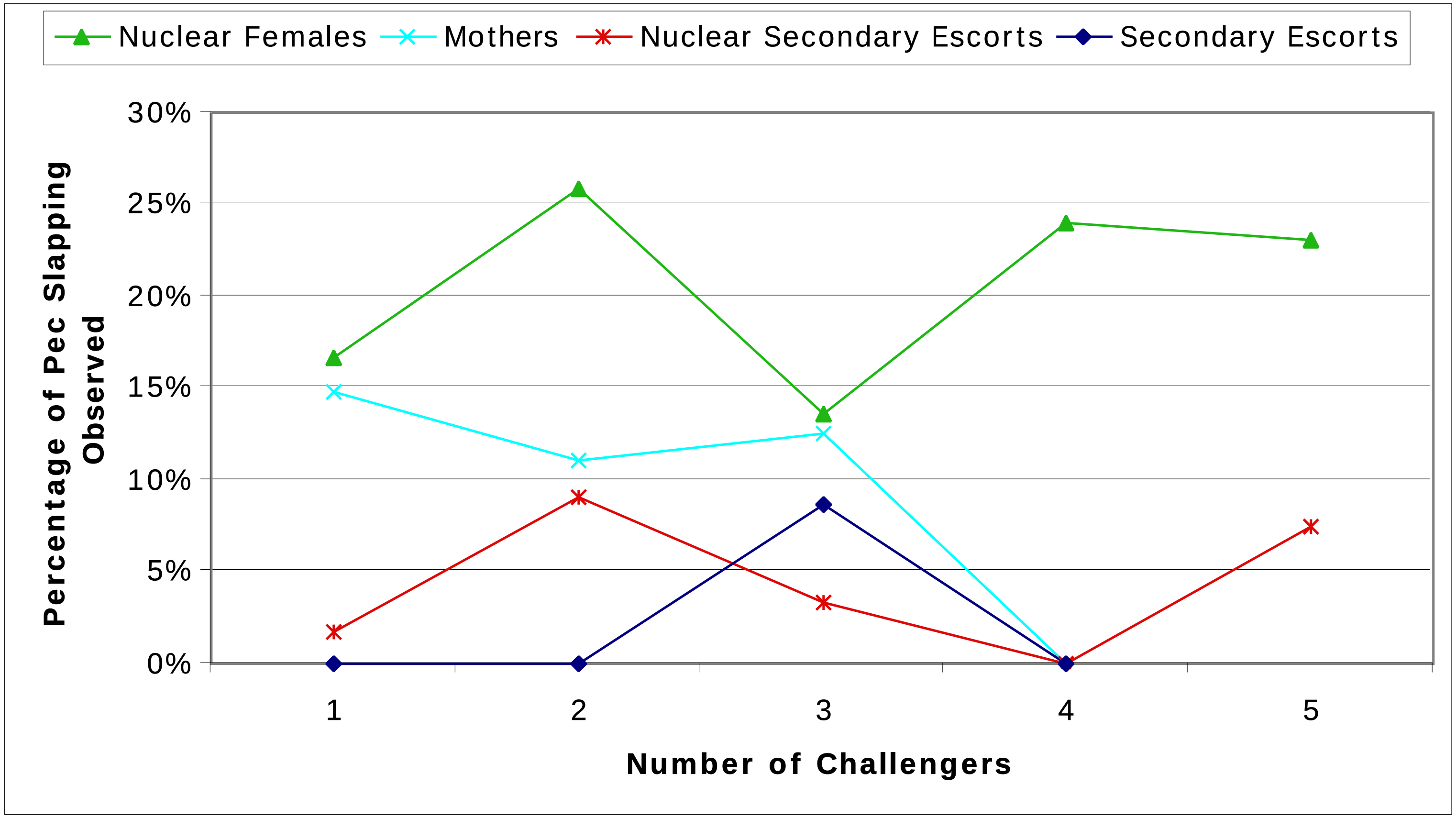


Figure 16. Percentage of pec slapping observed with increasing numbers of challengers for 2 female and 2 male behavioral roles.

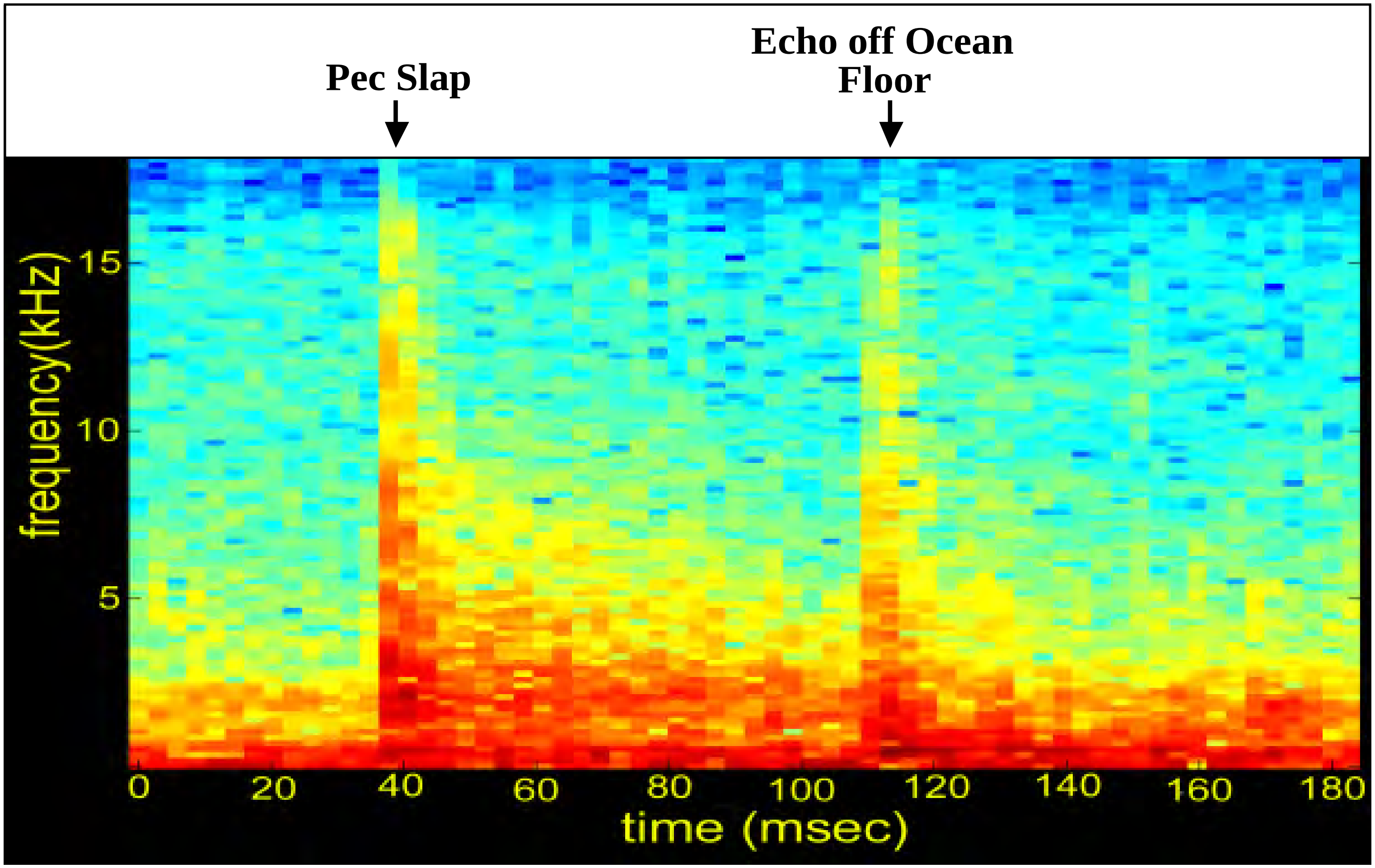


Figure 17. Spectrogram of a broadband sound signal produced by a pec slap followed by an echo from the ocean floor.

APPENDIX C. PEC SLAPPING ANECDOTES

The following anecdotes describe real observations of whales in particular behavioral roles that were observed pec slapping. Each anecdote was chosen as a typical representation of what is observed for that behavioral role.

- Female Yearling

"This Y was a resight of an injured female calf we documented on three occasions during 1999. A whale watch boat sighted this whale two weeks earlier still together with her mother (verified with fluke photo-identifications). Our research group sighted the yearling, no longer with its mother, approximately 4 miles off Olowalu. Several other pods were in the area. The Y was logging quietly at the surface, and consistently performed a shallow, low fluke-up dive before diving for 6-8 minutes. The large gash just ahead of the dorsal fin was very dramatic and looked very similar to the way it did the previous season. The injury on the yearlings left side was pink in color and extended nearly a third of its height. The wound was also visible on the right side, but no pink tissue could be seen. The flukes were concave in shape arching towards the dorsal side. A period of surface activity and slow travel southeast began, during which 18 pec slaps with her left pectoral fin and 84 with her right were observed. She also rolled frequently at the surface. Surface intervals were long and dive times were between 1 and 4 minutes when they occurred. Two separate dyads were observed passing within 150 yd but the pec slapping behavior occurred both prior to and after their passing. Pec slapping also continued with our research boat over 500 yd away. After two hours of observation, her behavior became quiet once again. She went stationary and had dive times of 7-9 minutes. Two divers were deployed who obtained body size measurements and documented the new appearance of the wound on underwater video and using an underwater still camera.”

- Female Juveniles

“We were alerted to this singleton by our shore station crew who observed this whale rolling and pec slapping at the surface. We observed this unusual behavior for 4 hours and 7 minutes during pod#23 and #23a. In close proximity to the boat, this whale, small in size, did a lot of rolling just below the surface. After 20 min. she began traveling SW continuing to perform lateral fluke displays, tonal blows, rolling, tail behaviors, and pec slaps even when 300 yd away from the boat. The whale watch vessel Windjammer approached from the east. The whale turned towards them and approached the boat. For the next 12 minutes the whales moved around their stationary boat remaining close to the surface. She was seen rolling and doing head rises. A diver was deployed earlier who sexed this whale as a female and noted her small size. After moving away from Windjammer she continued rolling just under the surface 100 yd from their boat. A diver was deployed again who noted this whale manipulating a large piece of mesh-like material with her pectoral fins. She pushed it from one pec fin to the other and was seen lifting the mesh with her rostrum, releasing it, and catching it on her pec fin again. This continued for another 12 minutes until a dyad was seen approaching from the NE traveling NW. Our whale began to travel parallel to this dyad 100 yd to the side. A peduncle slap was performed by on of the adults in the dyad but the two pods never got closer than 100 yd from one another. The J female slowed, continued rolling at the surface and reproached our boat and inspected it for the next 30 min. A diver was deployed who noted the whale no longer had the foreign material. The whale then moved away and began travel S during which she peduncle slapped twice and performed 4 breaches. Shortly after an affiliation occurred. She was seen with an adult who was being tracked by another research group. They indicated that they had been tracking our affiliate all morning, initially seen as the E in a MC pod, later as a singer. This whale had been singing up to the point of our juvenile breaches at which time he stopped singing, turned in the direction of the juvenile, and affiliated. The diver had heard loud song even during the surface activity. This new pod became pod #23a. She showed no interest in the affiliate who remained stationary more than 50 yd away. The juvenile was then seen manipulating a large piece of rope with her pectoral fins while it floated at the surface. In total this whale did 2 tail swishes, 1 tail extension, 5 tonal blows, 2 tail slaps, 4 pec slaps, 5 peduncle slaps, 2 peduncle lifts, 1 exaggerated fluke up, 22 head rises, 1 pec extension, 2 underwater blows, and 3 breaches.

- <u>Male Juvenile with Singer</u>

"After a disaffiliation by an adult we named "Tri" in pod #1b we continued to track "Spot", a male juvenile, and "Round" an adult male. The pod was stationary and dive times were initially 9 minutes for "Round" and 13 minutes for "spot". Song was heard through the hull of the boat and recorded on our underwater video camera. Two divers were deployed who recorded song and obtained size measurements of both whales. A competitive pod passed within 50 yd of this pair but behavior did not change and song was not disrupted. "Round" was determined to be the singer since the song attenuated when he surfaced alone. Dive times increased to 17 min for Round and 22-26 min for "Spot". Three hours later, singing stopped and slow travel began SW. We observed "Spot" perform 17 peduncle slaps, 9 inverted tail slaps, 6 pec slaps, 1 forty blow, and was seen inverted at the surface as "Round" did 2 tonal blows and moved away until finally disaffiliating. We continued to track "Spot" who traveled slowly SW. During the disaffiliation by "Round", "Spot", for the first time in over 5 hours of observation became surface active, performing 8 peduncle slaps, 38 pec slaps, 9 head rises, 14 breaches, 3 tail slaps, 2 tonal blows, and was seen bow riding the waves in just over a one hour period. Travel slowed and dive times increased from 2-3 min to 7 min and eventually the pod was lost due to increasing sea conditions."

- Mother with Calf

"This pod was initially observed stationary. The mother surfaced every 15 min. and the calf about every 2 min. After 35 min. of observation, the pod became surface active. The calf performed 1 head rise, 1 tail extension, 1 tail slap, 40+ breaches, 10+ head slaps, and 5 pec slaps. The mother performed 2 breaches, 10 head slaps, 1 peduncle slap, 10 tail slaps, 10 inverted tail slaps, 10+ pec slaps with right pectoral fin, and 8 inverted pec slaps (both pecs). Surface activity lasted 22 minutes while traveling westerly. Then, the mother and calf began to slow and went stationary once again. The calf was observed milling in a counterclockwise direction. Surface activity stopped and at no time were any other whales visible in the immediate area."

- Mother with Yearling

"This mother and yearling were initially observed stationary. The yearling had an average dive time of five minutes and would log at the surface in between dives. The mother had a longer dive time of 16 minutes. A diver was deployed who obtained size measurements of the whales and sexed the yearling as a male. The pair would travel short distances and go stationary again. The yearling performed a tail extension during one of the stationary periods. After we had been with this pod for almost 2 hours, the mother did a series of 4 peduncle slaps, 10 inverted tail saps and one regular tail slap. Four minutes later, the mother performed a peduncle slap. Following another four-minute pause, the mother performed a pec slap. Following another 4 minute dive, the mother performed 3 pec slaps, 2 head slaps, one head lunge, and a breach while the yearling performed 14 pec slaps. Two more breaches were performed by the yearling, the second one in synchrony with the mother's breach. We were forced to leave this pod due to rough water."

- Mother with Calf and Escort

"When we first observed this mother, calf and escort pod, they were alternating between slow travel in variable directions and going stationary. When stationary, the calf would frequently mill at the surface. A diver was deployed who observed the mother, calf, and escort stationary, about 60 feet below. The escort was positioned perpendicular to the mother with his rostrum 15-20 yd from her midsection. The escort extruded his penis. The mother and calf began to travel slowly away from the escort. The escort followed about 45 yd behind. All three whales surfaced and continued traveling slowly S/SE. Shortly after, the calf breached, followed by the escort and then the mother. The calf remained surface active performing numerous head slaps and breaches while the pod continued travel slowly S/SE. Again, the calf breached, followed by a synchronous breach by mother and escort together. Both adults then began pec slapping. The escort continued pec slapping while all three whales traveled at the surface. No whales were observed in the vicinity and we left this pod."

- Mother in Competitive Group

"After observing this quiet, stationary mother, calf, and escort pod for nearly 4 hours, this pod erupted instantaneously with a triple breach by all three whales. The mother immediately performed over 25 pec slaps (some inverted), and 1 head slap. The escort performed 3 pec slaps, 3 inflated head lunges, and a chase towards 2 new affiliating challengers. The calf performed 5 breaches, 2 tail slaps, 1 peduncle slap and about 4 odd sounding tonal blows (lions roar). The affiliation was brief and the two challengers were seen traveling away heading SW. The mother, calf, and escort activity returned to their original quiet behavior."

- Females without Calf in Competitive Group

"This pod was the result of an affiliation between a singer in a previous pod and 2 new adults. The former singer became a nuclear secondary escort in this 3-adult competitive pod. The nuclear primary escort observed numerous inflated head lunges, underwater blows, and tonal blows. The nuclear animal performed more than 10 pec slaps. At one point, the nuclear secondary escort was observed traveling 60 yd from the female and the nuclear primary escort turned and traveled in the direction of the challenger. Shortly thereafter, the N2E disaffiliated leaving this male female pair."

- Single Escorts

"This mother, calf, and escort pod was seen pec slapping from a distance. Once we began tracking the pod, the escort was observed to be pec slapping. The pod was traveling slowly SE. The calf milled for about 2 min and was followed by the surfacing of the mother and escort. The escort performed repeated pec slaps as he trailed the mother and calf. The calf breached and the escort performed at least 13 pec slaps while we were following this pod. "

- Primary Escorts

"The whale-watch boats reported a stationary MCE about 1 mi off Lahaina Harbor. As we approached we observed a MC2E pod and the activity level was increasing. We initially observed an adult peduncle slap. The 1E also pec slapped about 8 times, rolling pec slapped several times, breached once, and did one head rise. The M was peduncle lifting repeatedly and tail slapped once in the direction of the 1E as the 1E swam back and forth behind the MC. The C was active at the surface, rolling and performing lateral fluke displays. The 2'E remained about 30-40 yd from the MC with the 1'E between them. The 2'E disaffiliated after about 1 hour of observations. We continued to track the MCE. Surface activity subsided after the disaffiliation."

- <u>Nuclear Primary Escorts</u>

"Two secondary escorts left this 5 adult group and were replaced by 2 new secondary escorts ("Big" and" Chop"). This pod continued to track S/SE slowly with "Smooth" the NA, periodically rolling at the surface. A diver was deployed and gendered "Big" as male. Shortly after the diver was deployed, "Big" displaced "T2" as the primary escort. "Big" maintained the N1E position for the rest of the observation. A group of 3 whales approached the pod but did not affiliate. Shortly after this pod was seen, an unidentified whale breached twice and an unidentified whale did a tail slap. Shortly after, "T2", the displaced N1E, and "Chop", appeared to disaffiliate together. They were seen once more moving apart and "T2" breached. "Big" performed one pec slap and "Smooth" did 2 pec slaps. "Big" was seen following another whale closely in what could have been a chase and then returned to the side of "Smooth". Neither "T2" or "Chop" was seen after this point, bringing us to pod 5c."

- <u>Secondary Escorts</u>

"This competitive MC4E pod was seen doing large scale slow milling off Kaanapali. The 1E "Small" was positioned to the left of the M and C. "Small" performed, exaggerated fluke-up dives, and occasionally chased the 2Es. Small performed 1 LBT and UWB, and the C tail slapped frequently when diving. Two charge strikes were performed by "Small", one towards "Little" and one towards "Scratch", both 2Es. "Scratch" performed 2 pec slaps on separate occasions, both towards the left and right while trailing the M, C, and 1E. Competition was observed between the 2Es, including chasing of "Scratch" by "Chop", also a 2E. "Little" appeared to be chased and shortly after, both "Chop" and "Little" were seen surfacing 50 yd. away traveling parallel to the MCE. None of the 2Es were seen again after this point."

- <u>Nuclear Secondary Escorts</u>

"This 4A+ pod resulted from the disaffiliation of 2 whales from POD 6 about 2 mi off Mala. The whales continued traveling generally SE. Very little agonistic behavior was observed. Dive times were variable. Behaviors included a LBT, breach, peduncle slap, head lunge, pec slap, and bubble cloud but they were very infrequent. Three N2Es were photo-identified on the perimeter. One of these N2Es pec slapped while it disaffiliated. The remaining 3 whales became POD 6B."

- Singers

“”Point”, our singleton from pod #21, affiliated with this second whale "Block" traveling W. Initially they remained about 100 yd apart with "Point" trailing. "Block", a 75% with white pecs was heard singing when the boat moved over the puka. The song attenuated suggesting the whale was traveling. One pec slap was seen performed by “Bloc" prior to hearing the song. “Point” remained 100 yd behind. After song was heard, “Block” surfaced and did 6 more pec slaps to the left. Both whales then surfaced together; "Point" did 3 pec slaps to the left with "Bloc" who did 6 rolling pec slaps. A LFD and tail swishing was seen by "Block". Both whales moved in the direction of a M and C. When about 100 yd away M peduncle slapped and our pod changed direction from W to S to affiliate with MC. "Block" became 1'E and "Point" 2'E. Photo-identifications were taken of Point, a 25%.”

- Lone Adults

“This singleton was sighted 2 miles off Puu Grande, initially stationary with dive times of 7 min. increasing to 18 minutes. This whale performed 1 breach, 3 head slaps, and 5 right pec slaps. The adult then began traveling southwest with dive times of 4-7 minutes. Then a second adult was seen surfacing with this 75% white pec'd adult and this became a dyad.”

- Male-Male Dyads

"This pod is the result of an affiliation of an adult with a singer observed in Pod #1. The approaching adult had surfaced within 50 yd of the singer 20 minutes earlier with no noticeable interaction. The affiliation occurred when the singer stopped singing and the 2 whales surfaced together. Two pec slaps with the right pectoral fin were observed by the former singer as the affiliate began to travel away to the SE. The affiliation was brief and the original singer resumed singing."

- Male-Female Dyads

"We came across this dyad 1.5 miles off Lahaina Shores. Both whales spent most of their time at the surface in very close proximity. One whale was named "Long" who was confirmed to be female by a deployed diver. The other whale was named "Tri" and was sexed by the diver as a male. "Long" was observed logging at the surface, often inverted and rolling, performing pec slaps (four times unknown pectoral fin and 3 times with left pec), pec extensions, and 3 inverted pec slaps. She also performed tonal blows, farty blows, peduncle lifts, and two peduncle slaps to the right while "Tri" was positioned on her right side. "Long" was also seen on occasion to swim slowly backwards at the surface. "Tri" performed over 60 inverted pec slaps, frequently very close to and nearly touching "Long" at the surface. He also performed regular pec slaps (2 with an unidentified pectoral fin, 17 with the left pec during earlier observations, and 5 with the right pec later in our observations), 2 left peduncle slaps, and 3 right peduncle slaps, one tail slap, reversals, peduncle lifts, a pec extension, head rises, and some sharking at the surface. "Tri" frequently surfaced several whale lengths from "Long", swimming back towards “Long” at a very fast pace, and coming to a quick halt when positioned just to the side of "Long". A diver was deployed who obtained sizes on both whales. After approximately 1.5 hours, the whales began traveling slowly SE with approximately 5 minute dive times. The pair became stationary with dive times between 12 and 17 minutes.”

- <u>Male-Female Dyads Resulting from Competition</u>

“Five whales were observed initially in this group traveling in a northwesterly direction. Tail slaps were observed by unknown whales within the group. A whale traveling directly in front of the pod disaffiliated leaving 4 whales. A diver sexed the primary nuclear escort and a challenger as male. Following possible attempted fluke strikes by the defending male, the two challengers disaffiliated leaving only the male/female pair. They turned southwest and travel slowed. At this time, the nuclear animal did 22 pec slaps, 3 peduncle slaps, 3 tonal blows, and a tail extension. Dive times were 4 min. During the pec slapping, a breach was observed 200 yd to the North by a whale who shortly afterwards affiliated. The new affiliate immediately displaced the defending male. The nuclear animal continued to pec slap 17 times often rolling at the surface, and occasionally inverted with her genitals exposed. Underwater observations revealed the nuclear animal swimming ventral side up underneath the new defending male. The displaced male was chased by the new defending male and moved away from the pod. A new challenger joined. The defending male chased the new challenger, a charge strike was seen, and the defending male was observed to push down the new challenger below the water. The nuclear female continued with 2 more pec slaps. We then left this pod."

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