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FEMALE HUMPBACK WHALE (MEGAPTERA NOVAEANGLIAE) REPRODUCTIVE CLASS AND MALE-FEMALE INTERACTIONS DURING THE BREEDING SEASON

by

Meagan E. Jones

A dissertation submitted in partial fulfillment of the requirements for the degree of

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(Environmental Studies)

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For my nieces,

Chloe, Charlotte, and Curran
ACKNOWLEDGEMENTS

In the Hawaiian culture, 'ohana means family. Today, 'ohana still means family, but it often refers to one's extended family. In general terms, 'ohana refers to a group of people that share a common bond and treat and respect each other like family. I am indebted to my 'ohana – the family, colleagues and friends, whom have supported, encouraged and helped me along this unforgettable 9.5 year journey.

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ABSTRACT

This study examined whether female reproductive class (i.e., presence or absence of a calf) in humpback whales (*Megaptera novaeangliae*) affects female behavior and male-female interactions on the Hawaiian breeding grounds. From 2003-2008, 295 female-calf groups (with or without a male escort) and 256 female no-calf groups (with a male) were observed. Forty-one female no-calf groups were confirmed male-female pairs by genetic sexing or photo-identification. Focal follows of 36 male-female pairs and 50 female-calf groups (29 escorted and 21 unescorted female-calf groups) were analyzed for time budget and movement estimates. Relative fluke size (fluke photogrammetry, n=30) and sighting histories (n=9) were used to estimate age-class for 39 individuals within focal follows. Escorted female-calf groups spent significantly more time traveling and less time resting than male-female pairs and unescorted female-calf groups. Indeed unescorted female-calf groups had time budgets more similar to male-female pairs than female-calf groups with a male. Male behavior and relative body size also affected female behavior and movement patterns: lone males chased females with calves significantly more than females without calves. Fluke sizes of mothers who were chased were significantly smaller than mothers not chased, and the chasing males tended to have smaller flukes (i.e., younger age-class) than males that did not chase. I also conducted 34 playback experiments (broadcasting sounds of competitive males) with 14 female no-calf groups (male-female pairs) and 20 female-calf groups (11 escorted and 9 unescorted female-calf groups). Results of playback trials indicated that females with calves were significantly more likely to avoid playbacks of sounds produced by adult males than females without calves. Overall, the range and variability of female behavior and movement patterns, especially around males, was striking. Results indicate that female reproductive class is a key factor in determining how females respond and interact with males during the breeding season, but also suggest that male-female interactions during the breeding season are a reflection of a combination of factors, beginning with female reproductive class, but also including costs and benefits of specific male escorts, stage of the reproductive cycle, relative body size and/or age-class.

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CHAPTER 1

GENERAL INTRODUCTION

Humpback whales are found in all major oceans of the world. Despite over thirty years of global study of humpback whale (*Megaptera novaeangliae*) breeding populations, our knowledge of female reproductive behavior during the winter breeding season remains extremely limited (Cerchio 2003; Darling et al. 2006; Cartwright and Sullivan 2009). Virtually nothing is known about the timing and length of female estrus cycles (Clapham 1996), and little is known about how females interact with males on breeding grounds (Darling et al. 2006; Cartwright and Sullivan 2009), including whether females actively choose or select mates based on specific male attributes as is often found in polygynous mammals (e.g., Andersson 1994). These large gaps in our understanding of what role the reproductively active female plays within the breeding system currently hinders our understanding of how males and females acquire and obtain mates and thus what form of mating system best characterizes the humpback whale mating system. Initially researchers suggested that the humpback whale mating system was a form of polygyny, where males compete for females through displays and fights, with the dominant males securing the majority of matings (e.g., dominance polygyny: Darling 1983; Brown and Corkeron 1995; lek: Mobley and Herman 1985; Cerchio 2003; floating lek: Clapham 1996). However, recent genetic and behavioral studies have raised questions as to whether this is the appropriate context within which to view humpback whale behavior (Valsecchi et al., 2002; Cerchio et al., 2005; Darling et al. 2006).

Moreover, while it is tempting to compare and contrast breeding populations of humpback whales between different geographic locations and ocean basins, recent findings suggest that despite general similarities in social structure (e.g., migration, group composition) and behavior (e.g., singing males, male-male competition) on most breeding grounds, breeding populations may vary in terms of oceanographic (e.g., currents: see Rosenbaum et al. 2009) and ecological characteristics (e.g., prey availability: Mikhalev 1997; Papastavrou and Van Waerebeek 1997), potential differences in population density (e.g., Hawaiian Islands versus Cook Islands), migration patterns (Mikhalev 1997; Stevick et al. 2003; Barendse et al. 2010) and reproductive biology (e.g., sexual maturity: Clapham 1992; Gabriele et
al. 2007), which may impact and influence male and female behavior during the winter breeding season. Varying underwater topographic conditions within breeding populations, such as changes in water depth, may even impact female distribution patterns and thus behavior during the breeding season (Craig and Herman 2000). This variability adds complexity to our ability to understand the behavior and mating strategies in this species and may confound attempts to compare or generalize behavioral patterns between populations. Yet, because our knowledge of female mating strategies is currently based on anecdotal observations (repulsion/displacement of males: Glockner-Ferrari and Ferrari 1985; Clapham et al. 1992) or predictions based on general mating systems theory (Clapham 1996), comparing what is known from whaling and field studies carried out between oceanographic populations is a useful and appropriate starting point as we begin to unravel and define the role of the reproductively active female on humpback breeding grounds.

Female Reproductive Class

While female humpbacks migrate to winter breeding grounds for two reasons, mating and calving, whether or not these purposes are distinct and represent potentially conflicting reproductive objectives remains unclear. In humpbacks, female reproductive class has been shown to influence and characterize associations on feeding grounds (Sardi et al. 2005), the length of time spent on breeding grounds (Darling 1983; Glockner-Ferrari and Ferrari 1984; Gabriele 1992; Clapham et al. 1992) and feeding grounds (Dawbin 1997), and possibly even male mate choice (Craig et al. 2002), but little is known about if and how female reproductive class affects female behavior and male-female interactions during the breeding season. In other mammals, female reproductive class has been shown to influence the composition of male-female groups (chimpanzees, Pan troglodytes schweinfurthii: Matsumoto-Oda 1999; Grevy's zebra, Equus grevyi: Sundaresan et al. 2007), to influence the behavior of one sex toward the other (P. troglodytes: Matsumoto-Oda and Oda 1998; Matsumoto-Oda 1999) including rates of male harassment (Grevy’s zebra, E. grevyi: Sundaresan et al. 2007), and to affect seasonal movement patterns during the mating season (e.g., Equids: Rubenstein 1986; P. troglodytes: Matsumoto-Oda and Oda 1998; brown bears, Ursus arctos: Dahle and Swenson 2003). The importance of female reproductive class in
understanding male-female interactions during the winter breeding season is further suggested by what is known about female reproductive biology and the social organization on humpback breeding grounds.

Female Reproduction

Female humpbacks typically give birth to a single calf every 2–3 years (Chittleborough 1958, 1965; Dawbin 1966; Glockner-Ferrari and Ferrari 1990; Baker et al. 1987; Clapham and Mayo 1987; Straley et al. 2001) following an 11–12 month gestation period (Chittleborough 1958). The age of first calving has been reported at 5–7 years in the North Atlantic (Clapham 1992), but in the North Pacific Ocean, the age at first calving appears to occur between 8–16 years of age, with a reported average age of 11.8 years (Gabriele et al. 2007). Chittleborough (1958) reported that the mean length of lactation was 10.5 months, and field observations suggest that most calves are weaned by the end of their first year (Clapham and Mayo 1987, 1990), indicating that some mothers may return to breeding grounds with year-old calves called yearlings.

Not much is known about the duration of estrus cycles; however, female humpbacks are seasonally polyestrous (Mathews 1937; Chittleborough 1954), meaning that a female may ovulate more than once within the breeding season if an estrus cycle does not end in conception. Although interbirth intervals are highly variable, ranging from one to six years (Baker et al. 1987; Clapham and Mayo 1987, 1990; Perry et al. 1990; Straley et al. 2001), the number of females producing calves in one-year intervals represents a small percentage, with reports ranging from 8.5%–14.4%, of the overall population of breeding females (Chittleborough 1958; Glockner-Ferrari and Ferrari 1990; Clapham and Mayo 1990; Straley et al. 2001; Mikhailov 2000 cited by Noad and Cato 2007). It remains unclear how often post-partum estrus occurs (Chittleborough 1954, 1958, 1965), but clearly some females enter a post-partum estrus and may conceive shortly after parturition. The reproductive biology of females, specifically the intermittent and variable reproductive cycles, including the age of first calving, and relative rarity of consecutive year births, suggests that the majority of females may have different, and perhaps even conflicting, reproductive objectives (i.e., mating and newborn care) on breeding grounds.
Social Organization on the Hawaiian Breeding Grounds

Segregated migration patterns based on sex, age and reproductive class (Matthews 1937; Chittleborough 1958, 1965; Dawbin 1966, 1997) and a male biased operational sex ratio (Brown et al. 1995) also suggest that female reproductive class may be a critical component in understanding male-female interactions during the winter breeding season. Based on whaling catch records, Chittleborough (1958, 1965) and Dawbin (1966, 1997) showed that the migration to and from the breeding grounds involves a loose progression of individuals that generally begins with mature females terminating lactation (i.e., mothers and last year’s calves) and sexually immature individuals of both sexes. Mature males and females that were neither lactating nor pregnant (i.e., resting females) were in the center of the migration and late pregnant females carrying near term fetuses were in the rear of the migration. The return migration was similar with the first to arrive on the breeding grounds generally also being the first to leave for the feeding grounds. The earliest departures from winter grounds were resting and early pregnant females and immature or juvenile whales, while the last to leave were females with newborn calves. Humpback migration patterns thus appear to reflect the significance of a female’s reproductive class and support suggestions that newly pregnant females minimize time spent on breeding grounds to maximize feeding opportunities in higher latitudes to ensure good body condition during parturition (Gabriele 1992).

Despite a sex ratio of near parity at birth (Chittleborough 1958, 1965; Mathews 1937; Glockner-Ferrari and Ferrari 1990) and on summer feeding grounds (Clapham et al. 1995), a male biased operational sex ratio (OSR) of 2.4:1 for humpback whales migrating to and from southern hemisphere breeding grounds has been reported by Brown et al. (1995). Observations of fewer females on winter breeding grounds and along the migration have now been reported from whaling catch records (see Brown et al. 1995), molecular studies (Brown et al. 1995; Palsboll et al. 1997) and mark-recapture studies based on photo-identification of individuals on breeding grounds (e.g., Craig et al. 1997; Smith et al. 1999). Consequently, several researchers have suggested that not all females complete the migration each year (Brown et al. 1995; Craig et al. 1997; Mattila et al. 1999). Although individuals known to overwinter in higher latitudes do not reflect any clear patterns of age or sex-segregation (Straley 1990,
1999), some females may become pregnant en route to breeding grounds and thus may not complete the migration in its entirety (Craig et al. 1997).

The male biased operational sex ratio reported in this species along the migration (Brown et al. 1995) and on breeding grounds (Craig et al. 2003) coupled with typical 2–3 year reproductive cycles (Chittleborough 1958, 1965; Dawbin 1966; Glockner-Ferrari and Ferrari 1985; Baker et al. 1987; Clapham and Mayo 1987; Straley et al. 2001) suggests that females are a limited resource during the breeding season. Indeed, breeding populations of humpback whales include females that vary in terms of sexual maturity, body condition, estrus cycles and reproductive class. Male-male competition, predicted when the number of sexually receptive females is less than the number of males that are available (Emlen and Oring 1977), is a prominent feature of the humpback mating system (Darling 1983; Tyack and Whitehead 1983; Baker and Herman 1984; Clapham et al. 1992).

Evidence of segregated migration patterns based on age, sex and reproductive class (Matthews 1937; Chittleborough 1958, 1965; Dawbin 1966, 1997), a male-biased OSR on winter breeding grounds (Brown and Corkeron 1995; Craig et al. 1997), and intermittent reproductive cycles (Chittleborough 1958, 1965; Dawbin 1966; Glockner-Ferrari and Ferrari 1990; Baker et al. 1987; Clapham and Mayo 1987; Straley et al. 2001) collectively suggest that females are a limited resource. Some females may therefore be expected to be in conflict with breeding males that stand to maximize reproductive success by increasing access to females (Trivers 1972; Smuts and Smuts 1993). Given the small percentage of females that successfully reproduce in consecutive years, I would expect lactating females to experience more conflict with males than females that have migrated for the purposes of mating, and for female reproductive class to be an important factor in characterizing male-female associations.

**Male-Female Associations During the Breeding Season**

The regularity of associations between females with calves and males during the breeding season, however, complicates this hypothesis. Females (with and without calves) are rarely alone during the breeding season (Darling 1983; Gabriele 1992; Brown and Corkeron 1995; Craig et al. 2002). Similar
to females without calves, females with calves are most often found associating with a single male called an "escort" (Darling 1983; Glockner and Venus 1983; Glockner-Ferrari and Ferrari 1985; Craig et al. 2002), and/or at the center of multiple male groups (Brown and Corkeron 1995; Robbins et al. 2001) where males are believed to compete for access to a presumably estrus female (Darling 1983; Tyack and Whitehead 1983; Baker and Herman 1984). In addition, other than apparent preference for nearshore, shallow waters (Smultea 1994) there is little evidence of spatial segregation on humpback breeding grounds between mothers and other breeding males. Female-female associations, although not uncommon on feeding grounds (Weinrich and Kuhlberg 1991; Clapham 1993), are exceedingly rare on breeding grounds (Valsechhi 1997 cited by Valsechhi et al. 2002; Robbins et al. 2001; Craig et al. 2002; Pomilla and Rosenbaum 2006; Cypriano-Souza et al. 2010). Consequently, while female reproductive class appears to play a significant role in several aspects of female reproductive behavior, it seems to have a minimal affect on male-female associations during the breeding season.

Previous studies comparing the behavior of female humpback whales with and without calves, however, were limited by the difficulty of sexing individuals in the field when a calf was not present (e.g., Mobley and Herman 1985; Gabriele 1992; Craig et al. 2002). In these studies, female no-calf groups often included females in multiple male groups which made direct behavioral comparisons with females in single-males groups (i.e., escorted mother-calf groups) challenging, especially because the presence of multiple males has since been found to affect the behavior and movement of females (Cartwright and Sullivan 2009). Although genetic studies now indicate that the majority of pairs on breeding grounds are male-female (Brown and Corkeron 1995; Pomilla and Rosenbaum 2006; Cypriano-Souza et al. 2010), male-male pairs are also found on humpback breeding grounds (Darling 1983; Clapham et al. 1992), which further complicates these earlier descriptions as the behavioral differences between male-female pairs and male-male pairs have not yet been discerned in the literature. As a result, although pairs of whales are one of the most prevalent social groups on winter breeding grounds (Pomilla and Rosenbaum 2006; Cypriano-Souza et al. 2010), the social role and function of these pairs has not been systematically studied, and consequently little is known about sex-specific behavior within these groups.
Female body condition is an important indicator of reproductive success (Ralls 1976), and consequently successive gestation and lactation periods are not considered to be a sustainable or viable long-term reproductive strategy for females (Chittleborough 1955; Clapham and Mayo 1987; Wiley and Clapham 1993). Because whaling records have suggested that post-partum ovulation occurs only rarely in females (Chittleborough 1958) and only a small percentage of females successfully give birth on an annual basis (Chittleborough 1958; Glockner-Ferrari and Ferrari 1990; Clapham and Mayo 1990; Straley et al. 2001; Mikhalev 2000 cited by Noad and Cato 2007), the question of why females with calves are frequently observed with males has presented a conundrum for researchers. Most researchers agree that male’s escort lactating females to maximize potential mating opportunities (Darling 1983; Baker and Herman 1984; Mobley et al. 1985; Glockner-Ferrari and Ferrari 1985; Clapham et al. 1992); however, the question of why lactating females tolerate these associations with males is less clear. Cartwright and Sullivan (2009) have recently proposed that the seemingly paradoxical female-calf associations with a single male may be a counterstrategy to offset male harassment by multiple males. Indeed, reports of males working together to secure access to a female are increasing in the literature (Clapham et al. 1992; Brown and Corkeron 1995; Darling et al. 2006). But whether or not females without calves face similar pressures is not known.

**Female Reproductive Strategies**

Mature females without calves migrate to breeding grounds to maximize mating opportunities, while late pregnant females migrate primarily to give birth and/or to raise calves in warmer waters. It is possible that females with calves may behave differently around males than females without calves that migrate specifically for mating purposes, in spite of the frequency that both females with calves and without calves are observed with a male on the breeding grounds. Gabriele (1992) has hypothesized that females without calves should maximize associations with males on breeding grounds to ensure conception occurs as early in the breeding season as possible to maximize feeding opportunities in higher latitudes. In contrast to females without calves, the energetic demands of lactation during prolonged fasting periods (Lockyer 1981, 1984) and potential consequences of annual reproduction for
lifetime reproductive success (Chittleborough 1955) coupled with low rates of successful annual reproduction suggest that the majority of females with calves may try to avoid mating in successive years.

From this theoretical perspective, the overall reproductive objectives of females on the breeding grounds are different. The primary objective of females with calves is to ensure calf development and survival, whereas females without calves are primarily concerned with successful conception and balancing the need to conceive with the highest quality male while spending the least amount of time away from areas with access to food necessary for successful parturition. If meaningful, these different priorities and objectives should be reflected in male-female interactions during the breeding season. In this study, I hypothesized that female humpbacks may behave differently around males during the breeding season based on female reproductive class (i.e., presence or absence of a calf).

Overview of Dissertation

The purpose of this study is to investigate whether the potentially different reproductive objectives of mating and calving are reflected in differences in female behavior and male-female interactions during the breeding season. Because previous studies comparing the behavior of females with calves with females without calves in humpback whales have been limited by the difficulty of sexing individuals in the field when a calf was not present (Gabriele 1992; Craig et al. 2002), one of the primary objectives of this study was to sex individuals believed or presumed to be a female (without a calf) in order to compare and describe the similarities and differences between females with and without calves.

In Chapter 2, I examine whether the time budgets, associations and movement patterns in female humpback whales are related to the different reproductive objectives of mating and calving during the breeding season. I hypothesized that if female reproductive class were an important consideration in characterizing female behavior and male-female interactions, I would find significant differences between females with and without a calf in female time budgets, associations and movement patterns. Alternatively, I predicted that if female choice were a more important factor than female reproductive class in regulating male-female interactions, I would observe more differences within female reproductive
classes (i.e., within female-calf groups or within female no-calf groups) than between female reproductive classes (female-calf versus female no-calf groups).

In Chapter 3, I explore the variability and range characterizing male-female interactions during the breeding season in Hawaii. Specifically, I look at the role of relative body size (based on results of fluke photogrammetry), age-class (sighting histories based on photo-identification) and male behavior (e.g., chasing) in conjunction with females in different reproductive classes to determine if and how these factors influence male-female associations and interactions on the Hawaiian breeding grounds.

In Chapter 4, I utilize sound playback experiments to determine whether female reproductive class affects female responses to sounds produced by males in multiple male, surface-active groups (SAGs) that are associated with male-male competition around a presumably estrus female. I predicted that if female reproductive class was an important factor in understanding male-female interactions, females would respond differently to the male sounds based on the presence or absence of a calf. Specifically, I predicted that if females with calves were trying to minimize associations with males they would actively avoid the playbacks by traveling away from the projected sounds, whereas if females without calves were trying to maximize associations with males that they would respond either neutrally or positively to the same sounds.

In Chapter 5, I examine the overall trends and findings that resulted from this study and some of the implications for understanding female reproductive strategies in humpback whales.


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CHAPTER 2

TIME BUDGETS, ASSOCIATIONS, AND MOVEMENT PATTERNS IN FEMALE HUMPBACK WHALES
(MEGAPTERA NOVAEANGLIAE) ON THE HAWAIIAN BREEDING GROUNDS

ABSTRACT

This study examined whether time budgets, associations and movement patterns in female humpback whales (Megaptera novaeangliae) on the Hawaiian breeding grounds are related to female reproductive class (either mating or calving) during the breeding season. Between 2003-2008, 295 female-calf groups (with or without a male escort) and 256 female-no calf groups (females without a calf but with a male) were encountered. Forty-one groups from this sample were sexed and all were male-female. Focal follows with 36 female no-calf (male-female pairs) and 50 female-calf groups (29 escorted and 21 unescorted female-calf groups) were conducted and analyzed for time budget and movement estimates. Female reproductive class (presence or absence of calf) affected both the timing and duration spent on breeding grounds as well as the likelihood of being pursued by multiple males. Although female reproductive class did not affect the prevalence of associations between males and females, it did affect how females responded to males. Escorted female-calf groups spent significantly more time traveling and less time resting than other groups; and unescorted female-calf groups had time budgets more similar to male-female pairs (female-no calf groups) than female-calf groups with a male escort, suggesting that the presence of a calf significantly affects male-female interactions during the breeding season. Male-female pairs (without calf) moved the least and escorted female-calf groups moved most. The range and variability of female behavior and movement patterns, especially around males, was striking. These findings suggest that female reproductive class influences female behavior, association and movement patterns on the breeding grounds, but due to this variability there are other factors that also play a role in determining female behavior and movement during the breeding season. These factors may include estrus cycles, and both female and male age-class, body size and condition.
INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) are seasonally reproductive, migrating annually from higher-latitude feeding areas in the summer to lower latitude breeding and calving grounds during the winter (Scammon 1874; Kellogg 1928; Dawbin 1966). Although behaviors associated with reproduction (e.g., singing, male-male competition) occur along the migration (Brown and Corkeron 1995; Clark and Clapham 2004) and during the fall in higher latitude areas (Dolphin 1987; Straley 1990), humpback whale reproduction is generally separated in space and time from feeding activities, and food resources are largely absent during the breeding season (e.g., Chittleborough 1965). Over 50% of the North Pacific humpback whale population migrates each winter to the subtropical waters around the Hawaiian Islands (Calambokidis et al. 2008), creating one of the largest and densest aggregations of humpbacks in the world.

Despite over thirty years of global study of humpback whale breeding populations, our knowledge of female reproductive behavior during the winter breeding season remains extremely limited (Cerchio 2003; Darling et al. 2006; Cartwright and Sullivan 2009a). Female humpbacks migrate to winter breeding grounds for two reasons, mating and calving, but whether or not these purposes are distinct and represent potentially conflicting reproductive objectives remains unclear. Female reproductive class has been shown to influence and characterize humpback whale associations on feeding grounds (Sardi et al. 2005), the length of time spent on breeding grounds (Darling 1983; Glockner-Ferrari and Ferrari 1984; Gabriele 1992; Clapham et al. 1992) and feeding grounds (Dawbin 1997), and possibly even male mate choice (Craig et al. 2002), but little is known about if and how female reproductive class affects female behavior and male-female interactions during the breeding season. In other mammals, female reproductive class has been shown to influence the composition of male-female groups (chimpanzees, *Pan troglodytes schweinfurthii*: Mastumodo-Oda 1999; Grevy’s zebra, *Equus grevyi*: Sundaresan et al. 2007), to influence the behavior of one sex toward the other (*P. troglodytes*, Matsumodo-Oda and Oda 1998; *P. troglodytes*, Matsumodo-Oda 1999) including rates of male harassment by Grevy’s zebra (*E. grevyi*: Sundaresan et al. 2007), and to affect seasonal movement patterns during the mating season (e.g., Equids: Rubenstein 1986; chimpanzees, *P. troglodytes*: Matsumoto-Oda and Oda 1998; brown
bears, *Ursus arctos*: Dahle and Swenson 2003). In this chapter, I present results of a study exploring whether the presence or absence of a newborn calf affects female behavior and male-female interactions during the winter breeding season.

Low annual birth rates in humpbacks suggest that female reproductive class should play a crucial role in determining female behavior and association patterns during the breeding season. Female humpbacks typically give birth to a single calf every 2–3 years (Chittleborough 1958, 1965; Dawbin 1966; Glockner-Ferrari and Ferrari 1990; Baker et al. 1987; Clapham and Mayo 1987; Straley et al. 2001) after an 11–12 month gestation period (Chittleborough 1958). Some female humpbacks are capable of conceiving and calving annually (Glockner-Ferrari and Ferrari 1984, 1990; Clapham and Mayo 1990; Straley et al. 1994), confirming whaling reports that post-partum estrus exists in this species (Chittleborough 1958). However, the number of females producing calves on one-year intervals represents a small percentage, ranging from 8.5%–14.4% of the overall population of breeding females (Chittleborough 1958; Glockner-Ferrari and Ferrari 1990; Clapham and Mayo 1990; Straley et al. 2001; Mikhalev 2000 cited by Noad and Cato 2007). Given the small percentage of female humpbacks that give birth annually, it appears that at least the majority of females have different, and perhaps even conflicting, reproductive objectives (i.e., mating versus newborn care) on the breeding grounds. If this were the case, I would expect lactating females to avoid males more frequently during the winter breeding season than females without calves.

The regularity of associations between mothers with newborn calves and males during the winter breeding season, however, complicates this hypothesis. On the Hawaiian breeding grounds between 69% and 85% of females with calves are accompanied by male escorts (Darling 1983; Glockner and Venus 1983; Glockner-Ferrari and Ferrari 1985; Craig et al. 2002), and females with calves are found in the center of multiple male, surface-active groups (SAGs) where males compete for access to females. There is also little evidence of spatial segregation on humpback breeding grounds between mothers and other breeding whales, and female-female associations, although common on feeding grounds (Weinrich and Kuhlberg 1991; Clapham 1993), are exceedingly rare on breeding grounds (Valsechhi 1997 cited by
Given the different reproductive objectives of females with calves and females without calves on the breeding grounds, behavioral responses to males may be expected to differ. In other mammals, lactating females may be at odds with breeding males that stand to maximize reproductive success by increasing access to receptive females (Trivers 1972; Smuts and Smuts 1993). Conflict between the sexes is predicted in polygynous systems when reproductive objectives between the sexes are incompatible (Smuts and Smuts 1993). For lactating females, the energetic demands of lactation during prolonged fasting periods (Lockyer 1981, 1984) and the potential costs of successive births for lifetime reproductive success (Chittleborough 1955) coupled with low birth rates in consecutive years suggest that the majority of females with calves may try to avoid mating in successive years (Craig et al. 2002). Females with calves appear to avoid multiple-male, surface-active groups (Tyack and Whitehead 1983, Mobley et al. 1988; Chapter 4), and Cartwright and Sullivan (2009a) have proposed that the seemingly paradoxical female-calf associations with a single male may be a counterstrategy to offset male harassment by multiple males. Although few studies have investigated females without calves due to the difficulty of sexing humpbacks at sea (Gabriele 1992, Craig et al. 2002), most indications are that females without calves are rarely alone (Darling 1983; Gabriele 1992; Brown and Corkeron 1995; Craig et al. 2002; although see Robbins et al. 2001). Similar to females with calves, females without calves are most often found in association with a single male (i.e., male-female pair) or in multiple male groups (Brown and Corkeron 1995; Robbins et al. 2001).

As first suggested by Gabriele (1992), the reproductive success of females without calves may represent a balance between the need to locate and conceive with the highest quality male and the need to spend the least amount of time away from critical resources necessary for successful parturition. Whaling records show newly pregnant females (i.e., females without calves) are often the first to leave breeding grounds (Chittleborough 1958, 1965; Dawbin 1966, 1997). Meanwhile, the reproductive success of pregnant females arriving on the breeding grounds may hinge on successfully giving birth, and
protecting and strengthening the newborn for the return migration to the winter grounds. One of the largest obstacles to understanding female behavior in humpback whales is the difficulty in determining the sex of females without calves in the field and to associate this with known behavior patterns. In this study, I compared association, short-term movement patterns and time budgets of known females with and without calves, to examine whether or not the presence or absence of a newborn calf affects female behavior and male-female interactions during the winter breeding season.

**METHODS**

**Study Site**

The study was conducted between January and April in the Au’Au Channel off Maui, Hawaii over six winters between 2003 and 2008 (circa 20º48' N, 156º40' W). This region comprises one of the most concentrated aggregations of humpback whales in the Hawaiian Islands (Mobley et al. 1999), and the relatively calm sea conditions provide an ideal environment for conducting behavioral studies on breeding populations of humpback whales. The calm conditions were critical for tracking whales over extended periods of time for the focal follows.

**Focal Groups**

To investigate how female reproductive class (i.e., the presence or absence of a calf) affects the association patterns, time budgets and movement patterns of females with and without calves, I conducted focal follows with three different social groups on the Hawaiian breeding grounds: male-female pairs, unescorted mother-calf groups, and escorted mother calf-groups. Each day, I randomly selected focal groups in calm conditions (Beaufort Scale 2 or less) within the approximately 100-sq km study site. I attempted to select focal groups known or believed to contain a female as far away from boat traffic and other whales (<500m) as possible, which maximized the likelihood that extended behavioral observations could be completed. Selection of groups was likely biased because females without calves are often the
first to leave the breeding grounds and mothers and calves are typically the last to leave (Nishiwaki 1959, 1966; Chittleborough 1965; Dawbin 1966, 1997).

Calves were defined based on their size and mothers were defined based on physical proximity to the calf. An adult in association with a mother and calf was assumed to be a male escort (Glockner and Venus 1983). The sex of individuals within pairs was determined by one or more of the following: 1) photo-identification of individuals of known sex; 2) genetic determination of sex based on biopsy or opportunistic collection of sloughed skin samples; 3) photo-documentation of the hemispherical lobe in female humpbacks (Glockner 1983); 4) presumed sex based on previously described social behavior of males and females on the Hawaiian breeding grounds (e.g., singer, escort, male competition).

**Focal Follow Protocol**

Focal group sampling (Altmann 1974) was used to characterize female behavior, association and movement patterns in groups both with and without a calf during the winter breeding season. Both adults were used as the focal animals as described by Altmann (1974), but in female-calf groups, I also recorded if the calf was observed circling (see Ethogram, Appendix A) or engaged in active behavioral displays (e.g., breaching) as these calf behaviors were often indicative of the behavioral state of the group. If the group changed composition, I attempted to follow the female in the focal group and to begin a new focal follow to compare behavior and movement patterns before, during and/or after the change occurred.

Group focal follows were divided into three phases: 1) 20-minute habituation period; 2) a two-hour sampling period focused on movement, respiration and behavior patterns; 3) and a final phase where potentially more invasive methods were added to the protocol (e.g., biopsy sampling to determine sex in unknown whales). Focal follows varied in duration and typically lasted as long as weather, time and/or the whales permitted. For movement comparisons, a two-hour time period was selected for analyses because of the longer dive times typically associated with male-female pairs and so that I could compare movement (e.g., speed and distance traveled) over comparable timeframes. The dataset for movement
patterns showed little variation in times used (range: 1:47 hr – 2:12 hr; \(\bar{x} = 2:01 \pm SD\) 05:21 min) and was based on the two-hour period that directly followed the 20-min habituation phase. In contrast to movement comparisons, the purpose of time budget analyses was to examine the similarities and differences in behavioral patterns between females with and without calves. Because longer focal follows give a broader and more detailed representation of behavior patterns (including interactions with other whales) and are considered more statistically reliable than shorter follows (Rogosa and Ghandour 1991), I used the total duration of focal follows for time budget and activity budget analyses (range: 52 min – 7:29 hr, \(\bar{x} = 2:33\) hr \pm SD 1:17 hr).

**Focal Group Sampling Methods**

Throughout the focal follow, continuous and incident sampling methods were used when the group was visible at the surface. During each surfacing bout, continuous data on the group’s movement (i.e., travel direction, distance, speed), respiration (i.e., surface and dive time), and behavioral state (e.g., traveling, resting, socializing, active) were recorded; and incident sampling was used to record infrequent displays such as active behaviors (e.g., breaches). On most days there was more than one observer on the boat and the primary observer (MJ) kept eyes on the focal individual(s) and dictated the behavior to an assistant that recorded the data. In other situations, the primary observer either recorded the information directly (with assistance from the driver if needed) or dictated the data directly into a portable recorder for later transcription if the behavioral data was occurring too fast for reliable recording (e.g., during chasing bouts or interactions with other males). Because the duration of these surface intervals was typically limited and generally followed by a prolonged dive where the group is out of sight, observer fatigue was not considered a problem within this study (Altmann 1974).

During the initial 20-minute habituation phase, the group was monitored for any changes in behavior (e.g., from rest to travel) or travel patterns (e.g., increased speed, changes in travel direction) that might indicate our presence was affecting the natural behavior of the group (i.e., habituation period). Groups that were abandoned before the commencement of the second phase (due to behavioral changes, weather conditions, interactions with other whales, lost whales, etc) but were photo-identified
were included in more general analyses (e.g., overall composition of female-calf and female no-calf groups on the breeding grounds). If no changes were apparent during this time, the two-hour sampling period began. During both of these phases, any activity that could potentially disturb the whales was avoided, including close boat approaches (<50m), abrupt changes in vessel speed or position, or more invasive research techniques such as biopsy sampling or underwater observations. When whales surface and dive they often leave a series of ‘footprints’ on the surface of the water that allows an observer to reliably record the track of an individual without having to directly approach the whales during surfacing bouts. In order to minimize disturbance to the group, these ‘footprints’ were used to record the location of the initial surfacing and terminal dive. Biopsy sampling and underwater observations that helped determine the sex of focal individuals were carried out after the two-hour focal follow was completed.

For time budget sampling, one of four behavioral states was classified for the group during each surfacing bout: 1) resting (i.e., no change in location from terminal dive to subsequent surface location); 2) traveling (i.e., change in location from terminal dive to subsequent location or individuals traveling at the surface); 3) socializing (e.g., periods where one or both focal individuals spent prolonged periods at the surface, often rolling upside down while approaching the research vessel); 4) active (e.g., bouts where surface displays such as breaches, tail slaps, tail throws were observed). I assumed that a behavioral state continued through the out-of-sight period (i.e., the period of time that the group was underwater) if the behavioral state was the same as the previous surfacing (Mann 1999). If the behavioral state changed when the group resurfaced after being submerged (e.g., resting to traveling), then the previous terminal dive was considered to be the onset of the new behavior and the termination of the last behavioral state. Because active behaviors can occur singly or in rapid succession and are obvious and usually infrequent, I recorded both the frequency and the duration of these behavioral events, as well as the actor of the behavior when known. To determine the proportion of time spent in each behavioral state during the focal follow, the total time spent in each behavioral state was divided by the overall observation time.
For movement comparisons, the time and location of each surface and dive for focal animals within the group were recorded using a handheld Garmin GPSmap 76CSx global positioning system. The geographic distance moved was computed by measuring the distance between the first and last GPS coordinate in the follow and represented the minimum distance traveled. The cumulative distance moved was computed by measuring the distance of all successive GPS coordinates taken during the two-hour follow, which determined the travel route for each group. A ratio of the geographic distance to the cumulative distance was computed to quantitatively determine the linearity or circular nature of travel. The closer the ratio was to 1 the more linear (straight line) the travel path, and the closer the ratio was to 0 the more circular the travel path. Speed of travel was computed by dividing the cumulative distance traveled by the length of the observation period. Routes for each focal follow were plotted using Ozi-Explorer (vers. 3.95.4q) so that individual tracks could be overlaid with behavioral data to examine potential relationships between movement and behavior.

I also focused on obtaining the following information during each focal follow: 1) photographs of the underside of the flukes and other markings for individuals within focal groups for photo-identification; 2) presence of other groups observed within 400m of the focal group to examine how nearby groups influence behavior and movement patterns; 3) collection of skin samples for genetic determination of sex. I used biopsy sampling to determine the sex composition of pairs, while sloughed skin samples were used to determine the sex of individuals engaging in active behaviors (e.g. breaching, tail throws). Genetic sampling using a biopsy darting system has been used extensively with humpbacks and has been found to be reliable (Lambertson et al. 1988) and to evoke minimal reactions from humpbacks (Clapham and Mattila 1993). Biopsies were obtained by firing a small dart attached to a retractable and floating arrow from a crossbow. Because it is often difficult to biopsy both animals within a pair, and females are rarely found together on the breeding grounds (Valsechhi 1997 cited by Valsechhi et al. 2002; Robbins et al. 2001; Craig et al. 2002; Pomilla and Rosenbaum 2006; Cypriano-Souza et al. 2010), biopsies of presumed females were attempted first and males second in order to maximize the likelihood of sexing pairs whenever a female was confirmed; in these cases the other whale was presumed to be a male. I opportunistically collected skin fragments at the surface after behavioral displays (e.g., breaches)
when possible for DNA analysis to determine the sex of the individual engaging in the behavior. Although not as efficient as biopsy darting in making a link between sample and individual, Valsecchi et al. (1998) reported high compatibility between genetically determining sex and assigning sex in the field based on social role (e.g., mother or escort) from sloughed skin samples. Drs. Per Palsboll and Martine Berube of Stockholm University analyzed all DNA samples.

**Data Analysis**

During field work, data collected from female-calf and female no-calf groups encountered for periods of 30-minutes or less were used to examine the timing of females on the Hawaiian breeding grounds, general association patterns, and for photo-identification purposes. Photographs taken of the underside of the tail flukes of individuals (Katona et al. 1979) were matched within each field season to examine sighting histories of individuals included in this study. Re-sighting histories provided insight into the length of association patterns between focal whales and allowed us to determine if an individual had been sampled more than once, which would affect the assumption of independence for statistical tests. For statistical purposes, the later focal follow was discarded when focal follows were conducted more than once with the same individual or the focal group changed composition (e.g., new focal male joined, primary male and female split) during the two-hour observation. Focal follows that were interrupted (e.g., other whales joined, a focal whale left and the group composition changed) before the completion of the two-hour time period were analyzed separately from other two-hour focal follows used in movement data analyses.

Data analyses were conducted using SPSS (version. 17.0) software and results were interpreted as significant at the 0.05 level or better. All variables were tested for normality using one-sample Kolmogorov-Smirnov test and Levene’s Test for any violations in the homogeneity of variance. For comparisons within groups, a paired samples t-test was used when the data were normally distributed. When the dependent variables were not normal, I used the non-parametric Wilcoxon Ranks test. If the variance was unequal, the unequal t-test was used for comparisons between groups (Ruxton 2006). Because the calculation of degrees of freedom in this t-test generally leads to a non-integer value, these were rounded down to the nearest whole integer as Ruxton (2006) advises. When comparing the means
between groups with distinctly normal and homogenous data that were collected from independent samples, I used the one-way analysis of variance or the independent samples t-test. A chi-squared test or its non-parametric equivalent (e.g., Kruskal-Wallis H) was used to test proportional data associated with the activity budgets. If the data were non-normal, the non-parametric Mann-Whitney test was used.

RESULTS

From 2003-2008, a total of 551 groups were encountered during 210 days of field effort (Figure 1) that included a presumed or known female. This overall dataset was used to determine the timing and association patterns of females with calves and females without calves on the Hawaiian breeding grounds (Table 1). Only pairs of known sex were included in time budget and movement analyses. For these analyses, the sex of 41 male-female pairs was determined, 32 from genetic analysis, 4 from photographs of the hemispherical lobe (Glockner 1983), and 6 from photo-identification of known individuals.
Table 1: Summary of humpback whale groups encountered during field observations 2003-2007. Values represent monthly observations summed across the five years of sampling. MC = unescorted mother-calf pair; MCE = escorted mother-calf group; MY = mother, yearling; MYE = mother, yearling and escort. SAG-calf = surface-active group with mother and calf. MF Pair = confirmed male-female pair; PR = two individuals of unconfirmed sex; SAG = surface-active group with a female without a calf; Single Female = genetically sexed lone female; Trio = three individuals of unconfirmed sex.

<table>
<thead>
<tr>
<th>Reproductive Class</th>
<th>Group Type</th>
<th>Dec</th>
<th>Jan</th>
<th>Feb</th>
<th>March</th>
<th>April</th>
<th>Total</th>
<th>Proportion of Sample</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females with calves (FC)</td>
<td>Mc</td>
<td>1</td>
<td>10</td>
<td>16</td>
<td>42</td>
<td>5</td>
<td>74</td>
<td>25.1%</td>
</tr>
<tr>
<td></td>
<td>McE</td>
<td>0</td>
<td>31</td>
<td>50</td>
<td>92</td>
<td>15</td>
<td>188</td>
<td>63.7%</td>
</tr>
<tr>
<td></td>
<td>My</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>1.0%</td>
</tr>
<tr>
<td></td>
<td>MyE</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>.68%</td>
</tr>
<tr>
<td></td>
<td>SAG-Calf</td>
<td>0</td>
<td>2</td>
<td>15</td>
<td>7</td>
<td>2</td>
<td>26</td>
<td>8.8%</td>
</tr>
<tr>
<td></td>
<td>Unknown</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>.68%</td>
</tr>
<tr>
<td>Subtotal FC</td>
<td></td>
<td>1</td>
<td>48</td>
<td>83</td>
<td>141</td>
<td>22</td>
<td>295</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Proportion FC Groups per month</td>
<td>.34%</td>
<td>16.3%</td>
<td>28.1%</td>
<td>47.8%</td>
<td>7.5%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Females without calves (FNC)</td>
<td>Group Type</td>
<td>Dec</td>
<td>Jan</td>
<td>Feb</td>
<td>March</td>
<td>April</td>
<td>Total</td>
<td>Proportion of Sample</td>
</tr>
<tr>
<td></td>
<td>MF Pair</td>
<td>0</td>
<td>17</td>
<td>19</td>
<td>5</td>
<td>0</td>
<td>41</td>
<td>16.0%</td>
</tr>
<tr>
<td></td>
<td>Pair</td>
<td>2</td>
<td>77</td>
<td>57</td>
<td>17</td>
<td>0</td>
<td>153</td>
<td>59.8%</td>
</tr>
<tr>
<td></td>
<td>SAG</td>
<td>0</td>
<td>21</td>
<td>10</td>
<td>8</td>
<td>2</td>
<td>41</td>
<td>16.0%</td>
</tr>
<tr>
<td></td>
<td>Single Female</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>1.2%</td>
</tr>
<tr>
<td></td>
<td>Trio</td>
<td>2</td>
<td>6</td>
<td>7</td>
<td>3</td>
<td>0</td>
<td>18</td>
<td>7.0%</td>
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<tr>
<td>Subtotal FNC</td>
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<td>4</td>
<td>124</td>
<td>93</td>
<td>33</td>
<td>2</td>
<td>256</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Proportion FNC Groups per month</td>
<td>1.6%</td>
<td>48.4%</td>
<td>16.9%</td>
<td>12.9%</td>
<td>.78%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTAL</td>
<td></td>
<td>5</td>
<td>172</td>
<td>176</td>
<td>174</td>
<td>24</td>
<td>551</td>
<td></td>
</tr>
</tbody>
</table>
Sexing of Individuals

Between 2003 and 2007, 30 biopsies (from males and females without calves) and 51 sloughed skin samples were obtained from 72 individuals to genetically determine the sex of individuals observed in focal follows (Table 2). Of the 81 total samples collected, 43 were females and 38 were males. A total of 49 individuals (30 females, 21 males) from 38 different pairs were sexed, and samples of both individuals within a pair were collected in 13 different groups. As predicted (based on behavior), each of these 13 groups was comprised of a male and female, and none of the 13 pairs where both individuals were sampled were male-male or female-female. In pairs where only one individual was sampled (n=25), 18 of the samples were females. Because of the extremely rare occurrence of female-female pairs on humpback breeding grounds (Valsechhi 1997 cited by Valsechhi et al. 2002; Robbins et al. 2001; Craig et al. 2002; Pomilla and Rosenbaum 2006; Cypriano-Souza et al. 2010), I assumed that any pair genetically sampled that included a female was indicative of a male-female pair. In contrast, because male-male pairs are also observed on breeding grounds (Clapham et al. 1992), when only one sample was collected and the result was male, I classified the sex composition of the group as unknown. In total, 31 of the 38 pairs (82%) sampled were confirmed to be male-female using DNA analysis. An additional 10 male-female pairs were confirmed from photographs of the hemispherical lobe on the lobe on the female (see Glockner 1983) or photo-identification of known individuals.

Timing on the Breeding Grounds

Females without calves were more common earlier in the breeding season and females with calves were more common later in the season (Table 1, Figure 2). The highest proportion of groups including females without calves were sighted in January (48.4%, 124/256), while the highest proportion of females with calves were sighted in March (47.8%, 141/295). The most significant overlap between the two groups occurred during the month of February with 16.9% of females without calves groups and 28.1% of females with calves groups encountered. Similar results were found when the encounters of the 41 known male-female pairs were compared to this larger dataset of all possible groups that included females without calves. Nineteen of the 41 known male-female pairs (46.3%) were sighted in January and 17 of the 41 were sighted in February (41.5%), with the remaining five male-female pairs sighted during
March (12.2%). Known male-female pairs were sighted as early as the 9\textsuperscript{th} of January and as late as the 22\textsuperscript{nd} of March. Although less common, females with calves were also sighted early in the season.

Table 2: Sex Determination of Female-Calf and Female No-Calf Groups. Samples are divided into two categories, those determined by DNA analysis and those determined by identification photographs or photographs of the hemispherical lobe. Skin samples for DNA analysis were either sloughed skin or biopsy samples. Photo-Id refers to females within pairs that were sexed based on previous sighting/behavioral histories. Pair = two whales; Unescorted mother-calf group = Mc; Escorted mother-calf group = McE; Escorted mother-yearling (year old calf) group = MyE; Lone = single whale; Surface-Active Group = multiple male group.

<table>
<thead>
<tr>
<th>Group Type</th>
<th>Sex</th>
<th>Sample Type DNA</th>
<th>Sample Type PHOTO</th>
<th>Sub-Total DNA</th>
<th>Total Sample</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Skin</td>
<td>Biopsy</td>
<td>Photo-ID</td>
<td>Lobe</td>
</tr>
<tr>
<td>Pair</td>
<td>Female</td>
<td>17</td>
<td>14</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>11</td>
<td>13</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>Mc</td>
<td>Female</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>McE</td>
<td>Female</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>7</td>
<td>7</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>MyE</td>
<td>Female</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Lone</td>
<td>Female</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>SAG</td>
<td>Female</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>1</td>
<td>3</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>TOTALS</td>
<td></td>
<td>51</td>
<td>30</td>
<td>6</td>
<td>4</td>
</tr>
</tbody>
</table>
Figure 2: Proportion of female no-calf groups and female-calf groups encountered per month. Values represent monthly observations summed across the five years of sampling. Sample sizes are total number of groups encountered per month. Sampling effort was less in December and April but nearly equal in the months of January – March (see also Figure 1).

Females with calves were more likely to be sighted more than one time in one season (i.e., re-sighted) than females without calves in this study. Although only 3% of individuals photographed within this study were re-sighted more than once (34/1173), of the 13 females re-sighted, 10 were females with calves (77%) and only three were females without calves (23%). Females with calves were also sighted over longer time periods. The maximum number of days between sightings for a mother-calf group was 33 days (range: 2 – 33 days, $\bar{x} = 12.9$ days), while the maximum number of days for a female without a calf was 17 days (range: 1 – 17 days, $\bar{x} = 6.7$ days). None of the females photographed in this study twice within one season were seen both with and without a calf within one season.

Association Patterns

Both females with calves and females without calves were most often found in association with a single male (Table 1). Females without calves were found primarily in pairs and females with calves were found primarily in escorted mother-calf groups. Females without calves (41/256, 16%) were nearly twice as likely to be found in a multiple male surface-active group than females with calves (26/295, 8.8%). Only 26% (74/288) of mothers with newborn calves were unescorted by a male. Unfortunately, direct
comparisons of the proportion of females without a calf that did not include a male are challenging due to the difficulty of sexing lone females at sea. I rarely encountered known females alone (n=2) and none of the pairs for which I genetically sampled both individuals (n=13) were female-female pairs. However, of five skin samples opportunistically collected from lone whales, two were from females without calves; and two lone females were observed after they split from the focal male.

**Length of Associations**

Re-sights of individual males (n=21) and females (n=13) within one season provided some insight into the length of association patterns in male-female pairs and escorted mother-calf groups. Although it was more common for individuals re-sighted within one season to be found with different individuals on repeat sightings (Appendix B), two observations, one of a female with a calf and one of a female without a calf, indicated that the same male and female were sighted together on two separate occasions. Both of these male-female groups were sighted within three days of the first sighting. In the first case, a male-female pair was photographed together across two consecutive days spanning a 28-hour period, within 3km of first sighting. In the latter case, a mother with escort was fluke identified in the second sighting only; however, photographs of the left dorsal of the calf clearly indicate that it was the same mother-calf pair on the earlier date, indicating that the escort was sighted over a three-day period with the same mother-calf pair (Jan. 25, 2005–Jan. 27, 2005).

The majority of individuals re-sighted within 10 days of first sighting were found with a different individual or in a different role (e.g., singer and escort). Of the 14 individuals re-sighted within a 10-day period where photographs of both individuals were available for both dates, 11 (78.6%) were sighted with different individuals. For example, one other female without a calf was sighted twice in three days but was with a different male on the second sighting. Similarly, one mother was sighted twice in two days and another mother photographed twice in four days, but both were with different escorts. A third female without a calf was sighted twice within 17 days. On both occasions, male-male competition was observed around the female.
Despite the low number of individuals that were re-sighted together on more than one occasion, disaffiliations or splits (i.e., the male and female split during the observation) were rarely observed in groups with and without calves. In this study, only three of 89 groups (3.4%) including known (n=2) or presumed females without calves (n=1) split during the observation period (range: 27:32 min – 6:08 hr, $\bar{x} = 2:40$ hr ± SD 1:41 hr), and only three of the 103 (2.9%) escorted mother-calf groups (range: 27 min – 7:13 hr, $\bar{x} = 1:34$ hr ± SD 1:08 hr) split. In the two known male-female pairs that split, the male was heard singing before the split occurred. In addition to the splits between male-female pairs and escorted mother-calf groups described above, one unescorted mother-calf group that was joined by a male escort and one mother-yearling-escort group split from an escort during the observation.

Other males joined and interacted with 60 of the 551 female-calf and female no-calf groups encountered (10.9%). Males were equally likely to join females without calves as females with calves: 27 female-calf groups were joined during the study while 33 female no-calf groups were joined by other male(s) ($\chi^2 = 2.765$, df = 1, p = .096). The duration of interactions with other males varied in female no-calf groups from ≤ 1min – 1:34 hr ($\bar{x} = 30:50$ min ± SD 31:35 min) and from 2:38 min–33:21 min in female-calf groups ($\bar{x} = 16:50$ min ± SD 11:21 min). Of the 27 female-calf groups that were joined, 10 were escorted mother-calf groups followed for an hour or more, and 12 of the 33 female no-calf groups were known male-female pairs. In these groups, the mean duration of the interaction with other males was nearly twice as long in female no-calf groups than in female-calf groups, although these differences were not significant (unequal variance $t = 1.43$, df = 14, p = .175). However, escorted female-calf groups were more likely to be joined by two males ($\chi^2 = 4.08$, df = 1, p < .05), and were more likely to be joined more than once during the observation period (Fisher’s Exact Test, p < .05) than females without calves. Because observation times were longer for female no-calf groups than in female-calf groups that were joined ($t = 2.015$, df = 20, p = .057; $\bar{x}$ difference = 1:20 hr), the length of the focal follow did not affect the probability of being joined more than once.

There was no difference in the response of males to interactions with other males based on whether or not the female had a calf. Males responded to the presence of a new male by competitive or agonistic displays in 83.3% of female no-calf groups and 88.9% of female-calf groups. Displacements of
the focal male by other males were also very rare, occurring in less than 1% (1/103) of observations of escorted mothers and calves and 2.2% (2/89) of male-female pairs. However, none of the three displacements led to the focal male and female splitting during the observation.

Females responded to interactions with other males in four primary ways: 1) remaining stationary while the focal male fought with the joining male; 2) traveling; 3) engaging in active behavioral displays; 4) a combination of one or more of the above. Females without calves were more likely to remain stationary or engage in active behaviors during interactions with other males than females without calves. There were 58.3% of females without calves that responded with active behaviors (7/12), but none of the females in escorted mother-calf groups responded in this way. Similarly, 25% of females without calves (3/12) remained stationary throughout the majority of the interaction, while none of the females with calves remained stationary. However, the majority of females with calves (9/10) and half of the females without calves (6/12) responded by traveling at some point during the interaction.

**Time Budgets**

Time budgets were analyzed based on one-hour minimum focal follows ($\bar{x} = 2:33$ hr ± SD 1:17 hr) with 36 confirmed male-female pairs and 50 mother-calf groups. Mother-calf groups included 21 unescorted mother-calf groups and 29 escorted mother-calf groups (a single male was present with the mother and calf during the focal observation). The presence or absence of behavior states as well as the proportion of time spent in each state was examined. Although the duration of focal observations for time budgets varied for male-female pairs and mother-calf groups, the mean difference in observation times between the two groups was only 7 sec, which was not significant (Kruskal-Wallis $\chi^2 = .005$, df = 1, $p = .944$). Moreover, the length of the observation period did not affect the proportion of time spent resting (Wald chi-square = .451, df = 1, $p = .502$), traveling (Wald chi-square = 1.038, df = 1, $p = .308$), socializing (Wald chi-square = .799, df = 1, $p = .371$) or engaging in active behaviors (Wald chi-square = .151, df = 1, $p = .697$) between female-calf and female no-calf groups.
Resting and Traveling

Resting and traveling were the most prevalent behaviors observed in both females with calves and females without calves (Figure 3). However, escorted mother-calf groups spent significantly less time resting ($t = 2.70$, df = 46, $p = .005$) and more time traveling ($t = -2.97$, df = 46, $p = .005$) than unescorted mother-calf groups. Moreover, there was no difference in resting ($F(1,55)= .027, p = .870$) and traveling ($F = .459 (1,55), p = .501$) between unescorted mother-calf groups and male-female pairs. Therefore, it was not appropriate to pool the data for unescorted mother-calf and escorted mother-calf groups into one reproductive class comprised of both female-calf groups when comparing the time and activity budget data.

Both male-female pairs ($t = 6.01$, df = 35, $p < .001$) and unescorted mother-calf groups ($t = 5.43$, df = 20, $p < .001$) spent significantly more time resting than traveling (Figure 3), while escorted mother-calf groups spent nearly equivalent amounts of time resting (50.6%) and traveling (48.9%). Moreover, escorted mother-calf groups spent significantly more time traveling ($t = -2.97$, df = 46, $p = .005$) than unescorted mother-calf groups.

Figure 3: Mean proportion of time spent resting, traveling, socializing (e.g., rolling upside down, touching, twirling, approaching research vessel), or engaging in active behavior displays (e.g., breaching) for male-female pairs, unescorted mother-calf groups and escorted mother-calf groups.

...
\( t = 3.598, \text{df} = 49, p = .001 \) and less time resting \( (t = -2.683, \text{df} = 63, p = .009) \) than male-female pairs and unescorted mother-calf groups (rest: unequal variance \( t = 2.932, \text{df} = 46, p = .005 \); travel: unequal variance \( t = -2.979, \text{df} = 46, p = .005 \)). The majority of male-female pairs (23/36) and unescorted mother-calf groups (13/21) spent 70% or more of the observation period resting, whereas only 31% (9/29) of escorted mother-calf groups rested for 70% or more of the observation period. These differences were highly significant between both unescorted mother-calf pairs and escorted mother-calf groups (\( \chi^2 = 7.99, \text{df} = 1, p = .0047 \)) and male-female pairs and escorted mother-calf groups (\( \chi^2 = 12.28, \text{df} = 1, p = .0005 \)).

There were also significant differences between male-female pairs and unescorted mother-calf groups in the extensiveness of resting bouts. Male-female pairs were significantly more likely than unescorted mother-calf groups to spend 90% or more of the observation resting (\( \chi^2 = 5.78, \text{df} = 1, p = .016 \)). Thirty-six percent of male-female pairs rested for 90% or more of the observation period (\( \bar{x} = 2:16 \text{ hr} \pm 24:21 \text{ min} \)), and 22% (8/36) rested during the entire observation. In contrast, all of the unescorted mother-calf groups traveled at some point during the observation, and only 4 of 21 (19%) unescorted mother-calf groups rested for 90% or more of the observation period (\( \bar{x} = 2:30 \text{ hr} \pm 1:04 \text{ hr} \)).

Variability in the amount of time spent resting, however, was most pronounced in groups that contained a male (i.e., male-female pairs and escorted mother-calf groups, Figure 4). Interactions with other males during the observation also led to an increase in the proportion of time spent traveling (and a reduction in the time spent resting) for each of the three social groups (Figure 5).
Figure 4: Variability in the proportion of time spent resting in unescorted mother-calf groups, escorted mother-calf groups, and male-female pairs.

In 48.3% (14/29) of male-female pairs where resting was observed for the majority of the time (29/36), the male surfaced alone and circled above the resting and submerged female before the pair surfaced together several minutes later. As such, asynchronous diving patterns were not uncommon in male-female pairs, and the mean downtimes were significantly different between males ($\bar{x} = 9.31$ min ± SD 2.20 min) and females ($\bar{x} = 21.32$ ± SD 4.41 min) (paired $t = 4.58$, df = 5, $p < .01$). None of the males in escorted mother-calf groups were observed engaging in these circling behaviors during resting periods.
Figure 5: Comparison of the proportion of time spent traveling in male-female pairs (MF PR), unescorted mother-calf groups (Mc) and escorted mother-calf groups (McE) that interacted with other males (joined) versus those that did not interact with other males during the observation period (not joined).

Active and Social Behaviors

Because active behaviors (e.g., tail throws, breaches, tail slaps) are often single occurrences, the mean percentage of time spent engaging in these behaviors is low (Figure 3). Active behaviors were most often observed in male-female pairs (61.1%; 22/36), followed by escorted mother-calf groups (55.2%; 16/29) and unescorted mother-calf groups (42.9%; 9/21). Male-female pairs were significantly more likely to engage in active behaviors than unescorted mother-calf groups ($\chi^2 = 4.11, df = 1, p < .05$). Although I found no significant difference in the frequency of active behaviors observed between male-female pairs and escorted mother-calf groups ($\chi^2 = .33, df = 1, p = .566$), females within male-female pairs were significantly more likely to engage in these behaviors than females in escorted mother-calf groups ($\chi^2 = 5.80, df = 1, p = .016$; Figure 6).
Of the 22 male-female pairs where active behaviors were recorded and skin collected, genetic results indicated the female was involved in 90.9% (20/22) of cases and acted alone in 81.8% (18/22) of cases. Only three observations involved males (13.6%), and two of these three observations involved both the male and the female acting together (e.g., double breach). In contrast, 75% (12/16) of active behaviors in escorted mother-calf groups involved the male escort, and the mother acted alone in only three of sixteen observations (18.8%). Because there was no male present in unescorted mother-calf groups, the mother was responsible for each of the 9 active behaviors recorded. Females without calves also spent significantly more time engaging in active behaviors than females with calves ($U = .686, p < .05$), and the total time spent engaging in active behaviors was correlated with the likelihood of being joined by other males ($r = .244, p = .024$).

In contrast to rest and travel periods when whales typically spend time at the surface only between dives or during extended travel periods, social behaviors in this study involved situations where one or more individuals within the focal group remained at or near the surface for extended periods of time, often approaching the research vessel. Similar to descriptions by Darling (1983), these interactions often involved the female rolling upside down at or near the surface, and/or engaging in other surface behaviors, including 'head rises' (whale rises its head vertically out of the water while remaining

Figure 6: Proportion of male-female pairs (MF Pairs) and escorted mother-calf groups (McE) where the male and/or female was responsible for the active behaviors (i.e., breaching, tail slapping) observed.
stationary) and ‘flippering’ (raising one or both flippers out of the water). In the two cases where social behaviors were observed in unescorted mother-calf groups, the mother approached or remained close to the boat while repeatedly rolling at the surface and occasionally raising her head out of the water while the calf engaged in surface behaviors, including flippering, rolling, and head rises nearby.

Social behaviors were far more common in females without calves than in females with calves ($\chi^2 = 6.293$, df = 1, $p = .012$). These behaviors were observed in 25.0% (9/36) of male-female pairs but in none of the 29 escorted mother-calf groups and in only two of twenty-one unescorted mother-calf groups (9.5%). When I examined the larger female-calf dataset for social behaviors, I found that none of the mother-calf-escort groups observed for 30 min or more (n=103) were observed socializing and no further observations of social behavior were found in unescorted mother-calf pairs observed for 30 min or more (n=35).

I also found a relationship between social and active behaviors. In ten of the eleven cases where social behaviors (90.9%) were observed, the focal female was also engaging in active behaviors (e.g., breaching). In addition, females without calves that engaged in active and/or social behaviors were also likely to be joined by other males. In 66.7% (8/12) of interactions with other males in female no-calf groups, the female was identified as engaging in active behaviors before, during and/or after the interaction with the other male(s) occurred, and other whales joined five of the nine (56%) male-female pairs where social behaviors were observed. Social behaviors were not, however, a significant predictor of whether or not a group was joined (Wald chi square = 2.521, B = -1.273, df = 1, $p = .112$). In contrast, neither of the two social unescorted mother-calf groups was joined.

**Movement Patterns**

I found a highly significant relationship between distance and speed ($r = .997$, n=50, $p < .001$). Escorted mother-calf groups moved the most, while male-female pairs moved the least (Table 3). Although unescorted female-calf groups tended to move shorter distances and travel at slower speeds than escorted female-calf groups, there were no significant differences found between these two groups.
in any of the movement patterns examined (Table 4). As a result, I pooled unescorted and escorted mothers and calves into one female-calf group for comparisons with females without calves.

Table 3: Comparison of movement patterns between male-female pairs, unescorted female-calf groups, and escorted female-calf groups. Movement was measured in terms of the geographic distance moved (GD, i.e., first and last waypoint), the cumulative distance moved (CD, i.e., all successive waypoints during 2-hr follow), speed of travel (i.e., distance traveled/time = km/hr), and the ratio of geographic distance to cumulative distance moved during the 2-hr focal follow.

<table>
<thead>
<tr>
<th>Movement Pattern</th>
<th>Male-Female Pairs (n=18)</th>
<th>Unescorted Female-Calf Groups (n=11)</th>
<th>Escorted Female-Calf Groups (n=21)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Geographic Dist (km)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>2.3</td>
<td>2.2</td>
<td>3.0</td>
</tr>
<tr>
<td>Median</td>
<td>1.8</td>
<td>1.5</td>
<td>2.4</td>
</tr>
<tr>
<td>Std Dev</td>
<td>1.8</td>
<td>1.7</td>
<td>2.5</td>
</tr>
<tr>
<td>Range</td>
<td>.482 – 7.49</td>
<td>.080 – 5.12</td>
<td>.198 – 11.4</td>
</tr>
<tr>
<td>Cumulative Dist (km)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>2.9</td>
<td>3.3</td>
<td>4.3</td>
</tr>
<tr>
<td>Median</td>
<td>2.4</td>
<td>3.0</td>
<td>3.5</td>
</tr>
<tr>
<td>Std Dev</td>
<td>2.1</td>
<td>1.7</td>
<td>2.6</td>
</tr>
<tr>
<td>Range</td>
<td>.701 – 8.2</td>
<td>1.27 – 6.1</td>
<td>1.29 – 12.2</td>
</tr>
<tr>
<td>Speed (km/hr)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>1.4</td>
<td>1.7</td>
<td>2.2</td>
</tr>
<tr>
<td>Median</td>
<td>1.4</td>
<td>1.5</td>
<td>1.8</td>
</tr>
<tr>
<td>Std Dev</td>
<td>1.0</td>
<td>.85</td>
<td>1.4</td>
</tr>
<tr>
<td>Range</td>
<td>.377 – 4.36</td>
<td>.63 – 3.02</td>
<td>.584 – 6.15</td>
</tr>
<tr>
<td>Ratio (GD: CD)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>.78</td>
<td>.58</td>
<td>.65</td>
</tr>
<tr>
<td>Median</td>
<td>.85</td>
<td>.69</td>
<td>.66</td>
</tr>
<tr>
<td>Std Dev</td>
<td>.16</td>
<td>.28</td>
<td>.22</td>
</tr>
<tr>
<td>Range</td>
<td>.44 - .95</td>
<td>.06 - .92</td>
<td>.15 - .93</td>
</tr>
</tbody>
</table>

Table 4: ANOVA results comparing the mean geographic distance (km), cumulative distance (km), speed (km/hr), and movement ratio (GD:CD) (with outliers). Comparisons include: unescorted female-calf groups (n=11) and escorted female-calf groups (n=21); pooled female-calf groups (i.e., female-calf and female-calf with escort; n=32) with females without calves (n=18); and male-female pairs (n=18) with escorted mother-calf groups (n=21). All groups, including outliers, are included in these comparisons (n=50). * = Significant at .05 level.

<table>
<thead>
<tr>
<th>Type of Movement</th>
<th>Female-Calf and Female-Calf with Escort Groups</th>
<th>Female No-Calf and Female-Calf Groups</th>
<th>Male-Female Pairs and Female-Calf with Escort Groups</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F df  sig</td>
<td>F df  sig</td>
<td>F df  sig</td>
</tr>
<tr>
<td>Geographic Distance</td>
<td>.984 1, 30 .329</td>
<td>.552 1, 48 .461</td>
<td>1.12 1, 37 .298</td>
</tr>
<tr>
<td>Cumulative Distance</td>
<td>1.35 1, 30 .255</td>
<td>2.91 1, 48 .095</td>
<td>3.80 1, 37 .059</td>
</tr>
<tr>
<td>Speed</td>
<td>1.85 1, 30 .272</td>
<td>2.80 1, 48 .101</td>
<td>5.38 1, 37 .065</td>
</tr>
<tr>
<td>Ratio</td>
<td>.512 1, 30 .480</td>
<td>5.29 1, 48 .026*</td>
<td>3.88 1, 37 .056</td>
</tr>
</tbody>
</table>
Most striking was the variability in movement patterns evident within each of the three social groups (Table 3, Figure 7). Groups that included both a male and a female exhibited the greatest variability in movement patterns except for the ratio of cumulative distance to geographic distance traveled (Table 3) in which unescorted mother-calf groups had the largest range. The cumulative distances moved ranged from .701 km (70.1 m) to 8.4 km in male-female pairs and from 1.3 km to 12.2 km in escorted mother-calf groups during the two-hour sample period. Similarly, speeds ranged from .38 km/hr to 4.4 km/hr in male-female pairs and from .5 km/hr to 6.2 km/hr in mother-calf-escort groups.

When comparisons were made between male-female pairs and escorted mother-calf groups (Table 5), marginally significant differences were found, with male-female pairs traveling shorter distances ($F = 3.8 \ (1,37) \ p = .059$) and at slower speeds ($F = 5.4, \ (1,37), \ p = .065$) than escorted mother-calf groups. Only two of eighteen male-female pairs (11.1%) traveled more than 5 km, while 29% (6/21) of mother-calf-escort groups traveled more than 5 km in a two-hour period.
Figure 7: Boxplot illustrating the variability (+/- 1 SD) and the presence of outliers in the cumulative distance moved in 2-hours for male-female pairs (n=18), unescorted mother-calf groups (n=11) and escorted mother-calf groups (n=21).

The only significant difference to emerge between females with and without calves was in the ratio measurement (Table 4) of geographic distance moved to cumulative distance moved (GD/CD; Table 3). Females with calves had a significantly lower movement ratio ($\bar{x} = .63 \pm .24$) than females without calves ($\bar{x} = .78 \pm .16$) ($F = 5.29 (1, 48), p = .026$). Although unescorted mother-calf groups (Mc) had the lowest mean ratio (.59) and exhibited the greatest range of all three social groups, there was no statistical difference between unescorted and escorted mother-calf groups ($F = .512 (1,30), p = .480$). Overall, females with calves demonstrated more variability in the ratio measurement than females without calves (Figure 8) suggesting that the presence of a calf affects the linearity of travel more than the presence of a male escort. Nearly 70% (12/18) of females without calves had a ratio of .83 or higher,
while only 28% of female-calf groups had a ratio of .83 or higher, indicating that male-female pairs (no calf present) had a more linear movement pattern than females with calves.

Two outlier groups (Figure 7 and Figure 8), one in the escorted mother-calf dataset and one in the male-female pair dataset, significantly affected the movement patterns of these groups. As a result, I reanalyzed movement comparisons without the presence of these outliers (Table 5), and found significant differences between females with calves and females without calves and between male-female pairs and unescorted mother-calf groups in all comparisons except for the geographic distance (i.e., distance between first and last waypoint) moved during the two-hour period. Removing the outliers, however, did not affect the outcome of comparisons between unescorted and escorted mother-calf groups reported earlier.
Figure 8: Histogram showing the presence of outliers in the cumulative distance moved in two-hours by escorted mother-calf groups (McE) and male-female pairs (MF PR). Mother-calf groups (Mc) were normally distributed.

Table 5: ANOVA results comparing the mean geographic distance (GD), cumulative distance (CD), speed (km/hr), and the movement ratio (GD: CD) (without outliers). Comparisons include: male-female pairs (n=17) and escorted female-calf groups (n=20); pooled female-calf groups (i.e., escorted female-calf groups and unescorted female-calf groups, n=31) with females without calves (FNC) (n=48).

* Significance < .05.

<table>
<thead>
<tr>
<th>Movement</th>
<th>Male-Female Pair and Escorted Female- Calf Groups (without outliers)</th>
<th>Female-Calf and Female No-Calf Groups (without outliers)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>df</td>
</tr>
<tr>
<td>Geo Distance (GD)</td>
<td>1.69</td>
<td>1, 35</td>
</tr>
<tr>
<td>Cum Distance (CD)</td>
<td>5.89</td>
<td>1, 35</td>
</tr>
<tr>
<td>Speed (km/hr)</td>
<td>5.65</td>
<td>1, 35</td>
</tr>
<tr>
<td>Ratio</td>
<td>4.17</td>
<td>1, 35</td>
</tr>
</tbody>
</table>
DISCUSSION

Similar to other studies, I found that female reproductive class affected both the timing and the length of time spent on the breeding grounds (Darling 1983; Glockner-Ferrari and Ferrari 1984; Gabriele 1992; Clapham et al. 1992; Craig et al. 2003) but not the prevalence of associations between males and females during the winter breeding season (e.g., Darling 1983; Mobley and Herman 1985; Glockner-Ferrari and Ferrari 1985; Gabriele 1992). Females without calves were more common earlier in the breeding season and females with calves were more common later in the season, with the biggest period of overlap occurring during the month of February. Interactions with other whales (i.e., joinings) were also most common in February, which coincided with the highest number of observations of surface-active groups (SAGs) involving female-calf pairs. Females with calves were also more likely to be re-sighted in one season and over longer time intervals than females without calves corroborating reports that females without calves are often the first to leave the breeding grounds (Chittleborough 1965; Dawbin 1966; Baker and Herman 1984; Craig et al. 2003) and suggestions that females without calves spend shorter periods on breeding grounds than females with calves (Darling 1983; Gabriele 1992; Craig et al. 2003).

As expected, female reproductive class did not affect the pervasiveness of male-female associations during the winter breeding season. The majority of females, regardless of reproductive class, were found in association with one male, and similar to other studies (Darling 1983; Gabriele 1992; Craig et al. 2002), known females, although not the subject of this study, were rarely found alone. Females without calves were primarily in pairs and females with calves were primarily in escorted mother-calf groups. Only 26% (74/288) of mother-calf groups were unescorted by a male, a finding that falls within the previously reported range where 69 – 85% of mother-calf groups were escorted by males on the Hawaiian breeding grounds (Darling 1983; Glockner-Ferrari and Ferrari 1985; Craig et al. 2002).

Despite the comparatively longer focal follows used in this study (see Tyack and Whitehead 1983), disaffiliations were rare in both female-calf and female no-calf groups, occurring in less than 3.5% of female-calf and female no-calf groups. Two of the three disaffiliations that occurred in female no-calf
groups involved groups where the male was singing, suggesting that male behavior may affect the longevity of associations between males and females during the winter breeding season. The length of associations in humpbacks is considered short-lived and transient (Mobley and Herman 1985; Clapham et al. 1992) and results of this study indicated that despite only a few observed disaffiliations, the majority of individuals that were re-sighted within a few days were with different partners on the second sighting. I found two exceptions to this trend, with one male-female pair sighted across two consecutive days, and one female and calf with the same escort sighted over a three-day period. Baker and Herman (1984) reported finding the same mother, yearling (year old calf) and escort together over 2 days, but no reports show associations lasting longer than 2-3 days. The sighting of a female without a calf in a male-female pair associated with male competition, and then 17 days later as the nuclear animal (presumed female) in a surface-active group either suggests that the duration of estrus is much longer (see Robbins et al. 2001), or that polyestrous cycling does occur in this species (Mathews 1937; Chittleborough 1965).

The primary difference in association patterns between females with calves and females without calves was the likelihood of a female being found in a multiple male group. Comparable to results reported by Gabriele on the Hawaiian breeding grounds (1992) and Clapham et al. (1992) in the West Indies breeding ground, I found that females without calves were nearly twice as likely to be found in multiple male groups (4 or more whales) than females with calves. Although little is known about estrus in this species, researchers have often presumed that females in multiple male groups are in a sexually receptive state (e.g., Darling 1983) and differences in a female’s reproductive state may explain the difference in multiple male associations between females with calves and females without calves. How frequently lactating females enter a post-partum estrus is unknown, but in contrast to the prevalence of female-calf associations with males, whaling records have suggested that it might not be a regular occurrence in this species (Chittleborough 1965). Alternatively, this finding could be interpreted to lend support to suggestions made by Gabriele (1992) and Craig et al. (2002) that male humpbacks prefer females without calves to females with calves. In support of this possibility, the mean duration of interactions with other males was nearly twice as long in male-female pairs as it was in escorted mother-calf groups, but the finding that males were equally as likely to join female-calf groups as they were female no-calf groups questions this interpretation.
Female reproductive class also affected the general behavior, activity and movement patterns of male-female groups. While there were extremes in both female-calf and female no-calf groups with males (i.e., one pair traveled the entire time and one escorted mother-calf group rested the entire time), the majority of male-female pairs were characterized by extensive resting periods that lasted for the majority (70% or more) of the observation period, whereas the majority of escorted mother-calf groups divided their time between intermittent periods of resting and traveling. Indeed, the amount of time devoted to resting was significantly higher in females without calves than females with calves that were accompanied by males. Escorted mother-calf groups also traveled significantly further distances and speeds than male-female pairs. Of the three social groups followed during this study, male-female pairs traveled the least and escorted mother-calf groups the most.

The presence of a male escort significantly changed the proportion of time spent resting and traveling in female-calf groups. Unescorted mother-calf groups spent significantly more time resting and less time traveling than escorted mother-calf groups and were surprisingly more similar to male-female pairs than escorted mother-calf groups. Escorted female-calf groups spent significantly less time resting and more time traveling than male-female pairs and unescorted mother-calf groups, which suggests that the presence of a calf significantly affects male-female interactions during the breeding season. These findings stand in contrast to a recent study by Cartwright and Sullivan (2009a) that found no statistically significant differences in time budgets between escorted and unescorted mother-calf groups. They reported that traveling was the most predominant activity for all mother-calf groups, accounting for about half of the calf’s time budget. This was not the case in our study; although similar to their results, there was substantial variation between groups. The difference in findings is most likely a result of the different sampling protocols used between the two studies.¹

¹ Cartwright and Sullivan (2009a) used predominant animal sampling (PAS) with calves as the focal animal, while in this study continuous sampling methods were used to determine periods of rest and traveling (stalled) with adults as the focal animal. Using calf versus adult as the focal animal should not affect the results as the mother and calf are usually within close physical proximity to one another (Glockner and Venus 1983) and periods of resting or traveling should be the same for both individuals. It is more likely that the differences in observation times and/or the sampling methods used influenced the results. The mean length of our observation period was 153 ± 77 min (SD) per group, longer than the mean observation time 51.8 ± 13.6 min (SD) per group used in their study and as such I had greater number of observations to draw from in our study (Wilson et al. 2008), and longer focal follows may lead to more statistically reliable results (Rhodosa and Ghandour1991).
The primary difference between unescorted mother-calf pairs and male-female pairs was the pervasiveness of resting in female no-calf groups versus female-calf groups. Resting was the most defining characteristic of male-female pairs, whereas female-calf groups, both with and without an escort were more prone to intermittent and longer periods of travel. These lengthy resting periods in pairs correspond to more anecdotal descriptions of “breath-holding” pairs on winter breeding grounds (Darling 1983; Gabriele 1992); a name that originated because of the apparent lack of movement and activity typically observed within these pairs.

Forty-one “breath-holding” or resting pairs were sexed in this study and all were male-female. Our observations support previous suggestions that these male-female pairs are primarily reflective of reproductive unions and are an integral part of the mating system in humpbacks. Indeed, previous genetic studies have found that male-female pairs on breeding grounds are unrelated (Cypriano-Souza et al. 2010), and contrary to descriptions of known male-male pairs traveling and joining groups containing a female together (e.g., Clapham et al. 1992; Brown and Corkeron 1995; Darling and Berube 2001; Darling et al. 2006), none of the male-female pairs sexed in this study traveled toward or joined other groups. Instead, as reported in Chapters 3 and 4, movement in male-female pairs was correlated with the presence and avoidance of other groups observed within 400-meters of resting pairs.

Other males, however, often joined male-female pairs, which resulted in male-male competition, a male behavior pattern commonly associated with mate guarding in other mammals where the male defends the female from other males during critical times associated with her estrus cycle (e.g., elephants, *Loxodonta africana*: Poole 1989; bighorn sheep, *Ovis canadensis canadensis*: Hogg 1987; giraffes, *Giraffa camelopardalis*: Bercovitch et al. 2006). Indeed, several researchers have noted the similarity in male-female pairs to mate guarding (e.g., Baker and Herman 1984; Mobley and Herman 1985; Gabriele 1992; Clapham et al. 1992). Similar to reports by Glockner-Ferrari and Ferrari (1985), male-female pairs were also both the starting and ending point of surface-active groups (SAGs), a social group associated with female estrus (e.g., Darling 1983). Moreover, several researchers (Darling 1983; Gabriele 1992; Craig et al. 2002) have found that in the majority of cases where a female without a calf (including both pairs and SAGs) was sighted in consecutive years, the second year she was sighted with
a calf, suggesting that pairs, as well as surface-active groups, are reflective of successful reproductive unions.

None of the females in our study that were observed in pairs were re-sighted within the same season with a calf, suggesting that breath-holding and extensive resting periods are an important and perhaps defining characteristic of females without calves and that these unions are not reflective of late pregnant females waiting to give birth. Our results are in concert with results reported from a collaborative study in the North Pacific Ocean where 2,179 sightings of 314 females yielded only 3 cases where a female was sighted without a calf and then with a calf in Hawaii (Gabriele et al. 2001). However, there was no reported information on the group composition of these females prior to being sighted with a calf, so whether or not some of the variability I observed in the activity and movement patterns within male-female pairs is reflective of this late pregnant reproductive state is unknown. Indeed, in the one male-female pair (outlier) that traveled throughout the duration of the follow (traveling over 8.5 km in 2-hours), the female had an unusually wide girth, appearing much larger in girth than the male companion, but whether or not she was pregnant was impossible to discern. In support of this latter possibility, results of fluke measurements (Chapter 3) indicate that despite noticeable differences in girth there was no discernable difference in the fluke sizes of these individuals.

Collectively, the data indicate that male-female pairs typically behave differently than male-male pairs during the breeding season and that these pairs are associated with courtship as has been presumed in the literature (e.g., Darling 1983; Gabriele 1992). Extensive resting in other female terrestrial mammals (e.g., red deer: Clutton-Brock et al. 1982) is associated with the pro-estrus part of the reproductive cycle and as such the dominant resting periods observed in female no-calf groups may be suggestive of the female’s reproductive state. In red deer, for example, the proportion of time the female spent inactive or resting increased significantly and the range of movement decreased significantly during estrus periods (Clutton-Brock et al. 1982). In the humpback male-female pairs followed in this study, not only was resting the most dominant behavior pattern, but the mean distance moved and speed traveled in two-hours was significantly less than that in females with calves. One male-female pair that was sighted together across two consecutive days was re-sighted less than 3km away from the location of the last
sighting on the previous day, strongly suggesting that in this case the lack of movement persisted over a 28-hour period. Whether the male in these groups is guarding the female pre or post mating is unclear.

Increased male attention and male-male competition typically suggest that the female is in a heightened state of estrus (e.g., Geist 1971; Darling et al. 1983). In contrast to the predominantly resting male-female pairs described above, surface-active groups (comprised of multiple males apparently competing for access to the female) are typically characterized by fast and erratic travel (e.g., Tyack and Whitehead 1983). I found that female groups that were joined spent significantly more time traveling and less time resting than groups that were not joined. Furthermore, in this study, only 25% of resting male-female pairs that were joined by an additional male resulted in the formation of a surface-active group comprised of three or more males. The fact that this did not occur in the majority of cases raises questions as to whether this is an indication of the female’s estrus stage or the result of some other factor (e.g., male escort successfully defending female). The questions nonetheless remain: why are females remaining stationary with a lone male and moving extensively with multiple males? If females in pairs and in surface-active groups are in the same stage of estrus, then why do these conspicuous behavioral differences exist?

Resting male-female pairs appear outwardly similar to resting escorted mother-calf groups; one noticeable difference, however, was the tendency of males within pairs to complete a half or whole circle at the surface above the resting and submerged female prior to both the male and female surfacing together several minutes later. Nearly 50% of males within male-female pairs engaged in this behavior while none of the escorts to females with calves exhibited this circling behavior. Asynchronous surfacings by males and females within the same pair led to significant differences in downtimes between males and females, with female dives averaging over twice as long as their male companions on average. I found similar results in 60-min focal follows conducted prior to a playback experiment with male-female pairs (Chapter 4). In contrast to female behavior, males closely attended and followed the female’s movements. I only observed a female within a pair surface alone without the male companion on two occasions, and both involved interactions with other incoming males where the male had temporarily left the female to address and block access of the new male.
While this circling behavior in males is reminiscent of calves circling at the surface as both the mother and escort rest below (Glockner and Venus 1983; Cartwright and Sullivan 2009b), and longer dives are associated with larger animals (e.g., Schreer and Kovacs 1997), there was no indication that these shorter dives by males in pairs were related to a difference in age-class between the male and the female within a pair (see Chapter 3). Based on sighting records, one known-age male that engaged in this circling behavior throughout the focal follow was 33 years old at the time of the observation (C. Gabriele, Personal Communication). Other known males that were circling were at least 11 years of age (Chapter 3) and thus were most likely both sexually and physically mature (Chittleborough 1965; Gabriele et al. 2007). Males in male-female pairs that were exposed to playback recordings of other males on breeding grounds often responded by circling the female underwater or at the surface (Chapter 4), suggesting that this male behavior may be related to guarding and/or the alertness of the male to nearby surroundings. In support of this possibility, when responding to a nearby disturbance, male sheep will sometimes make tight circles in one place (Geist 1971), and shorter downtimes in males have been reported and associated with mate guarding in male-female pairs of Dall's porpoises (Phocoenoides dalli) (Willis and Dill 2007).

Mate guarding usually involves close attendance by the male toward the female during periods associated with fertility and involves the attending male preventing potential rivals from interacting with the female, thereby reducing mating opportunities with other potential mates. To be successful, the male has to defend the female by monitoring the female’s movements and maintaining proximity to the female, especially during challenges from other males. Males in both female-calf and female no-calf groups behave in ways that are reminiscent of mate guarding. The finding that females with calves were equally as likely to be joined by other males as females without calves, and that males responded to these interactions with competitive and agonistic behaviors in nearly 90% of male-male interactions regardless of the female’s reproductive class suggests that the social role of the male within these groups may be similar.

While the behavior of the males was similar in these groups, I found significant differences in female behavior around males based on female reproductive class, as well as substantial variability within
reproductive classes, especially in male-female groups. In addition to the significant differences already reported in regards to rest and travel patterns, females without calves were significantly more likely to engage in active (e.g., breaching, pectoral or tail slapping, etc) and social behaviors (e.g., female repeatedly rolling upside down at the surface), and to respond to interactions with other males by remaining stationary or engaging in active behaviors than females with calves.

Social behaviors (i.e., rolling upside down, touching, spending more time at surface than underwater) occurred in 25% of male-female pairs but were absent in escorted mother-calf groups. Although the social function of these behaviors is not yet understood, females rolling upside down at the surface have been associated with both courtship (e.g., right whales, *Eubalaena glacialis*: Kraus and Hatch 2001) and avoidance of mating attempts in other baleen whales (e.g., gray whales, *Eschrichtius robustus*: Swartz 1986). Darling (1983) reported that a female within a pair that was engaging in similar behaviors was re-sighted the following year with a calf, suggesting that these behaviors may be part of the behavioral repertoire associated with courtship. In support of this possibility, pairs engaging in these behaviors were seen swimming belly to belly underwater, and on one occasion the male's penis was visible but mating was not observed. Behaviors correlated with a female’s estrus cycle are unknown in humpbacks. As such, whether or not these behaviors are related to a female’s reproductive state is not clear, but multiple males competing for a female are often presumed to be indicative of a female’s estrus cycle (Darling et al. 1983), and one or more males eventually joined the majority of male-female pairs that engaged in socializing behaviors. On the other hand, these types of behaviors were also observed in male-female pairs where either the female and/or male were likely sub-adults and have been reported in pairs of males (Glockner-Ferrari and Ferrari 1985; J. Darling, Personal Communication). In our study, one female that engaged in social behaviors for nearly 60% of the observation period eventually became the focus of two males that worked in apparent coordination to control her movements (see Chapter 3). As a result, whether or not these behaviors are reflective of the female’s reproductive state, willingness or unwillingness to mate, and/or social bonding action remains unclear.

In contrast, I observed active behaviors (e.g., breaches, tail slaps etc) in both escorted female-calf groups and male-female pairs, but there were highly significant differences in the sex of individuals
responsible for these behaviors. Over 90% of active behaviors in male-female pairs involved the female, whereas in escorted mother-calf groups 75% of active behaviors involved the male. The contrast in these results was surprising, but similar findings have been reported for females without calves in larger surface-active groups in Hawaii. For example, Deakos (2002) reported that females without calves in multiple male groups were significantly more likely to engage in flippering (pectoral fin slapping) than females with calves and suggested that females may use this behavior to solicit male competition.

Although the social function of active behaviors is not yet understood, researchers have speculated that females may use active behaviors to attract males, to solicit competition between males, or to displace an unwanted escort (Clapham 2000; Deakos 2002). If active behaviors attract other whales and females without calves are trying to maximize associations with males and females with calves are trying to minimize male interactions, then I might expect to find a difference between females engaging in active behaviors based on female reproductive class as I found in this study. Additionally, if whales were using active behaviors to attract other whales, then I would expect to find an increase in interactions with other whales after active behaviors were observed. In support of this possibility, active behaviors preceded or followed interactions with males in nearly 70% of the cases when other males joined known female no-calf groups, and preceded interactions in 40% of the escorted mother-calf groups that were joined. Overall, 55% of male-female groups that were joined were observed engaging in active behaviors immediately prior to these interactions occurring, and only 18% were stationary at the time of the joining. These results suggest that active behaviors are an important component of interactions with other whales and that the longer the activity occurs the greater the chances that other males will be attracted. However, unless there is some benefit to the male by attracting other males, it doesn’t explain why males in female-calf groups are significantly more likely to engage in active behaviors than in female no-calf groups.

If females with calves attempt to avoid male interactions (i.e., avoided males more often), then males might also use active behaviors to attract other males to help coerce or control a resistant female. In support of these possibilities, observations of pairs of males forming coalitions to displace a male escort (Clapham et al. 1992; Brown and Corkeron 1995) or to herd the movements of a resistant female
have been described in the literature (Darling et al. 2006; Chapter 3). In our study, females with calves were significantly more likely to engage in behaviors consistent with female avoidance of males (e.g., fast and circular travel, movement > 5km in 2-hrs, tail throws in the direction of the escort) than females without calves. Pairs of males were also significantly more likely to join females with calves than females without calves, and nearly 60% of female-calf groups that were joined by paired male’s involved situations where the escort was chasing the mother (female avoidance; see Chapter 3). In half of the observations of mothers (females with calves) that were engaged in active behaviors prior to having interactions with other males, the mother had an escort that was chasing her. On two such occasions I observed the mother turn directly toward and approach a pair of whales, presumably to displace the escort, which resulted in the pair joining the group and competitive behaviors, suggesting that at times, females may directly solicit competition to displace unwanted males. In the other half of these cases, however, the male was active prior to the interaction, which further suggests that both males and females in escorted mother-calf groups use active behaviors to attract other males, albeit for different reasons.

Females without calves also spent significantly more time remaining stationary and inactive around a male than females with calves. In elephants, Poole (1989) reported that females remained still and inactive with larger musth males while they attempted to outrun or avoid younger males. Anecdotal descriptions of female humpbacks rejecting males have been reported elsewhere (Mattila et al. 1989; Glockner-Ferrari and Ferrari 1985; Clapham et al. 1992) and certainly some of the extreme movements I observed involved situations where the female was trying to escape from or actively avoid a specific male escort. If lack of movement is indicative of tolerance of a male and movement indicative of avoidance, then females without calves rarely avoided interactions with males while females with calves frequently avoided males. In 89 focal follows with known or presumed male-female pairs, only two females clearly and actively avoided a male companion throughout the observation period, whereas nearly 30% of females with calves acted in ways consistent with female avoidance (e.g., fast and circular travel, movement > 5km in 2-hours, tail throws in the direction of the escort).

In contrast to the lack of movement I observed in male-female pairs, using satellite telemetry Mate et al. (1998) reported humpbacks in Hawaii moving distances of up to an average of 150 km/day,
including a mother and calf that traveled 670 km in 4.5 days. Although this result is presumably not representative of continuous travel, a mother and calf that traveled 670 km in 4.5 days would be traveling on average 6.2 km/hr. Only one out of the 50 focal follows I conducted involved females traveling between 6-7 km/hr and it was an escorted mother-calf group that traveled 12.2 km in 2-hrs, with clear avoidance from the female towards the male noted (fast circular travel, movement >5km in 2-hrs tail throws and displays toward the escort). Indeed, only 20% of our 50 focal groups traveled more than 5km in 2-hrs, and of those, 60% were escorted mother-calf groups, with the other 40% evenly divided between male-female pairs and unescorted mother-calf groups. In 83% of the escorted mother-calf groups and in one of two cases in male-female pairs where the distances exceeded 5km, the male was actively chasing the female, consistent with descriptions by Darling et al. (2006), and strongly suggesting that extreme movement in females may be related to the behavior of the male.

Male avoidance may be one explanation for more extensive short-term travel in mother-calf and male-female pairs, but it may be only part of the equation. I observed two unescorted mother-calf groups travel 5km or more in an observation period. Persistent travel has been related to the specific age-class of the calf (Thomas and Tabor 1984; Cartwright and Sullivan 2009b). These authors have suggested that increased travel in younger calves may stimulate the production of muscular myoglobin, an oxygen-binding protein that may lead to greater breath-holding capabilities. Cartwright and Sullivan (2009b) found that the age-class of the calf (based on the degree of dorsal fin furl) did not affect the number of male escorts around the mother, but did not investigate whether the behavior of the mother was different in escorted mother-calf groups with younger calves versus older calves. Given the critical implications for calf growth and survival on female reproductive success, it is plausible that calf age and avoidance of the escort are interrelated. Although not examined in our study, mothers with the youngest calves may actively avoid males more often than mothers with older calves, and may explain some of the variability I observed in activity and movement patterns in female-calf groups.

Other indications that females with calves may avoid interactions with males while females without calves may tolerate or even encourage interactions with males came from our observations that females with calves were more likely to move away (travel) in response to interactions with other males,
while females without calves were more likely to remain stationary or engage in active behaviors (e.g., breaching, flippering). Nearly 60% of females without calves responded to interactions with other males by engaging in active behaviors and 25% responded by remaining stationary; however, none of the female-calf groups responded in these ways. Instead, 90% of females with calves responded to interactions with other males by traveling, and the duration of these interactions was shorter than in female no-calf groups.

Previous studies comparing the behavior of female humpback whales with and without calves were limited by the difficulty of sexing individuals in the field when a calf was not present or the behavior of the individual had not previously been associated with one sex (e.g., singing or escorting females) (e.g., Mobley and Herman 1985; Gabriele 1992; Craig et al. 2002). In these studies, female no-calf groups often included females in multiple male groups which made direct comparisons with escorted mother-calf groups (i.e., single male groups) challenging, especially because the presence of multiple males has since been found to affect the behavior and movement of females (Cartwright and Sullivan 2009a). Although genetic studies now indicate that the majority of pairs on breeding grounds are male-female (Brown and Corkeron 1995; Pomilla and Rosenbaum 2006; Cypriano-Souza et al. 2010), male-male pairs are also found on humpback breeding grounds (Darling 1983; Clapham et al. 1992), which further complicates these descriptions as the behavioral differences between male-female pairs and male-male pairs have not yet been discerned in the literature. As a result, although pairs of whales are one of the most prevalent social groups on winter breeding grounds (Pomilla and Rosenbaum 2006; Cypriano-Souza et al. 2010), the social role and function of these pairs has not been systematically studied, and consequently little is known about sex-specific behavior within these groups. One of the primary goals of this study was to determine the sex of the individuals within pairs in order to compare and describe the similarities and differences in behavior between females with and without calves.

Overall, I found that female reproductive class (i.e., presence or absence of a calf) influenced and characterized some, but not all aspects, of female behavior, association, activity and movement patterns. Female reproductive class affected the length of time spent on breeding grounds, the likelihood of being pursued by multiple males, the extent of time spent resting and traveling, the degree of short-term
movement and specific behaviors (e.g., socializing, active behaviors). While female reproductive class did not affect the overall prevalence of associations with males, it did affect how females responded to males, and in time budgets, unescorted mother-calf groups were more similar to male-female pairs than escorted mother-calf groups. Because escorted mother-calf groups were significantly different from both unescorted mother-calf groups and male-female pairs strongly suggests that the presence of a newborn calf is a significant factor in male-female interactions during the breeding season. One of the most striking findings to come from this comparative study was the variability I found within the different female groups. This variability suggests that there are a number of factors influencing female behavior during the breeding season, beginning with female reproductive class, but also including costs and benefits of specific male escorts, stage of the reproductive cycle, and relative body size/age-class.

Clearly, the most critical gap and limiting factor in all studies of humpback reproductive behavior is our current lack of knowledge around the female estrus cycle. Separating male behavior from female behavior is a formidable challenge for behavioral studies, and our results suggest that there is significant flexibility governing male-female interactions during the breeding season. This variability adds complexity to our ability to understand the behavior and mating strategies in this species and may confound attempts to compare or generalize behavioral patterns between populations. Developing a more complete understanding of male-female relationships and interactions during the breeding season depends upon our ability to isolate and consider the influence of other variables, including how female estrus cycles and varying oceanographic, topographic, ecological and social characteristics influence these interactions. In the meantime, future studies aimed at investigating how male-female interactions are affected by variables other than reproductive class, such as male behavior, male and female body size, and age-class (calf and adults), may help explain the substantial variability I observed between males and females and increase our understanding of how female choice operates in breeding populations of humpback whales.
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MALE-FEMALE INTERACTIONS IN HUMPBACK WHALES DURING THE BREEDING SEASON ARE AFFECTED BY RELATIVE BODY SIZE AND MALE AGGRESSIVENESS

ABSTRACT

Breeding aggregations of humpback whales (*Megaptera novaeangliae*) are comprised of mixed-sex individuals that vary in terms of female reproductive class (with or without calf), age-class (sub-adult/adult), body size and condition, but how this range of individual physical characteristics and physiological states influences male-female interactions during the breeding season is poorly understood. The purpose of this study was to investigate how reproductive class, relative body size, age-class and aggressive behavior by lone male humpbacks interrelate and contribute to the variability found in female time budgets, behavior, and movement patterns. Focal follows with 36 female no-calf groups (male-female pairs) and 29 female-calf groups (escorted mother-calf groups) were conducted on the Hawaiian breeding grounds; and relative fluke size (n=30; fluke photogrammetry) and age-class (n=9; sighting histories) was determined for 39 individuals within these groups. I found that multiple and direct approaches by males to <1 body length of the female, and chasing, which included multiple approaches, and led to high-speed, energetic chases that persisted over time significantly impacted female behavior. Chasing significantly affected distance and speed traveled, and the proportion of time a group spent resting versus traveling. Females with calves were significantly more likely to be chased by lone males than females without calves suggesting that these short-term increases in energy expenditure are significant and greatest for lactating females. I also found a significant relationship between fluke size, age and male behavior. Although fluke sizes ranged up to 4.53m in males and 4.61m in females, none of the males that chased females or females that were chased had flukes larger than 4.1m, and none of the females or males of known maturity chased or were chased. The mean fluke size for mothers in chasing
groups was significantly smaller than mother’s not being chased. Our results indicate that body size, age-
class, female reproductive class and aggressive behavior by lone males significantly influence male-
female interactions on breeding grounds.

INTRODUCTION

Humpback whales (Megaptera novaeangliae) are seasonally reproductive, migrating annually
from higher latitude feeding areas in the summer to lower latitude breeding and calving grounds during
the winter (Scammon 1874; Kellogg 1928; Dawbin 1966). Over 50% of the North Pacific humpback whale
population migrates each winter to the subtropical waters around the Hawaiian Islands (Calambokidis et
al. 2008), creating the largest and densest aggregation of humpbacks in the North Pacific Ocean.
Although humpbacks migrate for the purposes of reproduction, individuals arriving on breeding grounds
are of mixed-sex and vary in terms of reproductive class (e.g., with or without calf), age-class (sub-
adult/adult), body size and condition. This wide range in physical characteristics and physiological states
present in both sexes undoubtedly leads to substantial variability and potential conflict in how any two
individuals, both of the same or different sex, interact with each other. Indeed, I found a wide range in
activity, behavior and movement patterns of females, especially around males, during the winter breeding
season (Chapter 2). In this study, I investigate some of the potential sources of variability in male-female
behavior during the winter breeding season.

Female humpbacks, both with and without calves, are most often found in association with a lone
male during the winter breeding season (Glockner and Venus 1983; Glockner-Ferrari and Ferrari 1985;
Gabriele 1992; Brown and Corkeron 1995; Craig et al. 2002). These pairings or associations, with or
without a calf, reflect one of a number of different physiological and social combinations that may result in
different behavioral interactions: 1) age-class: sub-adult female and adult male, adult female and sub-
adult male, or adult female and adult male; 2) female reproductive condition: lactating (with calf) or non-
lactating (without calf); parous or nulliparous; estrus or anestrous; good or poor physical condition; recent
completion of weaning or one or more years since lactation; non-pregnant, newly pregnant or late
pregnant. How these different physiological states and physical characteristics interact with and influence male-female interactions in humpback whales during the breeding season is not yet understood.

Furthermore, male status and age-class, reflected in body size, has been found to play an important role in male-female interactions and associated strategies to acquire mates. Body size and condition influence male and female reproductive success (Ralls 1976; Andersson 1994), and may characterize social relationships between males and females (Rubenstein 1986), including aspects associated with female mate choice (equids: Rubenstein 1986; elephants: Poole 1989; elephant seals: Galimberti 2000a; orangutans: Stumpf and Boesch 2010). Female preference for dominant males, for example, may lead to selection for increased size, strength and fighting ability in males (Mesnick 1997). Male body size and age-class have also been correlated with aggressive behavior in males toward females in several species of polygynous mammals (e.g., elephants: Poole 1989; polygynous ungulates: Clutton-Brock and Parker 1995; orangutans: Stumpf and Boesch 2010). As a result, relative body size and age-class, as well as aggressive behavior in males, have been found to have a profound effect on female movement patterns (Clutton-Brock and Parker 1995), mate selection (Wiley and Poston 1996), and male and female reproductive strategies used to obtain mates (Clutton-Brock and Parker 1995). This includes the evolution of mate guarding (Wrangham 1979), a prominent feature of male-female interactions during the humpback winter breeding season (e.g., Baker and Herman 1984; Mobley and Herman 1985; Gabriele 1992; Clapham et al. 1992; Brown and Corkeron 1995; Chapter 2). In humpback whales, body size may confer an advantage in male-male competition for estrus females (Spitz et al. 2002) and males may preferentially associate with larger females (Pack et al. 2009) that may have higher reproductive success (Ralls 1976). In this study, I explore how relative body size, age-class, and aggressive behavior by lone males interact and contribute to the substantial variability found in female behavior and movement patterns during the winter breeding season.
METHODS

Study Site

The study was conducted between January and April in the Au’Au Channel off Maui, Hawaii over six winters between 2003 and 2008 (circa 20º48’ N, 156º40’ W). This region comprises one of the most concentrated aggregations of humpback whales in the Hawaiian Islands (Mobley et al. 1999), and the relatively calm sea conditions provide an ideal environment for conducting behavioral studies on breeding populations of humpback whales. The calm conditions were critical for tracking whales over extended periods of time for the focal follows.

Focal Groups

To investigate how relative size, age and behavior of individual males and females affect the range and variability in movement and behavior patterns, I conducted focal follows with male-female pairs and escorted mother-calf groups on the Hawaiian breeding grounds. Each day, I randomly selected focal groups in calm conditions (Beaufort Scale 2 or less) within the approximately 100-sq km study site. I attempted to select focal groups known or believed to contain a female as far away from boat traffic and other whales (<500m) as possible, which maximized the likelihood that extended behavioral observations could be completed. Our selection of groups was likely biased because females without calves are often the first to leave the breeding grounds and mothers and calves are typically the last to leave (Matthews 1937; Chittleborough 1958, 1965; Dawbin 1966, 1997).

Calves were defined based on their size and mothers were defined based on physical proximity to the calf. An adult in association with a mother and calf was assumed to be a male escort (Glockner and Venus 1983). The sex of individuals within pairs was determined by one or more of the following: 1) photo-identification of individuals of known sex; 2) genetic determination of sex based on biopsy or opportunistic collection of sloughed skin samples; 3) photo-documentation of the hemispherical lobe in female humpbacks (Glockner 1983); 4) presumed sex based on previously described social behavior of males and females on the Hawaiian breeding grounds (e.g., singer, escort, male competition).
Focal Follow Protocol

Focal group sampling (Altmann 1974) was used to characterize behavior, association and movement patterns in groups with and without a calf during the winter breeding season. As described by Altmann (1974) both adults were used as the focal animals. Focal follows varied in duration and typically lasted as long as weather, time and/or the whales permitted. Because longer focal follows are considered more statistically reliable than shorter follows (Rogosa and Ghandour 1991), a two-hour focal sampling period was used for movement comparisons and the total duration of the focal follow, with a minimum of one-hour, was used to determine the proportion of time spent resting or traveling for time and activity budgets. Following Mann (1999), female-calf and female no-calf groups that were observed for 30-minutes or less were considered survey data and were included for photo-identification purposes to determine the relative reproductive span or age-class of individuals in different social groups.

Group focal follows were divided into three phases: 1) twenty-minute habituation period; 2) a two-hour sampling period focused on movement, respiration and behavior patterns; 3) and a final phase where potentially more invasive methods were added to the protocol, including biopsy sampling, underwater observations to determine sex in unknown whales and measurement techniques using fluke photogrammetry techniques first described by Calambokidis et al. (2001).

Focal Group Sampling Methods

Throughout the focal follow, continuous and incident sampling methods were used when the group was visible at the surface. During each surfacing bout, continuous data on the group’s movement (i.e., travel direction, distance, speed), respiration (i.e., surface and dive time), and behavioral state (e.g., traveling, resting, socializing, active) were recorded for movement, activity and time budget analyses. Incident sampling was used to record infrequent displays such as active behaviors (e.g., breaches). Instantaneous sampling (during each exhalation when both focal adults were visible) was used to record the relative proximity estimated in body lengths of the focal individuals to one another (e.g., 0 -1 body
lengths), using the female’s body as a reference clock (e.g., 12:00 directly ahead of female; 6:00 directly behind female).

On most days there was more than one observer on the boat and the primary observer (MJ) kept eyes on the focal individual(s) and dictated the behavior to an assistant that recorded the data. In other situations, the primary observer either recorded the information directly (with assistance from the driver if needed) or dictated the data directly into a portable recorder for later transcription if the behavioral data was occurring too fast for reliable recording (e.g., during chasing bouts or interactions with other males). Because the duration of these surface intervals was typically limited and generally followed by a prolonged dive where the group is out of sight, observer fatigue was not considered a problem within this study (Altmann 1974).

During the initial 20-minute habituation phase, the group was monitored for any changes in behavior (e.g., from rest to travel) or travel patterns (e.g., increased speed, changes in travel direction) that might indicate our presence was affecting the natural behavior of the group (i.e., habituation period). If no changes were apparent during this time, the two-hour sampling period began. During both of these phases, any activity that could potentially disturb the whales was avoided, including close boat approaches (<50m), abrupt changes in vessel speed or position, or more invasive research techniques such as biopsy sampling or underwater observations. When whales surface and dive they often leave a series of ‘footprints’ on the surface of the water that allows an observer to reliably record the track of an individual without having to directly approach the whales during surfacing bouts. In order to minimize disturbance to the group, I used these ‘footprints’ to record the location of the initial surfacing and terminal dive. Biopsy sampling and underwater observations that helped determine the sex of focal individuals were carried out after the two-hour focal follow was completed.

For time budget sampling (proportion of time spent engaging in a behavioral state), one of four behavioral states was classified for the group during each surfacing bout: 1) resting (i.e., no change in location from terminal dive to subsequent surface location); 2) traveling (i.e., change in location from terminal dive to subsequent location or individuals traveling at the surface); 3) socializing (e.g., periods
where one or both focal individuals spent prolonged periods at the surface, often rolling upside down while approaching the research vessel; 4) active (e.g., bouts where surface displays such as breaches, tail slaps, tail throws were observed). I assumed that a behavioral state continued through the out-of-sight period (i.e., the period of time that the group was underwater) if the behavioral state was the same as the previous surfacing (Mann 1999). If the behavioral state changed when the group resurfaced after being submerged (e.g., resting to traveling), then the previous terminal dive was considered to be the onset of the new behavior and the termination of the last behavioral state. Because active behaviors can occur singly or in rapid succession and are obvious and usually infrequent, I recorded both the frequency and the duration of these behavioral events, as well as the actor of the behavior when known. To determine the proportion of time spent in each behavioral state during the focal follow, the total time spent in each behavioral state was divided by the overall observation time.

For movement comparisons, I recorded the time and location for each surface and dive for focal animals within the group using a handheld Garmin GPSmap 76CSx global positioning system. The geographic distance moved was computed by measuring the distance between the first and last GPS coordinate in the follow and represented the minimum distance traveled. The cumulative distance moved was computed by measuring the distance of all successive GPS coordinates taken during the two-hour follow, which determined the travel route for each group. I then computed a ratio of the geographic distance to the cumulative distance to quantitatively determine the linearity or circular nature of travel. The closer the ratio was to 1 the more linear (straight line) the travel path, and the closer the ratio was to 0 the more circular the travel path. Speed of travel was computed by dividing the cumulative distance traveled by the length of the observation period. Routes for each focal follow were plotted using Ozi-Explorer (vers. 3.95.4q) so that individual tracks could be overlaid with behavioral data to examine potential relationships between movement and behavior.

During surface intervals, I also collected the following information: 1) photographs of the underside of the flukes and other markings for individuals within focal groups for photo-identification and fluke photogrammetry purposes (described below); 2) presence of other groups observed within 400m of the focal group to examine how nearby groups influence behavior and movement patterns; 3) collection of
skin samples for genetic determination of sex; 4) the approximate location of the male in relation to the female using a clockwise method (directly behind the female was 6:00 and directly in front was 12:00); 5) estimation of the distance of the male in relationship to the female using body lengths rounded to the nearest whole number (e.g., 0-1 body lengths, 1-2 body lengths, etc). We recorded the presence of other groups observed within 400m of the focal group because whales at this distance could consistently and reliably be recorded by observers (e.g., blows could often be heard if a surfacing was missed), and recordings with the laser range finder are reliable from this distance.

Fluke Photogrammetry (Relative Body Size and Age)

I used a photogrammetric technique first described by Calambokidis et al. (2001) to estimate the relative size of tail flukes of individual whales within focal groups. This method has successfully been used in field studies of humpback whales (Calambokidis et al. 2001; Jones et al. 2005; Sousa-Lima and Groch 2010), sperm whales (Jaquet 2006) gray and blue whales (Calambokidis et al. 2001) to determine the relative size and age-class of individuals (e.g., juvenile, mature). The technique involves taking identification photographs of a whale’s tail fluke (during dives) at a perpendicular angle while simultaneously measuring the distance to the whales. I used a calibrated Canon EOS digital camera with a calibrated fixed 300mm lens in combination with a Bushnell laser range finder to photograph and estimate the distance of the photographer to the whale’s tail as the picture is taken. In our calibration tests, the calculated measurements were within .1m of actual length; that is, flukes within .2m of each other would be considered the same size. Digital cameras have successfully been used with this technique before (Jacquet 2006), and I further calibrated the technique by measuring objects of known size. Two critical factors in accurately determining the relative size of flukes from this method are relying only on photographs taken at a perpendicular angle and using multiple photographs of the same tail (Calambokidis et al. 2001; Jones et al. 2005; Jacquet 2006). Consequently, our analyses were primarily based on individuals where I obtained a minimum of three high quality photographs taken at a perpendicular angle (although in reported instances I used two high quality photographs that were both taken at perpendicular angles and resulted in consistent measurements). Two independent observers (MEJ, JDD) measured each high quality fluke included in our sample (i.e., angle was 90 degrees). I then
averaged the multiple measurements to determine the relative width of the tail fluke for each individual. Sousa-Lima and Groch (2010) have reported a positive correlation between fluke width and body length in humpbacks.

**Sex Determination**

I used biopsy sampling to determine the sex composition of pairs, while sloughed skin samples were used to determine the sex of individuals engaging in active behaviors (e.g. breaching, tail throws) during focal follows. Genetic sampling using a biopsy darting system has been used extensively with humpbacks and has been found to be reliable (Lambertson et al. 1988) and to evoke minimal reactions from humpbacks (Clapham and Mattila 1993). Biopsies were obtained by firing a small dart attached to a retractable and floating arrow from a crossbow. Because it is often difficult to biopsy both animals within a pair, and females are rarely found together on the breeding grounds (Valsechhi 1997 cited by Valsechhi et al. 2002; Robbins et al. 2001; Craig et al. 2002; Pomilla and Rosenbaum 2006; Cypriano-Souza et al. 2010), biopsies of presumed females were attempted first and males second. I also opportunistically collected skin fragments at the surface after behavioral displays (e.g., breaches) when possible for DNA analysis to determine the sex of the individual engaging in the behavior. Although not as efficient as biopsy darting in making a link between sample and individual, Valsecchi et al. (1998) reported high compatibility between genetically determining sex and assigning sex in the field based on social role (e.g., mother or escort) from sloughed skin samples. Drs. Per Palsboll and Martine Berube of Stockholm University analyzed all DNA samples.

**Photo-Identification**

To determine individual sighting histories, I matched photographs taken of the underside of the tail flukes of individuals (Katona et al. 1979) within and between field seasons. Within season comparisons allowed us to determine if an individual had been sampled more than once, which would affect the assumption of independence for statistical tests. For statistical purposes, I discarded the second focal follow when focal follows were conducted more than once with the same individual or the focal group changed composition (e.g., new focal male joined, primary male and female split) during the
two-hour observation. Focal follows that were interrupted (e.g., other whales joined, a focal whale left and the group composition changed) before the completion of the two-hour time period were analyzed separately from other two-hour focal follows used in movement data analyses.

Comparisons of individuals between years and comparisons with other catalogues in the North Pacific Ocean allowed us to determine the relative age-class and/or the reproductive history of known individuals sighted within this study. Minimum age was calculated based on the number of years between the first sighting and the sighting year in this study plus one additional year as all whales were assumed to be at least one year of age unless noted as a calf in the first sighting (n=1). Minimum reproductive histories were based on the first year that a female was sighted with a calf.

Data Analysis

Data analyses were conducted using SPSS (version. 17.0) software and results were interpreted as significant at the 0.05 level or better. All variables were tested for normality using one-sample Kolmogorov-Smirnov test and Levene’s Test for any violations in the homogeneity of variance. For comparisons within groups, I used a paired samples t-test when the data were normally distributed. When the dependent variables were not normal, I used the non-parametric Mann Whitney test. If the variance was unequal, I used the unequal t-test to compare between groups (Ruxton 2006). Because the calculation of degrees of freedom in this t-test generally leads to a non-integer value, these were rounded down to the nearest whole integer as Ruxton (2006) advises. When comparing the means between groups with distinctly normal and homogenous data that were collected from independent samples, I used the one-way analysis of variance or the independent samples t-test. A chi-squared test or its non-parametric equivalent (e.g., Kruskal-Wallis H) was used to test proportional data associated with the activity budgets. I used an ANCOVA analysis using general linear models in SPSS to test the relationship between male behaviors and activity budgets. I used an ANCOVA regression analysis to examine the effect of female reproductive class (i.e., presence or absence of a calf) and relative fluke size of individuals on the speed and distance traveled during focal follows.
RESULTS

Between 2003 and 2008, I encountered 295 female-calf groups and 256 groups containing females without calves (see Chapter 2, Table 1). Of those 551 groups, 227 groups were followed for a minimum of 30 minutes (survey, general observations, photo-identification), 86 groups were followed for a minimum of 1-hr (activity and time budget data), and 50 were followed for 2-hours or more (movement data). In the overall dataset (n=227), females without calves included groups with known females (n=36) and groups that were presumed to include females without calves (n=53). The 53 presumed male-female pairs were included because they were observed “breath-holding” for 70% or more of the observation period, a defining characteristic of male-female pairs in Hawaii (see Chapter 2), or because the male was observed fighting with other male challengers during the observation. Female-female pairs are extremely rare on humpback breeding grounds (Valsechhi 1997 cited by Valsechhi et al. 2002; Robbins et al. 2001; Craig et al. 2002; Pomilla and Rosenbaum 2006; Cypriano-Souza et al. 2010), and the behavior patterns I observed are typical of male-female pairs (see Chapter 2) and have not been documented in male-male pairs.
Table 1: Composition of groups observed between 2003 and 2008 and included in study. The focal follow time (e.g., $\geq 30$ minutes) is the minimum amount of time a group was followed to be included within the dataset. General comparisons were used for purposes of photo-identification and to examine association patterns. Behavioral comparisons were used as the basis for time budget data.

<table>
<thead>
<tr>
<th>Dataset</th>
<th>Females without calves</th>
<th>Females with Calves</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex Determined (genetics, ID)</td>
<td>41 male-female pairs</td>
<td>103</td>
</tr>
<tr>
<td>General Comparisons ($\geq$ 30-minute focal follow)</td>
<td>36 Male-Female pairs</td>
<td>53 Presumed Male-Female pairs</td>
</tr>
<tr>
<td>Behavioral Comparisons ($\geq 1$hr focal follow)</td>
<td>36 Male-Female pairs</td>
<td>29 Mother-Calf Escort groups</td>
</tr>
<tr>
<td>Movement Comparisons ($\geq 2$-hr focal follow)</td>
<td>18 Male-Female pairs</td>
<td>21 Mother-Calf Escort groups</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Unescorted Mother-Calf Groups</td>
</tr>
</tbody>
</table>

The mean observation time for focal follows used to analyze time budgets was 2:33 hr (range: 52 min - 7:29 hr $\pm$ SD 1:17 hr). The mean difference in observation times was not significantly different between females with calves and females without calves (Kruskal-Wallis chi-square = .005, df = 1, p = .944). The dataset for movement patterns was based on two-hour time intervals with little range in time intervals (range: 1:47 hr – 2:12 hr; $\bar{x} =2:01 \pm$ SD 05:21 min).

**Variability in Male-Female Behavior Patterns**

I found substantial variability in short-term movement patterns within male-female groups both with calves and without calves (Figure 1). While the majority of females, with or without calves, moved 3.5 km or less in the two-hour sampling period, other groups moved 6 - 12 km (Figure 2). Similarly, speeds ranged from <1 km/hr to 4.4 km/hr in male-female pairs and up to 6.2 km/hr in escorted mother-calf groups.

The behavior of males and females within groups also ranged from passive and tolerant to aggressive and intolerant. Male behavior ranged from passive (resting, maintaining a distance of 1-2 body lengths from the female) to aggressive (chasing, active displays including head lunging) and female behavior ranged from tolerant (no movement away) to extreme avoidance (e.g., frequent changes in
direction, fast and extended travel, tail displays toward the escort) in both female-calf and female-no calf groups.

Figure 1: Variation in distance traveled during a 2-hour observation period for male-female pairs (MF PR) and escorted mother-calf groups (McE).
Figure 2: Routes of two escorted mother-calf groups, illustrating the variability in movement patterns over a two-hour time period for females with calves. Route A is an example of a mother that was being actively chased by the escort. Route B is an example of an escorted mother-calf group that was not being chased.
Male Approaches and Female Behavior and Movement Patterns

Approaches were defined as direct movement by the male toward the female that resulted in a decrease in distance of less than one body length between the two individuals. There was little difference in the frequency of male approaches to females with and without calves; however, multiple approaches were more common in female-calf groups and led to significant differences in activity patterns. Males approached females <1 body length (Figure 3 and 4) in 58.3% (21/36) of the focal follows with male-female pairs and in 65.5% (19/29) of escorted mother-calf groups. When approached females with calves spent significantly more time traveling ($F(1, 27) = 10.188, p = .004$) and less time resting ($F(1, 27) = 10.255, p = .003$) than groups where the escorts were not observed directly approaching females. In contrast, close approaches did not affect the proportion of time traveling ($F(1, 34) = 1.359, p = .252$) or resting ($F(1, 34) = 1.760, p = .193$) in females without calves.

![Figure 3: A male approaching a female directly from behind and within one body length of the female. Photo by Meagan Jones.](image-url)
However, males escorting mother-calf groups approached the female significantly more often than males escorting females without calves ($U = 364.5$, $Z = -2.161$, $p = .031$). The mean number of approaches made by a male in a female-calf group was $5.07 \pm SD 7.23$ (range: $1 - 30$, median = 2.0), while the mean number or approaches by a male within a male-female pair was $1.92 \pm SD 4.64$ approaches (range: $1 - 26$; median = 1.0). Multiple approaches by a male significantly affected the proportion of time spent resting (GLM Model: $B = -2.466$, df = 1, $p < .001$) and traveling (GLM Model: $B = 2.175$, df = 1, $p < .001$) for both female-calf and female no-calf groups (Figure 5).

The circumstances surrounding approaches differed between unescorted mother-calf groups and male-female pairs. In male-female pairs (without calf), 66.7% (14/21) of the approaches occurred at the same time another individual or group was observed within 400m of the focal group, but in female-calf
groups other nearby groups (i.e., ≤ 400m) were simultaneously observed with male approaches in only 26.3% (5/19) of the observations ($\chi^2 = 16.0$, df = 1, p < .001).

Figure 5: The number of approaches made by a male toward a female significantly affected the proportion of time a female spent resting.

Females also responded to male approaches differently based on female reproductive class. Nearly 80% of females with calves responded to close male approaches by diving and moving away; however, females without calves were more mixed in their responses. Six of 21 females without calves (28.6%) that were approached by males showed no overt response (i.e., continued to rest), five of the 21 (23.8%) responded with an active behavioral display (e.g., tail displays; Figure 6) and 47.6% responded by diving and moving away. In contrast, only two of 19 females with calves responded by resting and two
by engaging in active behaviors. Eight of the 11 (72.7%) active behaviors observed in response to male approaches involved tail or peduncle throws by the female.

Figure 6: A male humpback whale approaching a female from < 1 body length behind the female; the female responds with a tail lash. Photo by Meagan Jones.

**Male Chasing and Female Behavior and Movement Patterns**

Chasing was defined by the presence of the following factors: 1) multiple and direct approaches by the male towards the female; 2) fast (≥ 3km/hr) and/or frequent changes in direction (circular swimming) over sustained periods led by the female; 3) evasive active behaviors by the female including tail throws, tail slaps, and/or tail lashes. In all groups where males chased females, close approaches by the male toward the female were observed, but not all groups with close approaches involved chasing. Male approaches towards the female (within one body length of the female) were significantly more
common \((U = 25.0, z = -4.91, p < .001)\) in groups classified as chasing \((\bar{x} = 11.2 \pm SD 8.0)\) than in groups where males were not chasing \((\bar{x} = 1.96 \pm SD 1.4; \text{Figure 7})\).

Females with calves were significantly more likely to be chased by males than females without calves \((\chi^2 = 15.95, df = 1, p < .001)\). Chasing was observed in 22 of 103 female-calf groups (21.4%) and in two of 89 groups with females without calves (2.2%) that were followed for 30-min or more.

**Figure 7:** The number of approaches made by males toward females within one body length (≤1 BL) in groups where a male was chasing the female versus groups where chasing was not observed (n=29). Number 39 is indicative of an outlier in the data (number of approaches observed equaled 30 in this case).
The proportion of time a group spent resting \( (F(1,63) = 46.02, p < .001; \text{Figure 8}) \) and traveling (unequal variance \( t = -6.82, df = 19, p < .001 \)) was significantly greater in chasing groups than in non-chasing groups.

Figure 8: The proportion of time spent resting for female groups that were chased and female groups that were not chased. Differences were highly significant \( (F(1,63) = 46.02, p < .001) \).
Chasing also significantly affected the distance (unequal variance $t = -4.15$, df = 13, $p = .001$; Figure 9) and the speed traveled (unequal variance $t = -4.06$, df = 12, $p = .002$) in all cases. Indeed, when I removed groups where chasing was observed from a study comparing movement patterns between females with and without calves (Chapter 2), I found that the reported differences were no longer significant for distance ($F = 1.798 (1,28)$, $p= .191$) and speed traveled ($F =1.658 (1, 28)$, $p = .208$). In female no-calf groups that were not chased (n=16), the mean distance moved in two-hours was 2.64 km ± SD 1.6 km and the average speed was 1.3 km/hr compared to 7.1 km ± SD 1.9 km (distance) and 3.4 km/hr ± SD 1.4 km/hr (speed) in female no-calf groups that were chased (n=2). Similarly, in female-calf groups the mean distance traveled for groups that were not chased (n=14) was 3.2 km ± SD 1.1 km and the mean speed was 1.6 km/hr ± SD .56 km/hr. In female-calf groups that were chased (n=10), the mean distance traveled was 7.4 km ± SD 2.9 km and the mean speed was 4.0 km/hr ± SD 1.8 km/hr. One of the most extreme examples I observed was an escorted mother-calf group that traveled 8.93 km in 59 minutes. At an average speed of 9.1km/hr, the speed was so extreme that there was a visible wake coming off the mother as she moved away from the escort. While the actual distance covered was 8.93 km, the distance from the first to the last waypoint was only 4.78 km, indicating that the group changed direction frequently, traveling nearly twice as far as necessary to reach the same destination (ratio = .54).
Figure 9: Difference in the cumulative distance (km) traveled in 2-hours for female groups that were chased (n=12) versus female groups that were not chased (n=30). Differences were highly significant (unequal variance $t = -4.15$, df = 13, $p = .001$).

In groups where chasing was observed and time budgets were collected (n=17), the proportion of time a male spent chasing a female ranged from 17.2% of the observation period to 100% ($\bar{x} = 64.3\% \pm$ SD 33.5%). Although chasing was less common in female no-calf groups, the longest continual period of chasing I observed lasted 4:04 hr and involved a male-female pair, while the longest chasing bout in a female-calf group was 3:14 hr.

Females both with and without calves avoided chasing males by fast or circular travel over extended distances and/or by engaging in active behaviors. Seven of the 17 chased females (41.2%) responded with tail displays, and one female without a calf that was being chased by two males
simultaneously responded with head lunges (Figure 10), an uncharacteristic behavior for females. In addition, five of the 17 chased females (29.4%) approached other whales or the research vessel during chasing bouts.

Figure 10: Photograph of a female humpback fleeing (head lunging) away from two males that were chasing at the time. A scar on the lower jaw confirmed this was the female, and not one of the males. Photo by Meagan Jones.

Agonistic behaviors by males usually associated with male-male competitive behavior were observed in 35.3% (6/17) of chasing groups. These behaviors were directed toward the female and included head lunges, jaw claps, tail throws, head lifts (whale swims with back arched and head above water), tail throws, and bubble trails (see Figure 11). Blocking, a behavior where a male moves horizontally in front of the female thus blocking her line of travel and resulting in a change in travel direction, was also common in chasing groups. Blocking was observed in 52.9% (9/17) of the groups classified as chasing, but blocking also occurred in three groups that were not chasing. In each of these situations where blocking but not chasing was observed, other whales were noted within 400m of the
focal group. Overall, blocking was observed in four of 36 male-female pairs (11.1%) and eight of 29 escorted mother-calf groups (27.6%), but there were no significant differences between the occurrence of blocking between female-calf groups and female no-calf groups ($\chi^2 = 2.90$, df = 1, p = .089).

Figure 11: A photograph of a male chasing a female with the male's head on top of the female's tail as she tries to initiate a dive. Photo by Meagan Jones.

In 35.3% (6/17) of observations, other males joined chasing groups during the observation period, including one of the two female no-calf groups (described above) and five out of 15 female-calf groups (33.3%). Because one group (the one described above) was joined twice during the observation, five of seven (71.4%) interactions with other males in six groups led to competitive behaviors between the males. However, interactions with other males tended to be much shorter than the total proportion of time the male spent chasing the female. In groups that were joined, chasing lasted on average 56.2% (± SD 39.1%) of the observation period, whereas interactions with other males lasted 19.1% (± SD 12.97%) of
the observation period. In two of the six observations where chasing groups interacted with other males, the other male displaced the original male (i.e., was now in closest proximity to the female), and one escort split or disaffiliated from the female (with calf) during the observation.

The Effect of Male Singing on Female Behavior

Singing males rarely accompanied females with or without calves in this study. Singing was only heard in six of the 194 pairs (3.1%) and in 17 of the 188 (9.0%) escorted mother-calf groups encountered in this study. Females with calves were significantly more likely to be accompanied by a singing male than a female without a calf ($\chi^2 = 7.56$, df = 1, $p < .001$). Of the six female no-calf (pairs) groups where singing was heard, three were known male-female pairs, one was presumed male-female based on behavior, and the other two pairs were likely male-female but unconfirmed.

Although disaffiliations between focal males and females were rare in this study, occurring in only 3.4% of female no-calf groups (3/89) and 2.9% of female-calf groups (3/103), three of the six disaffiliations observed (2 females without calves, 1 female with calf) involved groups where the male was singing. In two of the three splits (1 female-calf, 1 female no-calf), the female left the group within < 10 minutes of the singing beginning, and in the third situation, the split occurred 20-minutes after a 2:05 hr singing bout had stopped. Singing did not lead to a higher occurrence of interactions with other males than groups where the male was not singing ($\chi^2 = 0.05$, df = 1, $p = .823$). Interactions with other whales occurred in only six of the 15 (40%) male-female groups where singing was heard, including three female no-calf and three female-calf groups.

Although there was no significant difference in the observation times between female-calf and female no-calf groups with singing males (unequal variance $t = 1.42$, df = 6, $p = .207$), the proportion of time spent singing relative to the total observation period was highly variable in male-female groups, ranging from 5.5% - 86.7% in female no-calf groups ($\bar{x} = 31.64\% \pm SD 30\%$) and from 5% up to 100% in female-calf groups ($\bar{x} = 69.42\% \pm SD 36.7\%$; Figure 12). Differences in the proportion of time singing were only marginally significant between female-calf and female no-calf groups ($F = 4.34$ (1, 13), $p = $
however, singing was heard \(<25\%\) of the time in the majority of female no-calf groups (4/6) and \(\geq70\%\) in the majority of female-calf groups (6/9).

Figure 12: The proportion of time the male was heard singing during observation periods for females with calves (FC) and females without calves (FNC).

**Relative Size and Age-Class of Males and Females**

The relative size of individuals within groups was determined using fluke photogrammetry; Table 2 summarizes the individuals and groups measured and included within the analyses reported here.
Table 2: Number of individuals measured using fluke photogrammetry. Female no-calf groups include male-female pairs (MF PR), presumed pairs based on behavior (Presumed PR), pairs of unconfirmed sex composition (Unknown PR), and multiple male, surface-active groups (SAG). FC groups include unescorted mother-calf groups (Mc), escorted mother-calf groups (McE) and multiple male, surface-active groups with a calf (SAG-calf).

<table>
<thead>
<tr>
<th>Sex Measured</th>
<th>Females without Calves (n=15)</th>
<th>Females with Calves (n=19)</th>
<th>TOTALS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MF PR</td>
<td>Presumed PR</td>
<td>Unknown PR</td>
</tr>
<tr>
<td>Male Only</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female Only</td>
<td>3</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Both Male and Female</td>
<td>4</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Unknown</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Both Unknown</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTAL</td>
<td>7</td>
<td>4</td>
<td>2</td>
</tr>
</tbody>
</table>

No significant differences were found between the mean fluke size of females with or without calves (*unequal variance t = -1.19, df = 12, p = .255; Figure 13). Although there was variability in fluke sizes in both reproductive classes, the range in sizes was greatest in female no-calf groups, from 3.4m – 4.61m, whereas females with calves ranged from 3.86m – 4.53m. There was no statistical difference in the mean fluke size of unescorted mothers and escorted mothers (*F = .887 (2, 12), p = .437); however, mothers in unescorted mother-calf groups tended to be larger, ranging from 4.21m – 4.60m (n=3) while mothers in escorted groups (n=12) ranged from 3.86m – 4.53m (Figure 14). Of the five smallest females I measured (<4m), three were females without calves (3.37m – 3.73m) and two were females with calves (3.86m, 3.93m). The smallest female measured (3.37) was a nuclear animal in a surface-active group, and the second smallest female (3.4m) was in a male-female pair.
Figure 13: Mean fluke width (m) as measured by fluke photogrammetry in males and females within groups containing a female with a calf (FC) or female without a calf (FNC). The sample size for female-no-calf groups consisted of 7 males and 9 females (n=16), whereas the sample size for female-calf groups included 11 males and 15 females (mothers; n=26).

Males tended to have smaller flukes than females (Wilcoxon z = -1.96, p = .05, n=12; Figure 13). For example, while 80% (20/25) of the females measured had a fluke size of 4m or larger, only 39% (7/18) of males had a fluke size of 4m or more. Although the mean fluke size of males did not differ between female-calf and female no-calf groups ($F = .016 \ (1, 16), p = .901$), the range in fluke sizes was greatest for males escorting females with calves (Figure 15). In pairs, males ranged in fluke size from 3.75m – 4.29m (n=7), whereas in mother-calf-escort groups males ranged in fluke size from 3.44m – 4.52m (n=10). Male escorts had significantly smaller flukes than mothers ($paired t = -2.55, df = 5, p = ...$)
.05), but the flukes of males within male-female pairs were not significantly smaller than the females they accompanied (paired \( t = -0.719, \text{df} = 4, p = .512 \)).

Figure 15: Variability in mean fluke size (m) of males photographed as escorts to females without calves (i.e., pairs, PR; \( n=7 \)) compared to males escorting females with calves (i.e., escorted mother-calf groups, McE groups; \( n=11 \)). One male (3) within a pair is shown as an outlier on this figure.

Relative Age of Individuals in Pairs

I was able to determine the age of one male within a male-female pair in our study at 33 years based on an identification record of this individual as a calf in 1974 (C. Gabriele, Personal Communication). In addition, I estimated the minimum age (\( n=5 \)), and minimum reproductive histories (\( n=3 \)) of 5 females and 4 males observed in pairs on the Hawaiian breeding grounds through sighting histories. Results of age estimations indicated that it was not uncommon for individuals within male-
female pairs to be physically and sexually mature (Chittleborough 1965; Gabriele et al. 2007). Individuals ranged in age from 11 years up to at least 33 years of age, and some females found in male-female pairs had been reproductively active for a minimum of 15 years (range: 4 – 15 years). Table 3 summarizes the histories of individuals photographed in this study with known life history information.

Table 3: Minimum age or reproductive span of known individuals found in male-female pairs on the Hawaiian breeding grounds. Min Age or Min Repro = Minimum age and/or minimum reproductive span based on sighting history. Breath-holding pair refers to pairs resting for ≥ 70% of the observation period.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Year/Location First Observed</th>
<th>Observation Date Hawaii</th>
<th>Min Age or Min Repro (f)</th>
<th>Behavior</th>
<th>Catalogue ID Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>1999 a w/calf in Hawaii</td>
<td>Jan 16, 2006</td>
<td>Calf 7 years earlier</td>
<td>Breath-holding</td>
<td>HI06-0027 M-6</td>
</tr>
<tr>
<td>Female</td>
<td>2002 a w/calf in Hawaii</td>
<td>Feb 23, 2006</td>
<td>Calf 4 years earlier</td>
<td>Breath-holding</td>
<td>HI06-0178 M-13</td>
</tr>
<tr>
<td>Female</td>
<td>1991b w/calf in Alaska</td>
<td>March 3, 2006</td>
<td>Calf 15 years earlier</td>
<td>Breath-holding</td>
<td>HI06-0209 SEAK 1126</td>
</tr>
<tr>
<td>Male (d)</td>
<td>1996c Alaska</td>
<td>March 3, 2006</td>
<td>11 years (min age)</td>
<td>Breath-holding</td>
<td>HI06-0210 SEAK 1472</td>
</tr>
<tr>
<td>Female (e)</td>
<td>1996c Alaska</td>
<td>Jan 21, 2007</td>
<td>12 years (min age)</td>
<td>Breath-holding</td>
<td>HI07-0077 SEAK 1776</td>
</tr>
<tr>
<td>Male (e)</td>
<td>1996c Alaska</td>
<td>Jan 21, 2007</td>
<td>12 years (min age)</td>
<td>Breath-holding</td>
<td>HI07-0078 SEAK 1292</td>
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<tr>
<td>Female</td>
<td>1986c Alaska</td>
<td>Feb 9, 2007</td>
<td>22 years (min age)</td>
<td>Breath-holding</td>
<td>HI07-0112 SEAK 972</td>
</tr>
<tr>
<td>Male</td>
<td>1989c Alaska</td>
<td>Feb 28, 2007</td>
<td>19 years (min age)</td>
<td>Breath-holding</td>
<td>HI07-0170 SEAK 1940</td>
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<tr>
<td>Male</td>
<td>1974c Alaska</td>
<td>March 6, 2007</td>
<td>33 years (known age; g)</td>
<td>Breath-holding</td>
<td>HI07-0194 SEAK 516</td>
</tr>
</tbody>
</table>

a. Rachel Cartwright, Keiki Kohala, ID Catalogue
b. Jan Straley, Southeast Alaska Catalogue
c. Jan Straley and Christine Gabriele, Southeast Alaska Catalogue
d. Male and Female sighted together as a pair in Hawaii
e. Male and Female sighted together as a pair in Hawaii
f. Assumes not a calf in first year sighted unless indicated
g. Whale of known age; first sighted as a calf in 1974
Fluke Size and Male-Female Interactions

Mothers with smaller sized flukes tended to travel significantly further distances and at higher speeds than larger females based on an ANCOVA test (Table 4a). The equivalent ANCOVA test showed that male size had no effect on the speed and distance moved for females with or without calves (Table 4b).

Table 4a: ANCOVA results showing the effect of fluke size of females with (n=8) and without calves (n=13) on the cumulative distance moved and speed traveled. Reproductive class was treated as the random factor and fluke size as the covariate. Interaction terms correspond to the slopes of the regression lines of speed and distance versus fluke size for each reproductive class separately. The main effects of reproductive class and female fluke size were non-significant.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Distance</th>
<th>Speed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>B</td>
<td>Std. Error</td>
</tr>
<tr>
<td>Intercept (Female)</td>
<td>33.321</td>
<td>10.990</td>
</tr>
<tr>
<td>Females Without Calves * Female Size Interaction</td>
<td>1.121</td>
<td>2.061</td>
</tr>
<tr>
<td>Females with Calves * Female Size Interaction</td>
<td>-6.837</td>
<td>2.571</td>
</tr>
</tbody>
</table>
Table 4b: ANCOVA results showing the effect of fluke size of males accompanying females with and without calves on the cumulative distance moved and speed traveled. Reproductive class was treated as the random factor and fluke size as the covariate and both were non-significant. Interaction terms correspond to the slopes of the regression lines of speed and distance versus fluke size for each reproductive class separately. The main effects of reproductive class and male fluke size were non-significant.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Distance</th>
<th>Speed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parameter</td>
<td>B</td>
<td>Std. Error</td>
</tr>
<tr>
<td>Males with FC*Male Size Interaction</td>
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<td>2.727</td>
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</tbody>
</table>

I was able to obtain measurements for four females and four males in groups where the male was chasing the female. In the escorted female-calf groups where chasing was observed (5/15), I measured the flukes of three females (mothers) and four male escorts. Although sample sizes are small, the mean fluke size for mothers in chasing groups was significantly smaller than those of mothers not being chased (Mann Whitney U: Z = -2.456; p = .014; Figure 16). Indeed, of the four smallest mother’s measured (range: 3.86m – 4.08m) three were being chased by the escort. Although the difference between the mean fluke size of escorts chasing and escorts that were not chasing was only marginally significant (Mann Whitney U: Z = -1.837, p = .066; Figure 17), of the five smallest escorts measured (range: 3.44m – 3.83m), three were observed chasing the mother.
Figure 16: Boxplot illustrating the difference in mean fluke size (m) of mothers that were chased (n=3) and mothers that were not chased (n=8). The mean fluke size for mothers in chasing groups was significantly smaller than mother’s not being chased.

Females and males with large flukes were rarely involved in chasing (Figures 16 and 17). Although fluke sizes ranged up to 4.53m in males and 4.61m in females, none of the males that chased females (with or without calves) or females that were chased (with and without calves) had flukes larger than 4.1m. The largest fluke size for a male observed chasing was 4.06 m and for a female was 4.08 m. Although I was only able to collect multiple measurements in one of the two female no-calf groups that were chased, the second female was judged to be a sub-adult based on her relative and overall body size in comparison with our 19-foot research boat. For nearly two-hours before the chasing began, the female was circling, approaching and lying upside down next to our 19-foot boat, which allowed us to estimate with confidence her relative body size in relationship to our boat.
Although none of the sexually mature females (i.e., females with known reproductive histories) was involved in chasing, the overall behavior patterns in male-female pairs were similar despite differences in relative size and age. Both sexually mature females and females with flukes smaller (range: 3.37m – 3.73m) than the smallest measured mother (3.86m) were found in “breath-holding” pairs (i.e., resting ≥ 70% or more of the observation) and situations involving male competition. Of the three smallest females measured, the smallest was the nuclear animal (i.e., presumed female) in a surface-active group with male competition and the other two were found in male-female pairs.
I did detect a potential relationship between fluke size and the duration of associations between males and females, although sample sizes are small. The splits (disaffiliations) I observed, which were rare (see Chapter 2), involved females with smaller flukes, and the smallest male measured (3.44m) was an escort to a mother-calf pair that split. Indeed, 50% of the splits that occurred in this study (3/6), and all of the splits with individuals that were measured, involved individuals with relatively small flukes. In contrast, in the escorted mother-calf group sighted twice over a three-day period during this study (Chapter 2), both the escort (4.12m) and the mother (4.45m) had larger flukes than the mean fluke size reported earlier for mothers (4.3m) and escorts (4.0m).

**DISCUSSION**

In this study, individuals within male-female groups on humpback breeding grounds varied in terms of size and/or age-class, and these variables, coupled with female reproductive class, significantly influenced female behavior patterns, including aggression by lone males toward females, and female time budgets and movement patterns.

**Fluke Size Variability in Male-Female Groups**

Individuals within male-female groups showed considerable variation in relative fluke size, suggesting that different sized (aged) whales may occupy the same social roles and may contribute to the substantial variability in behavior and movement patterns observed within social groups containing females on the breeding grounds (see also Chapter 2). In our study, escorts to mothers and calves, and females within male-female pairs showed the greatest range in fluke sizes. Mothers (with newborn calves) also had a relatively wide range in fluke size (3.86m – 4.53m), perhaps reflecting the wide range in age of first calving reported for females in the North Pacific Ocean (8-16 yrs; Gabriele et al. 2007). Using a different measurement technique (video photogrammetry), Spitz et al. (2002) measured male humpback whales in different social roles and similarly reported a wide range in male body sizes on the Hawaiian breeding grounds.
Assuming a correlation between fluke size and overall body size (see Sousa-Lima and Groch 2010), these data suggest that individuals within social roles range from small to large, experienced to inexperienced, and immature to mature. Indeed, two of the smallest females without calves measured in this study were within the range of fluke sizes previously found for yearlings in Hawaii (unpublished data, M. Jones, J. Darling); one was in a male-female pair and one was the nuclear animal (presumed female) in a surface-active group associated with male competition. Sexually immature females have previously been reported in pairs (Spitz et al. 2002) and although unusual, as the nuclear animal in surface-active groups (Robbins et al. 2001; Pack et al. 2009). Taken together, these data indicate that at least some females associating with lone and multiple males on breeding grounds are sexually immature.

Spitz et al. (2002) proposed that pairs might largely reflect sexually immature individuals; but if that were the case, then I would have expected to find differences between the fluke sizes of females with and without calves. I found no statistical difference between the fluke sizes of females with and without calves, which suggests that while some male-female pairs may be reflective of immature individuals, the majority of females within pairs are likely sexually mature. Moreover, each of the individuals within pairs that I matched to other photo-identification catalogues indicated that males and females within these pairs were a minimum of 11 and up to 33 years of age, and thus were most likely comprised of sexually mature individuals (Gabriele et al. 2007). These data are in concert with observations that pairs are the starting and ending point of surface-active groups (Glockner-Ferrari and Ferrari 1985) that are typically associated with estrus females (e.g., Darling 1983; Tyack and Whitehead 1983; Baker and Herman 1984). Reports by Gabriele (1992) and Craig et al. (2002) similarly suggest that females within pairs are sexually mature. In these latter studies, of the females re-sighted within two consecutive years, the majority of females that were first sighted in a pair were re-sighted the following year with a calf. Data from photo-identification (sighting histories), video photogrammetry (Spitz et al. 2002) and fluke photogrammetry (this study) collectively indicate that there is a wide range in the sizes and/or age-classes of individuals in male-female pairs (with and without calf).
Aggressive Behavior by Lone Males and Female Behavior

I identified two male behavior patterns that significantly impacted female behavior, activity and movement patterns during the breeding season: 1) multiple, direct approaches made by the male to within 0–1 body lengths of the female; 2) and chasing, which often included multiple approaches, and led to high-speed, energetic chases that persisted over time. Because multiple and direct approaches significantly affected the amount of time a female spent resting and/or traveling and often led to chasing situations, I associated both multiple approaches and chasing with aggressive male behavior. Observations reported here are consistent with descriptions of aggressive behavior in other male mammals (see reviews Smuts and Smuts 1993; Clutton-Brock and Parker 1995). For example, agonistic behaviors typically associated with male-male competition including head lunges, jaw claps, tail throws, bubble trails and head lifts (whale swims with back arched and head above water) were often directed toward the female in chasing situations; and, female humpbacks that were chased actively avoided and/or fled from chasing males, consistent with female responses to male aggression in other mammalian species (southern elephant seals, *Mirounga leonina*: Galimberti et al. 2000a; Grevy’s zebra, *Equus grevyi*: Sundaresan et al. 2007; chimpanzees, *Pan troglodytes schweinfurthii*: Muller et al. 2007).

Male harassment of females is widespread in polygynous mammals (Smuts and Smuts 1993). Definitions of male harassment cover a wide continuum of aggressive male behaviors ranging from potentially lower levels of harassment including herding, chasing, biting, or pushing (Galimberti et al. 2000b; Scott et al. 2005) to more extreme levels, which may directly result in severe wounding, forced copulation, death or infanticide (Smuts and Smuts 1993). In cetaceans, aggressive male behaviors associated with male harassment include chasing, herding, blocking, pushing, and/or biting (e.g., bottlenose dolphins *Tursiops truncatus*: Scott et al. 2005). While some of the direct and extreme consequences associated with sexual coercion (e.g., forced copulation, severe wounding, death, infanticide) are unlikely to occur in humpback whales, anecdotal descriptions of aggressive male behaviors including herding, chasing and blocking have been reported in this species (Darling et al. 2006); and male harassment has recently been proposed as an explanation for the paradoxical
associations between mothers and calves and lone male escorts in breeding populations of humpback whales (Cartwright and Sullivan 2009).

In other mammals, female behavioral responses to male aggression range from fleeing (primates: Smuts and Smuts 1993) to mating to avoid further costs associated with aggressive males (bighorn sheep, Ovis canadensis canadensis: Hogg 1987). Because adult female humpbacks are nearly the same size as males and highly mobile, avoidance mechanisms would be a particularly effective strategy to avoid aggressive males (Mesnick 1997). Avoidance was the primary response from females humpbacks confronted with a lone aggressive male in this study; female humpbacks typically responded to chasing bouts by engaging in behavior patterns previously associated with male avoidance in the literature. For example, females responded by engaging in behaviors typically associated with aggression including head lunges, tail throws, and peduncle throws (e.g., Tyack 1981; Baker and Herman 1984; Craig et al. 2002), approached nearby boats (Glockner-Ferrari and Ferrari 1985), and/or engaged in repetitive tail displays (Clapham 2000; Deakos 2002).

Females that were chased traveled significantly further distances and swam at significantly higher speeds than females not chased, indicating that the more extreme movements I reported in Chapter 2 were related to male behavior. Females (with and without calves) that were chased typically swam over twice as far and over twice as fast as females not chased. Chasing bouts also persisted over time, lasting on average for nearly two-thirds of the observation period, and as long as 3:14 hr in one escorted mother-calf group and 4:04 hr in a male-female pair. Swimming at higher than optimal speeds can lead to an overall energetic cost for marine mammals (Williams et al. 2000). During chasing bouts, whales swam at significantly higher speeds than groups that were not chased. For example, I observed one chased female-calf pair traveling at an average speed of 9.1km/hr covering 8.93m in just under an hour, over four times faster than the average speed for escorted mother-calf groups that were not chased. Cartwright and Sullivan (2009) provided empirical evidence that over extended periods of time such increases in speed, travel and respiration rates may be biologically significant and ultimately reduce calf fitness in mother-calf pairs pursued by multiple males. The significant increases I found in distance and speed coupled with significant decreases in resting periods and the persistence of these behaviors over time indicate that
aggressive behaviors by lone males lead to significant, and at least short-term, increases in energy expenditure associated with male harassment (see Galimberti et al. 2000a).

Increased respiration rates (Whitehead and Moore 1982; Cartwright and Sullivan 2009), speed and travel rates (Whitehead and Moore 1982; Cartwright and Sullivan 2009) have previously been associated with multiple male groups on humpback breeding grounds, but not with groups including a female with a single male. While several researchers have now described or noted observations of pairs of males working together around a female in surface-active groups (Tyack and Whitehead 1983; Clapham et al. 1992; Brown and Corkeron 1995; Pack et al. 2002), reports of harassment by lone males have only rarely been reported. Darling et al. (2006) reported “several” cases where lone escorts were observed chasing a female and examples of non-agonistic and apparently coordinated male-male behavior around a female, which included both blocking and chasing by two males around a mother and calf. In contrast to the majority of these descriptions, all but one of the events I report here involved a lone male humpback. In some mammals, rates of aggression from a male towards a female, however, have been found to rise dramatically when a second male is present (Clutton-Brock and Parker 1995). In this study, one of the most agonistic encounters I observed involved two males aggressively pursuing a distressed female (without calf). This was the only observation where I observed physical contact (strikes) between the male(s) and the chased female.

**Female Reproductive Class, Fluke Size and Behavior**

Males were significantly more likely to chase and act aggressively around females with calves than females without calves. Nearly a quarter of escorted female-calf groups involved aggressive male behavior (e.g., herding, chasing and/or blocking) by a lone male and these led to significant differences in behavior and movement patterns. These findings indicate that male aggression toward females with calves is more commonplace than has been previously reported, and that at least some lone males may use this as an alternate mating tactic during the breeding season (Gross 1996). In other mammals, lactating females have been found to experience higher rates of harassment from males than non-lactating females (orangutans, *Pongo pygmaeus abelii*: Fox 2002; Grevy’s zebra, *Equus grevyi*:...
Sundaresan et al. 2007). The finding that females without calves were rarely chased by a lone male, while females with calves were commonly chased suggest that humpback whale mothers, not unlike other female mammals with offspring, may sometimes be at odds with breeding males that stand to maximize reproductive success by increasing access to receptive females (Trivers 1972; Smuts and Smuts 1993). Conflict between the sexes is predicted in polygynous systems when reproductive objectives between the sexes are incompatible (Smuts and Smuts 1993). The male biased operational sex ratio reported in this species along the migration (Brown et al. 1995) and on breeding grounds (Craig et al. 2003) coupled with typical 2-3 year reproductive cycles (Chittleborough 1958, 1965; Dawbin 1966; Glockner-Ferrari and Ferrari 1985; Baker et al. 1987; Clapham and Mayo 1987; Straley et al. 2001) suggests that females are a limited resource during the breeding season. Consequently, some degree of conflict, both within and between the sexes, is expected in humpback breeding aggregations.

In populations where male aggression occurs, many males may never exhibit or use aggressive behaviors toward females (Smuts and Smuts 1993; Mesnick 1997). Because smaller and/or younger males may have limited success in contests involving male-male competition, males that are younger and/or less dominant may resort to alternative tactics in order to ‘sneak’ or force copulations with uncooperative females (Andersson 1994; Gross 1996). In other mammals, smaller, younger and/or subordinate males harass females more frequently than older, larger, and more dominant males (elephants, *Loxodonta africana*: Poole 1989; *Equis spp.*: Rubenstein 1986; southern elephant seals, *Mirounga leonina*: Galimberti et al. 2000a; orangutans, *Pongo pygmaeus abelii*: Fox 2002). Similar to other mammals, I found a relationship between the fluke size of males and male behavior; males that chased females tended to have smaller fluke sizes than males that did not chase females. Although the fluke size of males ranged up to 4.52m, the largest escort that I measured chasing a female with a calf was 3.83m. Not all small males chased females, however, indicating that individual males may choose between different tactics. Our data suggest that male humpbacks may use different mating tactics at different ages, which if successful would increase reproductive success throughout their lifetime (Cerchio 2003). In other species, when females cannot effectively avoid males, females may respond by mating
(Smuts and Smuts 1993). If this occurs even occasionally, then younger, smaller males may engage in this tactic because it can sometimes be successful.

I also found a relationship between female size and chasing. The mean fluke size for mothers that were chased was significantly smaller than mother’s not chased, and three of the four smallest mothers measured were chased. Although the fluke size of females ranged up to 4.61m, none of the fluke sizes of females involved in chasing events was larger than 4.1m, similar to the pattern I found in male fluke size and chasing events. In this study only two females without calves were chased and both were smaller and/or younger females. Although sample sizes were limited, females with smaller flukes (< 4m) were significantly more likely to be chased by males than females with larger flukes, suggesting that males may be targeting smaller and/or younger females that might not have the experience, reserves and/or endurance to outlast or defend against chasing males.

Although sample sizes were small (n=9), there were hints that fluke size and male behavior also affected the duration of associations between males and females. Despite the longer focal follows and observation times used in this study (see discussion in Tyack and Whitehead 1983), displacements (3 of 192 male-female groups) and disaffiliations were rare (6 of 192 male-female groups). All of the disaffiliations involved groups where male behavior (singing, chasing) and/or individuals of smaller size were implicated in the splits; and chasing situations were more likely to lead to a displacement or a disaffiliation than groups that were not chased. In contrast, in the one escorted mother-calf group sighted together twice over a three-day period (Chapter 2), both the escort and the mother had flukes larger than the mean fluke size reported for mothers and escorts. The sample sizes limit conclusions; however, these are the type of results that would be expected if male and female humpbacks prefer associations with larger and/or older mates, which has been suggested by Pack et al. (2009), and/or mates that are less aggressive.
Male Harassment and/or Female Choice?

Because observations of copulation attempts are extremely rare in humpback whales and little is known about female estrus cycles, male harassment is more difficult to establish than in other species where harassment is clearly correlated with female reproductive cycles and copulation attempts (Smuts and Smuts 1993; Mesnick 1997). Moreover, mature female humpbacks are slightly larger than males (Ralls 1976), and as such, male humpbacks are probably unable to physically dominate mature females. As a result, the direct consequences associated with sexual coercion (e.g., severe wounding, infanticide) are unlikely to occur in this species. Nonetheless, the frequency of our observations taken in concert with results presented by Cartwright and Sullivan (2009) indicate that aggressive behaviors by males may impose significant short-term costs in terms of energy expenditure, especially for lactating females, and suggests that male harassment may be an important and underestimated component influencing male-female interactions.

From a theoretical perspective, male harassment is not unexpected in humpback breeding populations. Male harassment is generally associated with polygynous mating systems like humpback whales (e.g., Cerchio et al. 2005) that reflect a male biased operational sex ratio (humpback whales: Brown and Corkeron 1995) and where mate guarding is observed (humpback whales: Mobley and Herman 1985; Gabriele 1992). However, in order to demonstrate male harassment, there should be a significant cost to the female. Potential costs run along a continuum from long-term consequences that directly affect female reproductive success (e.g., infanticide) to short-term consequences (e.g., time and/or energy expenditure) that may or may not have long-term effects (Galimberti et al. 2000a). Time and energy expenditure is a cost that has been associated with male harassment in several different taxa, ranging from insects to mammals (see review Mesnick 1997). In this study, I demonstrated that female humpbacks subjected to aggressive males potentially experience short-term costs associated with time and energy expenditure and those are reflected in significant differences in movement patterns between females with and without calves. For example, in a study of short-term movement patterns on humpback breeding grounds I found significant differences in travel patterns between females with and without calves (Chapter 2). However, when I removed groups where chasing was observed, the differences
disappeared, and essentially there was little difference between male-female pairs and escorted mother-calf groups in travel patterns. These results indicate that aggressive male behavior plays a significant role in a female’s time and activity budget on breeding grounds, and suggest that these characteristics may influence female selection in humpback whales.

Male harassment in social breeding systems raises questions, however, regarding the degree and extent of female choice. Separating male behavior from female behavior is a formidable challenge, and the interplay between male competition, female choice, and male aggression is expected to be dynamic and context-specific (Smuts and Smuts 1993). Female resistance, for example, may be interpreted as an honest indicator of female choice or a risk avoidance response (Fox 2002; Stumpf and Boesch 2010). In theory, a female may resist a male to incite further male competition. Female bighorn sheep, for example, may run away from a group of chasing males, but then mate with the dominant male that emerges from the group (Smuts and Smuts 1993). Surface-active groups may serve a similar purpose in breeding populations of humpbacks. The difference, however, is that in those situations the female has an opportunity to discriminate between multiple males that is presumably reflected in differential reproductive success for males. In Sumatran orangutans (*Pongo pygmaeus abelii*), Fox (2002) has argued that in situations where a lone male vigorously and actively chases a female, potentially at some cost to her in terms of time and/or energy, the opportunity to discriminate between males is not present. The female is resisting the male in the absence of other potential mates, which may indicate that resistance is not a means of inciting further male-male competition (Cox and LeBoeuf 1977) but instead is an honest indicator of negative mate choice (Fox 2002).

Theoretically, male aggression in breeding populations of humpbacks may have led females to prefer associations with larger males that can offer greater protection from harassing males (Wrangham 1979; Smuts and Smuts 1993; Mesnick 1997; Cartwright and Sullivan 2009). Females should prefer males that offer the greatest benefits (e.g., protection from other males) and impose the least costs while minimizing the costs of others (Rubenstein 1994; Mesnick 1997). From this perspective, in species where male aggression occurs but is not evenly distributed throughout the entire population (e.g., tactic used by
male harassment and female choice may have co-evolved and be expected to co-exist. The relative size and age data I was able to collect suggests that aggressive behavior is likely associated with a subset of individual males within the population that are younger and/or smaller. Aggressive behavior by males, although not uncommon for females with calves, was not observed in groups containing mature females without calves. As such, mature females without calves that migrate specifically for mating purposes may still be choosing males, either directly or indirectly, based on specific male attributes such as male body size, strength and fitness, and those attributes may be intertwined with the presence of male harassment.

Indeed, the relative size and age data I was able to collect further suggests that size and/or age may be a critical component to female preference patterns in humpback whales. Even if only some males in the population are using harassment as a reproductive tactic to gain access to mates, then protection can become a valuable resource that other males use to attract females (Mesnick 1997). Female preference for larger, older and potentially more dominant males may lead to selection for increased size, strength and fighting ability in males and may be the primary criterion of female choice in mating systems where females seek out alliances with males as a form of protection from more aggressive males (Mesnick 1997). In support of this possibility, mate guarding is common on humpback whale breeding grounds (Mobley and Herman 1985; Cartwright and Sullivan 2009) and surface-active groups may function to allow females the opportunity to discriminate between males to select the fittest and strongest male that can withstand male-male competition and prevent access to the female during critical periods (e.g., Tyack and Whitehead 1983; Spitz et al. 2002). Spitz et al. (2002) reported significant differences in the size of primary escorts in surface-active groups compared to other social roles (e.g., secondary escorts, escorts to mothers and calves) also suggesting that body size and thus age confers an advantage in male-male competition and may be an important criterion for female choice.

Rubenstein (1994) has argued that the best option for a reproductively active female may be to associate with males that simultaneously keep other males away while not altering her time budget and activity pattern. Our results suggest that this scenario may be one of the most important factors governing
male-female interactions during the winter breeding season. The significant variability I found in female activity, movement and behavior patterns around lone males suggests that females are tolerant and accepting of males that do not act or behave aggressively and that might be older and/or of larger size. For example, females aggressively and energetically avoided aggressive males and tolerated and accepted other males; and avoidance and repulsive behaviors were typically associated with aggressive male behavior, which was related to relative body size and age-class. Preliminary data further suggest that the longevity of associations might also be affected by male behavior and/or relative body size. The significant differences I found between females with and without calves, based on male behavior, and related to size and/or potentially age-class, indicate that there are many factors governing male-female interactions during the breeding season, including the potential for both male harassment and female choice to co-exist.

The frequency of females with calves that were chased and pursued by males was surprising and warrants further study to determine the extent of this behavior within the social organization of breeding humpbacks. Aggressive behavior in males has been correlated with populations with higher densities (see review Knell 2009). The density of the population around the Hawaiian Islands (Calambokidis et al. 2008), especially around Maui which hosts one of the most concentrated aggregations within the Hawaiian Islands (Mobley et al. 1999), may influence the degree and frequency of male aggression toward females I report here. Smaller and more diffuse populations may not be subjected to the same degree of harassment. Some evidence that this may be the case comes from smaller sub-populations of humpback whales scattered around the South Pacific Islands where the frequency of males escorting female-calf groups decreases from between 69-85% reported in Hawaii (Darling 1983; Glockner and Venus 1983; Glockner-Ferrari and Ferrari 1985; Craig et al. 2002) to 0% in the southern Cook Islands (Hauser et al. 2000). As such, future studies may be aimed at determining whether or not this is a function of the dense aggregation in the Hawaiian Islands (Calambokidis et al. 2008) or even Maui (Mobley et al. 1999), or a more universal and defining characteristic of the mating system of humpbacks worldwide. This study also confirms that the use of fluke photogrammetry is a useful and cost effective tool for examining the influence of relative size and age-class and its impact on the variability and range of behavior observed on breeding grounds. Future studies aimed at increasing sample sizes of known
sized and/or aged individuals and correlating them with known sex-specific behavior patterns during the breeding season will help clarify the relationship on how male and female body size affect male-female interactions, including female choice patterns.
LITERATURE CITED


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CHAPTER 4

RESPONSE OF FEMALE HUMPBACK WHALES TO PLAYBACK RECORDINGS OF MALE SOCIAL SOUNDS VARIES WITH FEMALE REPRODUCTIVE CLASS

ABSTRACT

This study examined whether female humpback whale (*Megaptera novaeangliae*) behavior towards males is related to the different reproductive objectives of females during the breeding season, including mating or calving. I used playback recordings of social sounds produced by males in multiple male, surface-active groups, with females on the Hawaiian breeding grounds with and without calves to explore this question. I predicted that females with calves will attempt to avoid males, and will move away from the playback recordings, while females without calves would respond neutrally (no change) or positively (approach) to the playbacks. In 2006 and 2007, I conducted 34 playback experiments with 14 female no-calf groups (male-female pairs) and 20 female-calf groups (11 escorted and 9 unescorted mother-calf groups) in the Hawaiian breeding grounds. Focal follows with subject whales were conducted pre, during and post-playback. I recorded responses to the playback experiments as follows: 1) travel direction toward or away from playback; 2) distance moved (m); 3) travel speed (km/hr); 4) behavior changes (i.e., rest, travel, active, social); 5) changes in respiration. Females with calves were significantly more likely to avoid playbacks than females without calves. During playback trials, females without calves showed no significant changes in behavior, while females with calves typically changed from rest to travel. While females with and without calves significantly increased speed and distance traveled during playback trials, females with calves moved further and faster than females without calves. Five females, with and without calves, approached the playbacks. Results confirm that female reproductive class is a key factor in determining how females respond and interact with males during the breeding season, but also suggest that male-female interactions during the breeding season are likely a reflection of a combination of factors, beginning with female reproductive class, but also including possible costs and benefits of specific male escorts, stage of the reproductive cycle, and possibly female age and body condition.
INTRODUCTION

Female humpback whales (*Megaptera novaeangliae*) migrate to lower-latitude breeding areas for two potentially distinct reasons, mating and calving. Theoretically, mature females without calves migrate to breeding grounds to maximize mating opportunities, while late pregnant females migrate primarily to give birth and/or to raise calves in warmer waters. Whether these different reproductive objectives impact female behavioral interactions with males during the breeding season is not well understood. In other mammals, female reproductive class has been shown to influence the composition of male-female groups (chimpanzees, *Pan troglodytes schweinfurthii*: Mastumodo-Oda 1999; Grevy’s zebra, *Equus grevyi*: Sundaresan et al. 2007), the behavior of one sex toward the other (*P. trogiodytes*: Matsumodo-Oda and Oda 1998; *P. trogiodytes*: Matsumodo-Oda 1999), male harassment (Grevy’s zebra, *E. grevyi*: Sundaresan et al. 2007), and seasonal movement patterns during the mating season (e.g., equids: Rubenstein 1986; *P. trogiodytes*: Matsumodo-Oda and Oda 1998; brown bears, *Ursus arctos*: Dahle and Swenson 2003). In humpbacks, female reproductive class influences and characterizes associations on feeding grounds (Sardi et al. 2005), the timing and duration on breeding grounds (Darling 1983; Glockner-Ferrari and Ferrari 1984; Gabriele 1992; Clapham et al. 1992) and feeding grounds (Dawbin 1997), and possibly even male mate choice (Craig et al. 2002)

Evidence of segregated migration patterns based on sex, age and reproductive class (Matthews 1937; Chittleborough 1958, 1965; Dawbin 1966, 1997) and a male biased operational sex ratio (Brown et al. 1995) suggest that females are a limited resource during the breeding season, and that female reproductive class may be a key component in understanding female behavior. Female humpback reproduction is highly variable with intermittent reproductive cycles ranging from 1–6 years (Baker et al. 1987; Clapham and Mayo 1987, 1990; Perry et al. 1990; Straley et al. 2001). Female humpbacks typically give birth to a single calf every 2–3 years (Chittleborough 1958, 1965; Dawbin 1966; Glockner-Ferrari and Ferrari 1990; Baker et al. 1987; Clapham and Mayo 1987; Straley et al. 2001). The age of first calving in the North Pacific Ocean (8-16 years; Gabriele et al. 2007), and the relative rarity of consecutive year births (Chittleborough 1958; Glockner-Ferrari and Ferrari 1990; Clapham and Mayo 1990; Straley et al. 2001; Mikhalev 2000 cited by Noad and Cato 2007) suggest that females on breeding
grounds may represent different, and perhaps even conflicting, reproductive objectives (i.e., mating versus newborn care).

The regularity of observed associations between females with calves and males during the breeding season, however, complicates this hypothesis. Similar to females without calves, females with calves are most often found associating with a single male called an “escort” (Darling 1983; Glockner and Venus 1983; Glockner-Ferrari and Ferrari 1985; Craig et al. 2002), and/or at the center of multiple male groups (Brown and Corkeron 1995; Robbins et al. 2001) where males are believed to compete for access to a presumably estrus female (Darling 1983; Tyack and Whitehead 1983; Baker and Herman 1984). On the Hawaiian breeding grounds between 69% and 85% of females with calves are accompanied by lone male escorts (Darling 1983; Glockner and Venus 1983; Glockner-Ferrari and Ferrari 1985; Craig et al. 2002).

Why humpback females with calves are frequently observed with males has presented a conundrum for researchers. Female body condition is an important indicator of reproductive success (Ralls 1976), and successive gestation and lactation periods are not considered to be a sustainable or viable long-term reproductive strategy for females (Chittleborough 1955; Clapham and Mayo 1987; Wiley and Clapham 1993). Whaling records suggest that post-partum ovulation may not be a regular occurrence in this species (Chittleborough 1965). Most researchers agree that males escort lactating females to maximize potential mating opportunities (Darling 1983; Baker and Herman 1984; Mobley et al. 1985; Glockner-Ferrari and Ferrari 1985; Clapham et al. 1992); however, the question of why lactating females tolerate these associations with males is less clear. Cartwright and Sullivan (2009) have recently proposed that the seemingly paradoxical female-calf associations with a single male may be a counter-strategy to offset male harassment by multiple males. Reports of males working together to secure access to a female are increasing in the literature (Clapham et al. 1992; Brown and Corkeron 1995; Darling et al. 2006).
Observations of females with calves avoiding males and groups of multiple males (surface-active groups) on breeding grounds have been reported (Tyack and Whitehead 1983; Mobley et al. 1988). But whether or not females without calves avoid multiple male groups is not known. Gabriele (1992), for example, has hypothesized that females without calves should maximize associations with males on breeding grounds to ensure conception occurs as early in the breeding season as possible to maximize feeding opportunities in higher latitudes. Given the small percentage of females that successfully give birth in consecutive years, I would expect the majority of lactating females to avoid mating. Thus, I hypothesize that females may utilize different behavioral strategies to attract, avoid or repel males during the breeding season based on their reproductive class.

Vocalizations termed ‘social sounds’ (Tyack 1982; Silber 1986) are frequently heard in surface-active groups and have been correlated with aggressive behavior between males (Silber 1986). Silber (1986) found social sounds often occurred when a new whale entered the group and suggested that competing males were producing these sounds coupled with visual threats to convey aggression toward one another. Unlike more complex songs, which are usually produced by lone males and last from 5-20 minutes (Payne and McVay 1971; Tyack 1981; Darling 1983; Darling et al. 2006), social sounds are typically short, discrete sounds (2-20 sec, Tyack, 1983; 0.25 to over 5.0 sec, Silber 1986) that are markedly variable and are not repeated over time. Observations of males rapidly approaching surface-active groups as well as playback recordings of social sounds, and females with calves moving away from surface-active groups or social sounds (Tyack 1983; Tyack and Whitehead 1983; Mobley et al. 1988) indicate that social sounds may serve to alert other males to the location of a receptive or estrus female, and perhaps also alert females to the presence of competing, aggressive males.

In this study, I used playback recordings of social sounds recorded within surface-active groups on the Hawaiian breeding grounds to investigate whether female reproductive class (i.e., the presence or absence of calf) affects male-female interactions on the breeding grounds. I evaluated the hypothesis that females with calves try to avoid mating by minimizing interactions with males while females without calves try to maximize mating opportunities by tolerating or seeking out associations with males. I thus predicted that female-calf groups will avoid (i.e., travel away from) the playback sounds produced in
multiple male groups, while females without calves will either remain neutral (i.e., no change) or approach (i.e., move toward) the playback.

METHODS

Study Site

Playback trials were conducted between January and April in the Au’Au Channel off West Maui, Hawaii in 2006 and 2007 (circa 20°48’ N, 156°40’ W). This region comprises one of the most concentrated aggregations of humpback whales in the Hawaiian Islands (Mobley et al. 1999), and the relatively calm sea conditions in this area provide an ideal environment for conducting behavioral studies on breeding populations of humpback whales. The calm conditions were critical for the playback experiments to be carried out, for tracking whales before, during and after playback trials, and locating and identifying other non-focal whales in the vicinity of the focal groups.

Playback Subjects

Playback subjects included male-female pairs, unescorted mother-calf groups (no male present), and escorted mother-calf groups (male escort present). Calves were defined based on their size and mothers were defined based on physical proximity to the calf. An adult in association with a mother and calf was assumed to be a male escort (Glockner and Venus 1983). The sex of individuals within pairs was determined by one or more of the following: 1) photo-identification of individuals of known sex; 2) genetic determination of sex based on biopsy or opportunistic collection of sloughed skin samples; 3) photodocumentation of the hemispherical lobe in female humpbacks (Glockner 1983); 4) presumed sex based on previously described social behavior of males and females on the Hawaiian breeding grounds (e.g., singer, escort, male competition).
**Playback Recording**

The playback recording consisted of a series of ‘social sounds’ which are often produced by males on the Hawaiian breeding grounds in multiple male/single female groups, known as surface-active groups or SAG’s (Silber 1986). The social sounds used in the playback experiments were recorded, over the course of several years (1999-2004), when surface-active groups (SAGs) were encountered and conditions allowed as part of another research project (JDD). Because the specific meaning behind individual social sounds is currently unknown, I chose a sample of the highest quality sounds (high signal to noise ratio), and combined them to make an exemplar tape. To mimic the most common natural conditions reported by Silber (1986), individual social sounds were looped and interspersed with silences of variable length onto a cassette tape.

A common criticism of playback studies is the use of a singular set of stimuli across multiple trials and groups (Kroodsma 1989, Kroodsma et al. 2001). Because the specific meaning of social sounds is currently unknown, I chose to use the exemplar tape to minimize any potential confounding of results that might be attributable to broadcasting sounds, which might convey different meanings (e.g., dominance) to playback subjects. Although these experiments violate some issues associated with pseudoreplication, the strong differences and consistent responses of focal whales coupled with responses of females to social sounds or surface-active groups observed in natural field observations (e.g., Tyack and Whitehead 1983; this study) and across other playback studies (Tyack 1983; Mobley et al. 1988) suggest that the use of the sounds used were appropriate.

**Equipment**

Sounds were broadcast using a Marantz PMD101 portable cassette recorder and a Lubell LL-9162 Underwater Acoustic Transducer. The system was calibrated to determine sound source levels. Calibration indicated the source level of the playback was 163db re 1uPa, which was the same average source level used by Mobley et al. (1988) in earlier playbacks of social sounds to humpback whales. These source levels are within the range of natural song source-level measurements of 151-173db (Au et al. 2006) and humpback whale social sounds of 149 +/- 5 dB pp re 1uPa and 185 +/- 5 dB pp re 1uPa.
Thompson et al. (1986) reported similar source levels of social sounds measured on feeding grounds (range: 161-172 dB for pulse trains to 181-185 dB for trumpet blasts).

**Playback Conditions**

In order to control the experimental situation as much as possible, the following a priori conditions had to be met in order for the playback experiment to be conducted: 1) focal group was followed for approximately one-hour (range: 52:48-1:16:48) prior to the onset of the playback experiment to document natural behavior (e.g., resting, traveling) and movement patterns (i.e., speed, distance, direction); 2) if focal group behavior changed within 15-minutes prior to the playback (e.g., resting to traveling), the onset of the playback experiment was delayed until either the initial behavior resumed (e.g., stopped traveling) for at least one prolonged dive or the new behavior pattern had been documented for a period of at least 15-minutes; 3) no other visible groups were observed within 400m of the focal group within 15-minutes of the playback experiment; 4) sea conditions were less than a Beaufort 3 (i.e., no more than 7-10 knots of wind) to prevent problems associated with vessel drift and to minimize the chance of losing the focal group during the playback.

**Playback Protocol**

Each playback trial consisted of three phases: pre-, during- and post-playback. One boat was responsible for conducting a group focal follow (Altmann 1974), and the same variables were recorded throughout each phase for comparison purposes. The sampling period was limited to times when the group was visible at the surface, and information on the group’s movement (i.e., travel direction, distance, speed), respiration (i.e., surface interval, dive time), and behavioral patterns (e.g., travel, resting, social, active) were recorded each time the group or an individual within the group surfaced and/or dove.

**Pre-Playback Phase**

Each group was followed for a minimum time period of approximately one-hour ($\bar{x} = 63:45 \text{ min } \pm \text{ SD 10:35 min}$) in the pre-playback phase. The 60-min time interval was selected for the focal follow during the pre-playback phase so that a representative picture of the natural behavior, movement and respiration patterns for each group could be compared with subsequent phases of the trial (i.e., during
playback and post-playback). The 60-minutes ensured that I could monitor the group’s behavior over several dive cycles, and allowed us to monitor whether observer effects (Deecke 2006) or our presence resulted in any visible disturbance (e.g., change in dive or movement patterns) within the group. To minimize disturbance, any activity that could potentially disturb the whales was avoided, including close boat approaches (closer than 50m), changes in engine speed, and underwater observations. If any change in behavior was observed due to our presence, the pre-playback phase was either extended until the group resumed previous behavior patterns and the focal follow was restarted, or the playback trial was not conducted. If the focal follow was prolonged for any reason (e.g., change in behavior, other whales observed, delay in second boat), the hour immediately preceding the playback was used in the analysis.

**Playback Phase**

The playback phase required the coordination of two research vessels: 1) one boat that remained with the focal group before, during and after the playback experiment; and 2) one boat from which the playback occurred. During this study, one playback trial was conducted with only one boat. In this case, the playback ended as soon as the focal whales were spotted from the playback vessel so that the playback vessel could monitor the movement of the whales.

The playback boat was positioned approximately 400m ($\overline{x} = 411.3m \pm SD = 62m$) upwind of the focal group to prepare for the playback trial. The distance from subject whales to playback boat was determined in the field with a Bushnell Laser Range Finder. In addition, GPS coordinates were taken to determine the precise distance between the playback boat and the whales at coordinated time intervals including the start of the experiment, surface and/or dive intervals, and the end of the experiment. The 400m distance was chosen because: 1) whales at this distance could consistently and reliably be recorded by observers (e.g., blows could often be heard if a surfacing was missed); 2) distance measurements with the laser range finder are reliable from this distance; 3) observations from our earlier research (2003-2005) indicated that whales within this distance could affect the movement and behavior of focal whales (Chapter 2, 3). All playback trials occurred when the whales were submerged, and every
effort was made to begin trials shortly following the terminal dive. I ended the playback trial after the 15-minute period had passed ($\bar{x} = 14:24 \pm SD = 3:34, Mdn = 15:04$), during the closest surface interval to the 15-min period trial, and/or if the playback vessel had drifted too close or too far from the subjects.

Underwater video was taken during the playback trial whenever possible with male-female pairs (MF pairs). With the exception of one escorted mother-calf group, this was not attempted with unescorted mother-calf (no male) or other escorted mother-calf group groups due to the increased possibility of disturbance with a calf present. To minimize disturbance, the videographer entered the water once the whales dove and remained at the surface and behind the whales during filming. If the presence of the underwater observer changed the behavior of the whales in any observable way (e.g., the whales moved and/or surfaced) the playback trial was abandoned. The video allowed us to monitor the time the focal individuals moved in response to the playback trial, and if so, which whale (i.e., the male or female) initiated the move. The video also allowed an audio record of any sounds heard during playback, and visual documentation of sex-specific behaviors that would otherwise be impossible to observe. Filming began as soon as the videographer entered the water, and a visual hand signal was made on the video to signal when the playback experiment began.

Post-Playback Phase

After the playback trial ended, the focal group was observed for a minimum period of 15-minutes or the duration of one typical dive cycle ($\bar{x} = 19:08 \text{ min} \pm SD 15:16 \text{ min}, Mdn = 14:06 \text{ min}$). However, sometimes circumstances (e.g., fast travel into rough seas, losing whales after playback trial ended, other whales joining and no longer being able to attribute movement to playback) made the length of this phase more variable (range: 00:00:00 – 01:02:00).

Experimental Controls

I collected data for purposes of experimental control in several different ways: a) I built-in a control through pre-playback documentation of naturally occurring behavior; b) I conducted focal follows with 36 female-no calf (male-female pairs) and 50 female-calf groups (29 escorted and 21 unescorted
female-calf groups) in another part of this study where no playback experiments were conducted; c) I opportunistically collected data from natural situations where surface-active groups passed within 400m of a focal group. During these latter naturalistic encounters, I recorded the same variables as were measured in playback trials.

**Data Analysis**

Data analyses were conducted using SPSS (version. 17.0) software and results were interpreted as significant at the 0.05 level or better. All variables were tested for normality using one-sample Kolmogorov-Smirnov test and Levene’s Test for any violations in the homogeneity of variance. Resighting histories of individuals allowed us to determine if an individual had been sampled more than once, which would affect the assumption of independence for statistical tests. For statistical purposes, I discarded the later playback trial from analyses when an experiment was conducted more than once with the same individual (n=1). For comparisons within groups, I used a paired samples t-test when the data were normally distributed. When comparing the means between groups with distinctly normal and homogenous data that were collected from independent samples, I used the one-way analysis of variance or the independent samples t-test. A chi-squared test was used to test data that was categorized based on presence/absence of the variable. Data were also analyzed using a repeated measures general linear model with a within-subjects factor of experimental phase (pre, during, or post-playback) for both speed and distance and a between subjects factor for group type (male-female pair, unescorted mother-calf, escorted mother-calf groups) or female reproductive class (female no-calf, female-calf). Post-hoc comparisons were made with the Dunnett’s T3 test when the variance between the measures and the groups were unequal.

**Conversion of Phase Duration**

In order to minimize potential observer effects and to clearly document the behavior of the focal group, the pre-playback phase of the experiment was longer than the playback trial and post-playback phase. For consistency I converted the pre and post-playback phases into relative time units that mirrored the playback phase so that all dependent variables could be measured over similar timeframes. I divided
the original time of the pre and post-playback phase by the denominator that brought the duration of these phases closest in length to the playback phase for each trial. For example, in one trial, the duration of the pre-playback phase was 59:26 minutes and the playback trial was 14:48 min. In order to make the pre-playback phase as close in duration to 14:48 as possible (i.e., playback trial duration), I divided the pre-playback phase duration by 4 to get a revised phase length of 14:52 (difference now of only 4 seconds). I then divided the distance traveled by the same number (i.e., 4 in this example), and recalculated the speed as revised distance traveled/revised time. The data conversion allowed us to compare the movement (i.e., distance, speed traveled), behavioral and respiration data over similar time frames, while accurately reflecting the natural behavior and movement patterns taken over a one-hour period as opposed to one abbreviated 15-min cycle.

Changes in Travel Direction

Response to the playback trial was categorized based on the direction of travel in relation to the playback boat. A neutral (0) response was assigned if the distance between the sound source and the focal group remained relatively equal, the total distance moved during the playback was consistent from the pre-playback phase, and there was no obvious change in direction of travel toward or away from the playback boat. An avoidance response (-1) was assigned if the distance between the sound source and focal group actively increased due to movement by the whales (as opposed to playback vessel drift). A positive response (+1) was assigned to groups that were observed visibly moving in the direction of the sound source (i.e., playback boat) and/or the distance between the playback boat and focal group decreased during the playback trial (beyond vessel drift). The drift of the playback boat was determined by comparing the location of the boat and its relative location to where the focal group was at the onset of the experiment, and by calculating the distance and speed the boat drifted during the trial. Scores were assigned a 0 for neutral drift (no obvious movement), +1 for positive drift (toward whales), or -1 for negative drift (away from whales). I used a Pearson’s chi-square analysis to investigate whether group type (male-female pair, unescorted mother-calf, escorted mother-calf groups) and/or reproductive class (female no-calf and female-calf) affected the directional response to playback sounds.
**Distance and Speed**

Distance and speed were compared across similar timeframes during all phases of the experiment. If I could not convert the pre-playback or post-playback phases to come within a minute of the duration of the playback trial, the data were not included in the analyses. While this was not generally a problem in the pre-playback phase, the shorter time frames in the post-playback phase due to a variety of factors (e.g., losing whales after the trial ended) led to smaller sample sizes in the post-playback phase across all groups. Paired (dependent) samples t-tests using a 95% confidence interval were used to examine the overall effect the playback had upon the speed traveled and distance moved at each stage of the playback experiment. I also examined the degree of change in both speed and distance that occurred between the pre-playback phase and the playback trial by calculating the difference in km/hr or meters (m) between the pre-playback and playback phase, and the percentage of change between the two phases. For example, a 100% change meant that the group essentially doubled the distance or speed traveled between the 15-min pre-playback and playback phases.

**Behavior Patterns**

I first categorized the behavioral data (i.e., rest and travel) into the presence (1) or absence (0) of behavior during each phase of the experiment. For example, if resting and traveling were both observed in the 15-min pre-playback trial a 1 was assigned for each behavior. I then created three binomial variables, which allowed us to determine if there were behavior changes in rest and travel between the three phases: before and during playback, during and post playback, and before and post playback. A value of 0 was scored if no change occurred and 1 if a change did occur. Change in behavior was analyzed through these dependent variables in generalized linear models with binomial logistic parameters against type of social group (e.g., male-female pairs, unescorted mother-calf pairs, escorted mother-calf groups). The null hypothesis was that no significant pattern of change of behavior could be detected (i.e. there was equal probability of obtaining 0 or 1). A high probability of a 0 response was indicated by a significant positive slope (logistic coefficient), and a significant negative slope indicated a high probability of 1. I used the Wald 95% confidence intervals of the logistic coefficients to determine whether behaviors were significantly different across reproductive classes.
Underwater Video Recordings

Underwater video recordings were analyzed for sex-specific behaviors (e.g., male circling, approaches of one individual to another, initiator of movement), response times (e.g., time and duration of behavior from onset of playback), general positioning (e.g., position, estimated proximity) and general response behaviors (e.g., stationary, traveling, diving deeper). Sex-specific behaviors were categorized as either being present (1) or absent (0), and the duration of specific behaviors was recorded. Proximity of the whales to one another was estimated to be between \( \frac{1}{4} \) body length or less (i.e., nearly touching) to greater than one body length if both individuals were not visible in the frame at one time. Since the video was taken from the surface to minimize any potential disturbance, the quality of the video recordings was variable based on the depth of the whales and general water quality. For instance, at times only one of the whales was discernable on the video (n=3). In these cases, only the behavior of the observable whale was documented and included in the analysis.

Respiration

Response times to playback trials of both males and females within focal groups were calculated from the surface and underwater video when data were available (i.e., male-female pairs). Response time from the surface was calculated by subtracting the time the playback trial began from the time of the first surfacing, or in the case of underwater videos, the time of first movement from either individual. Individual dive cycles (i.e., downtimes) were computed by subtracting the time the adult (i.e., adult male or female) surfaced from the time of the last terminal dive. If an individual did not have a pronounced arch signaling a terminal dive but was underwater for an extended period, the dive cycle was computed based on the time of the last surfacing during the cycle; however, if a whale did not dive because it was traveling just near or under the surface, it was considered to be part of the surface interval (i.e., time at the surface). Because each phase had a varying number of dive cycles, the mean length of the dive cycle ± 1SD for each adult within the focal group was calculated for each phase of the playback trial and used as the basis of comparison.
RESULTS

Responses to playback experiments were investigated in five ways: 1) travel direction during the playback trial (i.e., approach, avoid, neutral); 2) distance moved (m) including changes in distance before, during and after playback; 3) travel speed (km/hr) including changes before, during and after playback trial; 4) behavioral changes during the playback (i.e., rest, travel, active, social); 5) changes in respiration (response times, downtimes) before, during and after the playback. To further validate results, I compared playback responses to field observations where surface-active groups (SAGs) came within 400m of groups of the same composition. The overall results are summarized in Table 1.
Table 1: Summary of results for playback trials conducted with female-calf groups (FC) and female no-calf groups (FNC). Surface-active groups = SAGs.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Conclusion</th>
<th>Data</th>
<th>Stats Tests &amp; Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>Playback Response (Avoid, Neutral, Approach)</td>
<td>Female-Calf groups more likely to avoid SAGs than Female No-Calf groups</td>
<td>FNC Avoid: 28.57% (4/14)</td>
<td>$\chi^2 = 21.72$, $p &lt; .0001$</td>
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<tr>
<td></td>
<td></td>
<td>Neutral/Approach: 71.43% (10/14)</td>
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<tr>
<td></td>
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<td>FC Avoid: 71.43% (15/21)</td>
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<tr>
<td></td>
<td></td>
<td>Neutral/Approach: 23.8% (5/21)</td>
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<tr>
<td>Change in Distance Moved</td>
<td>Female-Calf groups more likely to increase distance moved, and to increase distance further</td>
<td>FNC % Sample Increase: 42.9%</td>
<td>Paired Samples T-Test: ($\bar{x} = 194.9m$, SE = 85.96, $t$ (13) = 2.260, $p &lt; .05$); 99% CI</td>
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<td></td>
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<td>Mean Increase: 194.9m</td>
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<td></td>
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<td>FC % Sample Increase: 90%</td>
<td>Paired Samples T-Test: ($\bar{x} = 630.73m$, SE = 112.52, $t$ (18) = 5.606, $p &lt; .001$)</td>
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<td></td>
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<td>Mean Increase: 631m</td>
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<tr>
<td>Change in Speed Traveled</td>
<td>Female-Calf more likely to increase speed, and to increase speed more than Female No-Calf groups</td>
<td>FNC % Sample Increase: 57.1%</td>
<td>Paired Samples T-Test: ($\bar{x} = .977$, SE = .321, $t$ (13) = 3.049, $p = .009$)</td>
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<tr>
<td></td>
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<td>Mean Increase: 1.03 km/hr</td>
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<tr>
<td></td>
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<td>FC % Sample Increase: 90%</td>
<td>Paired Samples T-Test: ($\bar{x} = 2.71$, SE = .43, $t$ (18) = 6.252, $p &lt; .001$); 99 CI</td>
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<td>Mean Increase: 2.7 km/hr</td>
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<tr>
<td>Change in Behavior</td>
<td>Female-Calf more likely to travel, and Female No-Calf groups more likely to rest in response to Playback</td>
<td>FNC % Sample Rest: 71.4% (10/14)</td>
<td>GLM, Binary Logistic: ($B = .916$, $p &lt; .121$) Change from Rest to travel</td>
</tr>
<tr>
<td></td>
<td></td>
<td>% Sample Travel: 42.9% (6/14)</td>
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<td></td>
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<td>FC % Sample Rest: 15% (3/20)</td>
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<td></td>
<td></td>
<td>% Sample Travel: 90% (18/20)</td>
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<tr>
<td></td>
<td></td>
<td>GLM, Binary Logistic: $B = -1.386$, $p &lt; .013$); Change from Rest to travel</td>
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<tr>
<td>Response Time to Playback</td>
<td>FC responded faster than FNC to playback</td>
<td>FNC Mean Response Time: 8:04 sec</td>
<td>ANOVA: ($F (1, 32) = 9.037$, $p = .005$)</td>
</tr>
</tbody>
</table>


Change In Travel Direction During Playback

If females with calves are trying to minimize interactions with males while females without calves are trying to maximize male interactions during the breeding season, I predicted that females with calves would avoid the playback, while females without calves would either remain neutral or approach the playback boat (see Figure 1). To test this hypothesis, I conducted 34 playback trials with 14 male-female pairs, 9 unescorted mother-calf groups, and 11 escorted mother-calf groups, which resulted in a total of 14 female no-calf groups (i.e., 14 male-female pairs) and 20 female-calf groups (9 unescorted mother-calf and 12 escorted mother-calf groups).

Figure 1: Potential Responses to Playback Experiments (Approach, Neutral, Avoid). Examples show movement patterns from focal groups before, during and after a playback trial as related to the location of the playback boat. From left to right, the figure illustrates examples of trials that were scored as an approach, avoidance or neutral response to the playback.

The 34 playback trials resulted in 5 approach responses, 10 neutral responses, and 19 avoidance responses (Figure 2). When travel direction (i.e., avoid, approach, neutral) was compared across group
types, I found highly significant differences between male-female pairs and unescorted mother-calf pairs ($\chi^2 = 11.08, p < .0039$) and escorted mother-calf groups ($\chi^2 = 16.99, p < .0002$). However, no significant differences were found between how unescorted mother-calf pairs and escorted mother-calf groups responded to the playback ($\chi^2 = 3.30, p < .192$). As a result, I combined unescorted mother-calf pairs and escorted mother-calf samples into one female-calf group (n=20) to investigate how the presence or absence of a calf (i.e., reproductive class) affected playback response.

![Figure 2: Responses to Playback Trials Based on Group Type.](image)

As predicted, I found highly significant differences in how female-calf groups and female no-calf groups responded ($\chi^2 = 21.72, p < .0001$) to the playback (see Figure 3). Avoidance was the most common response to playbacks by female-calf groups but not for female no-calf groups. While 71.43% (15/21) of female-calf groups moved away from the playback source, 71.43% of female no-calf groups responded neutrally or positively to the playback. Only 28.57% (4/14) of female no-calf groups avoided the playback. Moreover, in the four trials where female no-calf groups moved away from the playback sounds, the distance moved was generally less (range: 125m-1100m) than in female-calf groups (range: 200m-2000m).
Figure 3: Responses to Playback Trials by Females with a Calf and Females without a Calf. Travel direction during playback trials was classified as an approach (move toward), neutral (no observable change), or avoidance (move away) response.

**Playback Boat Drift**

The majority of responses in female no-calf groups were scored as neutral (8/14) because the whales were not observed actively moving toward (approaching) or away (avoidance) from the playback boat. The two trials (9.52%) that evoked a neutral response from female-calf groups were both from unescorted mother-calf groups (no male present). In 40% of the neutral responses (4/10) the measured distance between the focal group and the playback boat at the end of the trial had decreased. In contrast to an approach, however, the decrease was due to the playback boat drifting closer to the whales as opposed to the whale’s moving closer to the playback. In each of the four neutral trials where the distance decreased more than 50m from the start to the end of the playback, the playback boat drifted between 380m-594m ($\bar{x} = 462.3m \pm SD 102.8m$). As a result, even though the focal groups did not actively move toward or away from the playback, they were tolerant of the playback sounds, even when the playback boat approached the focal group from within 83.6m - 333m ($\bar{x} = 211.4m \pm SD 110.5m$).
Approach Responses

Five out of 34 playback trials (14.71%) resulted in the focal whales changing direction toward or actively moving closer to the playback boat during the trial (range: 133.1m-289.9m). Each of the five trials where whales approached the playback boat resulted in either an abrupt and initial change in direction toward the playback (n=2) or involved trials where the whales actively decreased the distance towards the playback at some point during the playback trial (n=3; see Approach, Figure 1).

Two of the five responses scored as an approach were from escorted mother-calf groups, one from an unescorted mother-calf group, and two from male-female pairs. Although 60% (3/5) of these focal groups met the criteria of an approach by actively decreasing the distance to the playback boat during the trial, in each of these three situations the whales did not alter their course toward the playback but kept traveling in the same general direction as the playback boat, eventually decreasing the distance and coming within 133-276m of the playback boat. In contrast, one male-female pair and one unescorted mother-calf group actively changed their course of travel towards the playback at the start of the experiment.

Interactions with Other Whales During Playback Trials

Although none of the targeted focal groups included in the study was observed directly joining or interacting with the playback boat during playback trials, other whales that were not targeted during the experiment directly approached (< 50m) the playback boat. In 38.24% (13/34) of playback trials, other whales ranging in group size from lone whales (n=8) to smaller surface-active groups (i.e., SAGs) of 3-5 individuals (n=3) approached and surfaced next to the playback boat. Because whales that approached the playback boat were mostly lone whales, and females are rarely alone on breeding grounds (e.g., Gabriele 1992), the whales that joined the playback boat were most likely males and not females.
Effect of the Playback on Movement Patterns in Female-Calf and Female No-Calf Groups

Figures 4a and 4b summarize the mean distance (m) and speed traveled (km/hr) for female-calf and female no-calf groups at all phases of the experiment. Both female-calf groups and female no-calf groups showed significant changes in the distance and speed moved between the pre-playback phase and playback phase of the experiment. During playback trials, female-calf groups (n=19) significantly increased the distance ($\bar{x}$ increase = 630.73m ± SD 490.45, paired samples $t$ (18) = 5.606, p < .001) and travel speed ($\bar{x}$ increase = 2.71 ± SD = 1.8, paired samples $t$ (18) = 6.252, p < .001; Table 1); female no-calf groups also showed significant increases in the distance moved ($\bar{x}$ = 194.31 ± SD 321.6, paired samples $t$ (13) = 2.260, p < .05) and speed traveled ($\bar{x}$ = .977 ± SD 1.2, paired samples $t$ (13) = 3.049, p = .009) between the pre-playback and playback phase of the experiment. However, females with calves (female-calf groups) moved significantly further distances ($F$ (1,31) = 13.66, p = .001) and traveled at faster speeds ($F$ (1,31) = 13.54, p = .001) than females without calves (female no-calf groups) during playback trials.
Figure 4a: Mean Distance Moved Before, During and After Playback Trials by Females with a Calf and Females without a Calf. Sample sizes differed depending upon the stage of the experiment and by group type: female no-calf groups (n=14) except for post-playback (n=10); female no-calf groups (n=19) except for post-playback (n=15).
Figure 4b: Mean Speed Traveled Before, During and After Playback Trials by Females with a Calf and Females without a Calf. Sample sizes differed depending upon the stage of the experiment and by group type: female no-calf groups (n=14) except for post-playback (n=10); FNC groups (n=20) except for post-playback (n=15).

Female-calf groups moved an average of 376.7m ± SD 246m (range 97m-1055m) at a mean speed of 1.7km/hr (± SD 1.1km/hr; range: .383 km/hr - 4.1km/hr) 15-min before the playback trial began (Figures 4a and 4b). However, during the playback trial, female-calf groups increased the distance moved to an average of 1007.4m ± SD 523.4m (range: 194m - 1,898m) at an average speed of 4.41 km/hr ± SD 2.21 km/hr (range: .65 km/hr – 9.87 km/hr; Table 1). Females without calves moved an average of 223.6m ± SD 111.8m (range = 44.9m - 410.4m) at a mean speed of .945 km/hr ± SD .536 (range = .179 km/hr – 1.89 km/hr) before the playback trial began, whereas during the playback trial female no-calf groups moved an average of 417.9m ± SD 337.7m (range: 31.6m – 849.2m) at an average speed of 1.92 km/hr ± SD .536 km/hr (range = .124 km/hr – 3.99 km/hr).
Change in Distance and Speed Traveled

Although both female no-calf and female-calf groups increased distance and speed traveled during playback trials, the degree of the reaction was strongest in female-calf groups (Table 1). Female-calf groups (n=19) moved on average 631m further ± SD 490m (range: -9.0m – 1568.7m; see Figure 5a) resulting in a mean 260% increase ± SD 300% (range = 5.9% - 1119.9%; see Figure 5b) during playback trials. In contrast, female no-calf groups (n=14) only moved an average of 194m further ± SD 322m (range: - 221.9m – 836.5m; Figure 5a) resulting in an average increase in distance of 116% further ± SD 203.6%; range: -61.2% - 566.4%; Figure 5b). Moreover, the most extreme distance of 1568.7m for one female-calf group during the playback trial was nearly twice (836.5m) that of the most extreme female no-calf group.
Figure 5a: Difference in Distance (m) Moved Before and During Playback Trials. Comparison of the differences in the distance moved (m) before and during the playback (PB) trial by females without calves (FNC) and females with calves (FC).
Figure 5b: Percent Difference in Distance Moved During Playback Trial. This figure illustrates the percentage of change in the distance moved in the 15-minute pre-playback phase compared to distance moved during the 15-minute playback trial for females with calves (FC) and females without calves (FNC). The shaded area gives a general indication of a neutral response, which is defined as up to a 50% increase or decrease in the distance of the focal group from the playback speaker.

Similar results were found for speed of travel before and during the playback trial (Figure 6a and 6b; Table 1). The mean difference in speed for female no-calf groups was less than 1km/hr ($\bar{x} = .98$ km/hr ± SD 1.20; range: -.919 km/hr – 2.918 km/hr) with an average 128.9% increase in speed (± SD 191.2%; range -60.97% - 535.99%), while the average difference in speed for female-calf groups was over twice that at 2.68 km/hr (± SD 1.90 km/hr; range: -.028 km/hr – 6.772 km/hr) resulting in a mean 230.3% increase in speed (± SD 271.5%; range = -4.12 – 1127.4%).
Figure 6a: Difference in Speed (km/hr) Traveled Before and During Playback Trials. Comparison of the differences in the speed traveled (km/hr) before and during the playback trial for females without calves (FNC; n=14) and females with calves (FC; n=20).
Figure 6b: Percent Difference in Speed During the Playback Trial. The percentage of change in the speed traveled in the 15-minute pre-playback phase compared to distance moved during the 15-minute playback trial for females with calves (FC) and females without calves (FNC). The shaded area gives a general indication of a neutral response, which is defined as up to a 50% increase or decrease in the speed of travel between the two phases.

Variability in Movement Between Social Groups

Despite an overall increase in speed and distance traveled during playback trials for all groups, results also indicated that there was a range in movement (i.e., speed and distance) for females within the same reproductive class (i.e., female no-calf and female-calf groups; Figures 5a and 6a) and based on group type (male-female pairs, unescorted mother-calf, escorted mother-calf groups; Figures 7a, 7b). For example, 100% of escorted mother-calf groups (10/10) increased movement and speed during playback trials, but two of the nine (22.2%) playback trials with unescorted mother-calf groups resulted in
no change in distance or speed traveled, and five of fourteen trials with male-female pairs (35.7%) resulted in either a decrease or no change in the distance or speed moved. Consequently, I also examined the effect of the playback trial on females within the three different social groups.

Figure 7a: Difference in distance moved (m) before and during the playback trial for male-female pairs (n=14), unescorted mother-calf pairs (mother-calf, n=9) and escorted mother-calf (mother-calf-escort, n=11).

Male-female pairs displayed the most conservative responses to playback trials, while escorted mother-calf groups showed the most extreme responses (Figures 8a, 8b; Table 1). Unescorted mother-calf pairs did not differ from either escorted mother-calf groups in distance (\(\bar{x}\) difference = -323.6m, Std. Error = 129.7m, \(p = .088\)) and speed traveled (\(\bar{x}\) difference = -1.4km/hr, Std. Error = .59km/hr, \(p = .094\))
or from male-female pairs in distance ($\bar{x}$ difference = 201m, Std. Error = 85.4, p = .088) and speed ($\bar{x}$ difference = .89km/hr, Std. Error = .41, p = .126). However, highly significant differences in distance ($\bar{x}$ difference = -524.6 m, Std. Error = 121.9, p = .003) and speed ($\bar{x}$ difference = -2.3km/hr, Std. Error = .54, p = .003) were found between male-female pairs and escorted mother-calf groups.

Figure 7b: Difference in speed traveled (km/hr) before and during the playback trial for male-female pairs (n=14), unescorted mother-calf pairs (mother-calf, n=9) and escorted mother-calf (mother-calf-escort, n=11).

Post-Playback Comparisons

Both female no-calf and female-calf groups showed a decrease in the distance and speed traveled after the playback trial ended (Figures 4a and 4b). However, the only statistically significant
decrease between the playback trial and the post-playback trial was in the distance moved after the playback trial ended for female-calf groups (paired samples $t$ (14) = -3.713, $p = .002$). Although both female no-calf and female-calf groups showed an average increase in the speed and distance traveled after the playback trial when compared to before the playback trial began, none of these increases were statistically significant. Although female-calf groups increased the average speed traveled from 1.68 km/hr prior to the experiment to 3.22 km/hr after the playback trial ended, this difference was only marginally significant ($paired samples t$ (13) = -1.846, $p = .088$), and the distance moved which ranged from 365m to 437.3m was not statistically significant ($paired samples t$ (14) = -.783, $p = .447$).

**Behaviors Observed During the Pre-Playback Phase**

As described in the methods, I compared the general behavioral state (e.g., rest, travel) of each focal group in 60-min and 15-min time periods prior to the onset of the playback experiment. Results indicated that there was little difference in the overall behavior patterns of groups between these two time periods. For example, 100% of focal groups (34/34) were resting during the 60-min focal follow preceding the playback trial, and 97.1% (33/34) were resting during the adjusted 15-min behavioral sample. Social (2/34) and active behaviors (2/34) were far less common in both 60-min and 15-min intervals. No active or social behaviors were observed in the 15-min sample, but this was intentional. To simplify results, the ideal situation involved whales that were resting as the experiment began.

**Behaviors Observed During the Playback Trial**

Resting decreased and traveling increased in both female no-calf groups and female-calf groups once the playback trial began (Figure 8). However, females with calves were significantly more likely to change from rest to travel during playback trials than female no calf groups ($B = -1.792$, Std. Error = .623, $df = 1$, $p = .004$). Female no-calf groups accounted for 76.92% (10/13) of observations where whales rested, and female-calf groups accounted for 75% (18/24) of cases where groups traveled (Figure 9).
Figure 8: Comparison of Resting and Traveling Before and During Playback Trial for Females with Calves (FC) and Females without Calves (FNC). Changes in resting and/or traveling behavior during the 15-min pre-playback (PB) phase compared to behavior observed during the playback (i.e., Rest PB, Travel PB) trial for females without calves (FNC) and females with calves (FC).

Figure 9: Percent of trials where resting or traveling was observed during playback (PB) trials by female-calf groups (FC) and female no-calf groups (FNC).
No significant changes in resting behavior before and during the playback trial were found for female no-calf groups ($B = .916$, Std Error = .5916, df = 1, p = .121). Indeed, only four of 14 (28.6%) female no-calf groups changed from rest to travel during the playback trial. In contrast, 95% of female-calf groups (19/20) were resting in the 15-min pre-playback phase, but only 15% (3/20) continued to rest during the playback trial. Of the three resting female-calf groups, one was an escorted mother-calf group and two were unescorted mother-calf groups, indicating that 90% of escorted mother-calf groups and 78% of unescorted mother-calf pairs changed from rest to travel during trials. The GLM binary logistic models showed a significant change from resting to travel behavior for escorted mother-calf groups during the playback trial ($B = -1.504$, Std Error = .7817, df = 1, p = .054) but not for unescorted mother-calf groups ($B = -1.253$, Std Error = .8018, df = 1, p = .118).

**Singing Behavior of Males in Response to Playbacks**

Because only male humpbacks are known to sing (Darling 1983; Glockner 1983) the only groups in which singing could have been heard in playback trials were in groups where a male was present (i.e., male-female pairs or escorted mother-calf groups). While no males were heard singing prior to the onset of the playback trial (n=25), in three playback trials (12%) where a male was present, the focal male began signing after the playback trial began. In one case, a male escorting a mother and calf (i.e., escorted mother-calf group) began singing within 40-sec of the onset of the playback, and in the remaining two events, two males within male-female pairs were heard singing after the playback trial ended. The onset of singing in the two male-female pairs ranged from 22 – 73 min after the playback trial ended, and consequently may not be directly related to the playback trial. The duration of these singing bouts was shorter than typical singer interactions (range: 3:40 min – 7:35 min). Given the low occurrence of males singing in the company of females reported within this study (Chapter 3), I felt it was worth reporting here.
Behaviors Observed from Underwater Video

Underwater video was collected and recorded in 12 out of 14 (86%) playback trials with male-female pairs and in one out of 21 trials (5%) with escorted mother-calf groups. These analyses indicated that males were significantly more likely than females within female no-calf groups (male-female pairs) to initiate movement ($\chi^2 = 9.8, p = .007$). In 11 of the 12 recordings where both the male and female are visible within the frame during the playback trial, the male initiated movement in $82.82\%$ (n=9) of recorded trials, and only two of the 11 trials resulted in the female moving first.

Where the female moved first during the playback trial, the male immediately followed the female ($\leq 6$-sec), but when the male moved first females were slower to respond ($\bar{x} = 3:15$ min $\pm$ SD $4:31$ min; range: $<1$min – 12 min). In 45.5% (5/11) of trials where both the male and female can be seen simultaneously on the video, the male was observed directly approaching the female to within $\leq \frac{1}{4}$ body length and three of the five approaches (60%) by males resulted in the female moving. In contrast, even when the female moved first, a female was never observed approaching a focal male. Similar results were found in two recorded field observations where a surface-active group approached a resting male-female pair and no playback trial was conducted. In both of these cases, the video showed the male moving first, circling in and out of the frame, presumably patrolling the perimeter around the female, while the female remained stationary throughout the encounters with other males.

Response Time to Playback Trials

I found no difference in the response times (i.e., time from the start of the playback to the time the female first surfaced) between females in unescorted mother-calf pairs and escorted mother-calf groups ($F (1, 18) = .011, p = .919$) during playback trials. Consequently, when comparing female response times I was able to pool unescorted and escorted mother-calf groups into one female no-calf reproductive class. Differences in female response times were highly significant ($F (1, 32) = 9.037, p = .005$; Figure 10). The mean response time for females in female no-calf groups was $8:04$ min $\pm$ SD $4:33$ min while the mean response time for females in female-calf groups was only $3:49$ min $\pm$ SD $3:40$ min.
The mean response time by males in escorted mother-calf groups was significantly longer than the response time of the mother (paired samples $t = 3.536$, df = 9, $p = .006$; $\bar{x}$ difference $= 5:11$ min $\pm$ SD 4:38 min). However, I found no difference in the response times of males and females within male-female pairs (paired samples $t = -1.109$, df = 13, $p = .287$; $\bar{x}$ difference $= 00:26$ sec $\pm$ SD 1:28 min).

Figure 10: Response Time to Playback Trials for Female No-Calf Groups (n=14) and Female-Calf Groups (n=20). Differences in female response times were highly significant ($F(1, 32) = 9.037$, $p = .005$).
Respiration Patterns

No differences were found in the mean downtimes (i.e., amount of time between the terminal dive and the next surfacing) between unescorted female-calf pairs and escorted mother-calf groups before \((F (1, 16) = .130, p = .724)\) and during the playback trial \((F (1, 16) = .157, p = .697)\). As a result, I was able to pool unescorted and escorted mother-calf groups into one group based on the presence or absence of a calf (i.e., female reproductive class) when comparing female dive patterns.

The playback trial significantly affected the downtimes of females in both female no-calf groups \((paired \ samples \ t = 4.337, df = 13, p = .001)\) and female-calf groups \((paired \ samples \ t = 3.586, df = 17, p = .002)\). While females in female-calf groups had significantly shorter dives than female no-calf groups before the playback \((F (1, 30) = 10.363, p = .003)\), I found only marginally significant differences during the playback trial \((F (1, 30) = 3.247, p = .082)\).

Responses to Surface-Active Groups (SAGs) in Natural Situations

I documented five responses (in four groups) by female no-calf groups (i.e., male-female pairs) and five responses by female-calf groups (i.e., unescorted mother-calf, escorted mother-calf groups) to surface-active groups (SAGs) that opportunistically passed within 400m of focal groups (i.e., distance to playback boat at start of experiment) before playbacks could be conducted. Although I can only confirm the presence of social sounds in two of the ten situations with SAGs passing focal groups, the presence of a SAG passing within 400m of focal whales provided us with a natural environment to observe what I were trying to simulate through experimental playbacks of social sounds produced within SAGs; that is, whether or not there was a difference in how females with calves and females without calves respond to the presence of multiple male groups on breeding grounds.

In general, the behavior and responses of male-female pairs exposed to naturally occurring surface-active groups (SAGs) were consistent with the results of experimental playback situations. Similar to experimental playbacks, 100% (5/5) of male-female pairs were resting when the SAG was first observed. SAGs were first observed from 300m-1000m away \((\bar{x} = 650m \pm SD \ 311m)\), and were observed
approaching within 25m-400m from the focal group (the same distance used in our playback experiments). The length of time that the SAG was observed in the area ranged from 4 – 19 min (\( \bar{x} = 11:03 \text{ min}; \pm \text{SD 07:40 min} \)), again within the same length of time that playback trials lasted. None of the five natural situations with females without calves involved the focal whales moving directly toward or away from the incoming SAGs. Instead, 100% (5/5) of the groups observed responded neutrally. However, similar to playback trials, in both of the interactions with SAGs recorded on video, the male approached and/or circled the female, frequently leaving the video frame, while the female remained stationary.

Three of the five (60%) natural encounters with SAGs led to the focal group being joined by a male, presumably approaching or leaving the SAG. These interactions with other males were typically short, lasting six minutes or less, and in two of the three situations involved only one surface interval. Bubble streams, fast dives, and approaches by the focal male toward the incoming whale were common, but higher levels of male-male competition typically observed on breeding grounds (e.g., body strikes, head lunges) were not observed and none of these interactions led to the formation of a SAG. In three situations SAGs approached within 100m (25 – 100m) but the female remained stationary. In one unusual observation of a pair, the focal male left the focal female when another male joined, and the two males traveled for 51:59 min at an average speed of 6.8 km/hr until joining another SAG 5.81 km away.

Overall behavior and response of female-calf groups exposed to naturally occurring SAGs was also consistent with the results of experimental playback situations. Three escorted mother-calf groups, one unescorted mother-calf group, and one unescorted mother-calf group with a male trying to join were included in this comparative sample. Similar to experimental playbacks, four of the five female-calf groups (80%) were resting at the time the SAG was first observed. SAGs were first observed from 200m - 387m away (\( \bar{x} = 260m \pm \text{SD 76m} \)) and were observed swimming within 125m - 353m (\( \bar{x} = 215.6 \pm \text{SD 90m} \)) to the focal group during the observation period. The length of interaction time (i.e., the amount of time the SAG was observed in the area) ranged from 10 - 26min (\( \bar{x} = 14 \text{ min} \pm \text{SD 6:47 min} \)). Thus, both the distance to the SAGs and the timeframe of the observations were nearly equal to playback trials. Similar
to results of the experimental playbacks, 80% of female-calf groups (4/5) exposed to SAGs within 400m responded by swimming away (i.e., avoidance) from the SAGs, noticeably increasing both the speed and distance traveled. One unescorted mother-calf group recently joined by a male escort swam directly toward a SAG (with the female in the lead), and I observed the male escort leaving the mother-calf to join the SAG. Within six minutes of the escort leaving to join the SAG, the mother and calf resumed resting.

In the one opportunistic observation of a confirmed traveling singer passing within 117m of a resting male-female pair, no underwater or surface reaction was observed. In fact, the singer was observed moving into the area, and although the singer was within 117m-200m from the pair for 18:52 min, the pair remained submerged for 22:16 min. Because the resting pair was visible from the boat, I could see that neither the male nor the female moved in response to the presence of the nearby singer. An experimental playback of social sounds with this same pair, however, resulted in the pair moving 1.14km away from the playback boat at an average speed of 3.99 km/hr, which was a 272% increase in the distance and speed traveled prior to the playback.

**DISCUSSION**

Both field observations (Tyack and Whitehead 1983) and playback studies (Tyack 1982; Mobley et al. 1988) have suggested that females with calves avoid SAGs, but nothing could be gleaned from these studies about whether females without calves would respond similarly. I found that unlike females with calves, females without calves did not avoid potential interactions with SAGs. Instead, the majority of females without a calf continued to rest during exposure to a playback trial and no significant changes in resting behavior were found between the pre-playback and playback phases in these females. Indeed the majority of resting responses came from females without calves, while the majority of traveling responses came from females with calves.

Although no playback studies conducted to date have specifically focused on how female humpbacks respond to acoustic cues in their environment, I found that females with calves responded significantly faster to playbacks, and swam further and faster away to avoid interactions with SAGs than
groups of females without calves. In contrast to Tyack and Whitehead’s (1983) observation that females with calves “occasionally made small changes of course or speed” (p. 145) in reaction to surface-active groups, our results suggest that females with calves reacted strongly after being exposed to sounds from SAGs, moving significantly further and faster during playback trials than compared to before. The avoidance responses by females with calves, and neutral responses by females without calves to playback trials were confirmed by field observations in this study and elsewhere (Tyack and Whitehead 1983) and suggest that social sounds are an important determinant of the movement and behavioral patterns of female humpbacks during the breeding season.

The degree and consistency of the reaction of females with calves to playbacks suggests that like other mammals (e.g., African lions, Panthera leo: McComb et al. 1993; baboons, Papio cynocephalus ursinus: Kitchen et al. 2003) female humpbacks may use acoustic cues to avoid interactions with multiple males during the breeding season. Male mammals often convey acoustic threats surrounding bouts of male-male aggression during the breeding season (e.g., harbour seals, Phoca vitulina richardsi: Hanggi and Schusterman 1994; baboons, Papio cynocephalus ursinus: Kitchen et al. 2003; red deer, Cervus elaphus: McComb 1991; elephant seals, Mirounga leonina: Sanvito et al. 2007; bison, Bison bison: Wyman et al. 2008), apparently similar to the social sounds of SAGs used in this study (Silber 1986). Studies of terrestrial mammals have shown that males may use these sounds to assess rivals and that they may impact the outcome of competitive male-male interactions (Reby and McComb 2003), while females may use these acoustic cues to avoid potentially aggressive males. For example, female African lions (Panthera leo) will flee in response to roars of unfamiliar males that may pose a threat to their cubs (McComb et al. 1993), and under natural conditions female baboons (Papio cynocephalus ursinus) will flee and hide, apparently to avoid notice in response to vocalizations produced within aggressive multiple male groups (Kitchen et al. 2003).

Because female humpbacks are slightly larger than males and highly mobile, avoidance mechanisms would represent a particularly effective strategy to avoid aggressive males (Mesnick 1997). Reported avoidance behaviors in female humpback whales include examples of energetic chases in which females try to escape males (Tyack 1981; Darling et al. 2006), females lying upside down at the
surface or rolling away from suitors (Darling 1983), females holding their tail-stock high out of the water for extended periods of time presumably making it more difficult for males to access the genital area (Darling 1983), and apparent preference of humpback females and calves for nearshore, shallow waters where they may be able to avoid harassment from sexually active males (Smultea 1994). Female avoidance of multiple male groups has been reported in gray whales (Swartz 1986), and in humpbacks (Tyack 1983; Glockner-Ferrari and Ferrari 1985; Mobley et al. 1988; Mattila et al. 1989). Observations of humpback females leading multiple male groups inshore (Glockner-Ferrari and Ferrari 1985) or into areas with shallow coral heads (Mattila et al. 1989) to displace an escort or disband the group have also been described. Our observations of females with calves traveling, sometimes at speeds approaching 10km/hr away from playbacks of social sounds indicative of multiple male groups, suggests that some female humpbacks flee from multiple male groups, and that active avoidance of these groups is common on breeding grounds.

In addition to female reproductive class, the composition of focal groups (male-female pairs, unescorted and escorted mother-calf groups) was also a factor in how groups responded to playbacks. For example, when comparing speed and distance moved during the playback trials, escorted mother-calf groups demonstrated the most extreme responses, male-female pairs the most conservative responses, with unescorted mother-calf pairs falling in between. While unescorted mother-calf groups did not differ significantly from escorted mother-calf groups or male-female pairs in speed and distance traveled when exposed to playbacks, male-female pairs and mother-calf-escort groups differed significantly from one another in each of the variables measured within this study. Previous playback studies with humpback whales on the Hawaiian breeding grounds have shown that responses to playback recordings differ based on group composition (e.g., Mobley et al. 1988) or even from one individual to the next (e.g., singers, Darling et al. 2006). For example, an individual singer will move toward a similar song and away from a dissimilar song (Darling et al. 2007), and some types of groups (e.g., singers) will ‘charge’ (Tyack 1983) or ‘rapidly approach’ (Mobley et al. 1988) feeding sounds or social sounds, while other types of groups (e.g., female-calf groups) move away. Because both male-female pairs and mother-calf-escort...
groups had a male present in our study, the differences found are likely due to female reproductive class (i.e., the presence of the calf), the variable that is different in these groups.

The consistent avoidance responses of females with calves compared to females without calves, coupled with the extreme reactions by escorted female-calf groups compared to unescorted female-calf groups, complement findings of Cartwright and Sullivan (2009) showing significant increases in travel and decreases in periods of resting in multiple male groups versus single-escort groups for females and calves. Based on estimations of calf metabolic rates and hourly calculations of energy expenditure, Cartwright and Sullivan (2009) have argued that these increases in travel and decreases in rest around multiple males require significantly more energy, and over extended periods of time, may impact the overall fitness of the calf. In our study, while the majority of unescorted female-calf groups moved away from playbacks of social sounds, they generally moved shorter distances and at slower speeds than escorted female-calf groups, suggesting that any potential cost in associating with multiple males may be even greater for females and calves with a male escort than females without a male escort. Indeed for escorted females and calves, any interaction with another male creates a multiple male group, potentially leading to increased energy expenditure over time due to male-male competition, and may explain the more extreme reactions I observed in escorted female-calf groups than other targeted groups in our study.

Speculating that these energetic costs are biologically significant, Cartwright and Sullivan (2009) propose that multiple male groups constitute a form of male harassment for female-calf pairs. The reproductive costs for females with calves interacting with multiple males during the breeding season are further suggested by an increasing number of observations of male humpbacks working together to secure access to a female (Tyack and Whitehead 1983; Clapham et al. 1992; Darling et al. 2006; Chapter 3), examples of females trying to escape aggressive males (Glockner-Ferrari and Ferrari 1985; Mattila et al. 1989; Chapter 3), rejection of specific males (Clapham 1992; Darling et al. 2006; Chapter 3), and studies showing that females with calves prefer nearshore, shallow waters possibly to avoid interactions with aggressive or competitive males (Smultea 1994). The active avoidance of SAGs observed in this
study by the majority of female-calf groups, but especially by escorted mothers and calves, are consistent with suggestions that interactions and associations with multiple males may impose a cost to females with calves, which may be even greater when a female is already in the company of a male escort.

Unlike females with calves, interactions with other males might be advantageous for females without calves and may explain why the majority of females without calves observed in this study did not move in response to playbacks. Sexual selection theory predicts that the reproductive success of resting females (i.e., non-pregnant, non-lactating females) is based on a female’s ability to choose the fittest male possible for mating. Because of the near absence of food resources on humpback breeding grounds (Chittleborough 1965) and the importance of these ecological conditions (e.g., fasting) to female reproductive strategies (Emlen and Oring 1977), females without calves may benefit from maximizing exposure to males. Gabriele (1992) suggested that females without calves might minimize the amount of time on breeding grounds to ensure quick conception in order to maximize feeding opportunities in higher latitudes during pregnancy. In support of this hypothesis, mature females are rarely found alone on breeding grounds (Darling 1983; Gabriele 1992), longer residency periods in feeding areas (Dawbin 1966) and shorter residency periods in breeding areas (Darling 1983; Gabriele 1992) have been reported for newly pregnant females, and migration records show that newly pregnant females are the first to depart for feeding grounds (Chittleborough 1958, 1965; Dawbin 1966, 1997). From this perspective, interactions with multiple males that might lead to male-male competition and provide an opportunity for a female to assess the relative fitness of her male companion (Tyack and Whitehead 1983; Glockner-Ferrari and Ferrari 1985; Clapham 1996) might be beneficial.

Multiple male groups are known to attract males from as distant as 9km away (Tyack 1982; Tyack and Whitehead 1983; Darling and Berube 2001), and I report that in natural conditions the presence of SAGs led to interactions with other males for the majority of females without calves that I observed. Moreover, 38% of our playback trials resulted in approaches by whales that were not the subject of the playbacks, often to within 5-25m of the underwater speaker. Because none of the 35 females targeted in this study directly or rapidly approached the playback as described by Tyack (1983) and Mobley et al.
(1988), and social sounds are known to attract other males (Tyack 1983; Tyack and Whitehead 1983; Darling and Berube 2001), females remaining within close proximity to a SAG may have an increased likelihood of interacting with other males. If females without calves are trying to maximize encounters and females with calves are trying to minimize interactions with males, then remaining in an area where multiple males are passing through might be a good strategy, and may explain why females without calves remained neutral during playbacks while females with calves moved away in our study.

Whether female humpbacks actively choose mating partners is unknown, and the potential mechanisms underlying female choice in this species are still speculative (see Clapham 1996; Cerchio 2003; Darling et al. 2006). As previously described, the similarities in responses within female reproductive classes were striking and clearly indicate that female reproductive class is an important predictor of male-female interactions during the breeding season. However, the variability in responses, including active avoidance of some SAGs and apparent tolerance or potential interest in other SAGs, suggest that male-female interactions during the breeding season are also influenced by a number of compounding factors, which include changes in female receptivity, and/or possible advantages or disadvantages of a male escort that might be indicative of female choice.

For example, despite the consistent avoidance of social sounds observed in females with calves and the neutral responses observed in females without calves, a small number of females within each social group responded in unexpected ways. In our study, five playback trials led to females, both with and without calves, actively changing direction toward or decreasing distance to the playback vessel (i.e., approaching) during the playback trial. Unlike other playback studies where social sounds recorded from SAGs were played back to whales (humpbacks: Tyack 1983; Mobley et al. 1988; right whales: Parks 2003), the focal groups that approached in our study moved closer and parallel to the playback, but not directly at the playback boat, and each of these groups ultimately ended up essentially the same distance from the playback vessel as at the start of the trial, or further. Why do some females with calves, and some females without calves, approach sounds made by multiple males during the breeding season, while others do not? Possible explanations for females approaching playbacks of social sounds include: a
pro-estrus female seeking out interactions with other males, possibly to incite male-male competition; or the result of a female strategy to escape, avoid or lose the current male escort. These differences are likely a reflection of the inherent variability in male-female groups with or without a calf (e.g., age, body size and/or condition of male, female, and/or calf; Chapter 3).

Virtually nothing is known about estrus cycles and behavior in female humpbacks. Consequently, I can only speculate about how female reproductive cycles influence female behavior and male-female interactions. Male humpbacks have been shown to compete for access to estrus females (Darling 1983; Tyack and Whitehead 1983; Clapham et al 1992). In the two female no-calf groups that approached the playback, male competition was observed, suggesting that the female was in a pro-estrus state (e.g., Darling 1983). Moreover, in one of these two cases the male was observed blowing bubbles underneath the female’s genital area, and I have observed males blowing fine streams of bubbles underneath a female’s genital area in slow moving SAGs (M.Jones, C. Nicklin, unpublished data) where the female is presumably in estrus (Darling 1983; Tyack and Whitehead 1983). In contrast to the approaching female no-calf groups, avoidance behaviors including frequent changes in travel direction, variable increases in speed and distance, and changing from resting to traveling were particularly evident in both of the pre-playback trials with escorted mother-calf groups that approached the playbacks, and may indicate that in these situations, females might be approaching the sounds in an effort to lose an unwanted male escort. I have observed at least three other situations where a mother and calf, with an apparent unwanted escort, used the same strategy of moving toward a SAG or pair of males.

Whether or not females sometimes approach nearby SAGs to incite male-male competition (Cox and Le Boeuf 1977) and/or to lose an unwanted escort by attracting other males, remains unclear but the evidence from this study, albeit largely anecdotal, suggests that females may use social sounds as a cue to avoid or approach multiple male groups depending upon the female reproductive cycle and/or specific characteristics associated with the male escort that are consistent with patterns of female choice. In other mammals, male body size, age, strength, fitness, fighting ability, endurance, and/or status may influence preference for one mate over another (Andersson 1994). Male acoustic displays are often associated with female choice in other species, but to date there is no evidence that the complex and continually evolving
male humpback song is a mechanism for active female choice (Darling et al. 2006). However, female mammals have been found to use various aspects of male vocalizations produced during aggressive encounters (like the social sounds used here) to discriminate between male competitive ability, physical condition, body size, and/or mating success (e.g., rates of display: red deer, *Cervus elaphus*: McComb 1991; *formant frequencies*: red deer, *Cervus elaphus*: Charlton et al. 2007; amplitude: bison, *Bison bison*: Wyman et al. 2008). Studies of the function of individual social sounds produced in SAGs on breeding grounds are virtually non-existent and thus whether or not female humpbacks are using social sounds as possible cues to male fitness or body condition is unknown. It is speculative but feasible that like other mammals, sounds produced in agonistic encounters might contain cues to a male’s body size or fitness that could be important to females. Indeed these sounds might prove to be more variable, and unlike humpback songs, may differ more between individuals thereby providing females with more individual acoustic cues than songs to discriminate between.

In about a quarter of our observations of female-calf groups, the responses to playbacks were neutral or positive (approaches), suggesting that multiple male groups may at times also be beneficial to female-calf groups. There are at least three ways that females with calves may benefit from interactions with nearby SAGs. First, females with calves may benefit if the interactions with the SAG cause an unwanted escort to join another group with a more receptive female. Second, SAGs may allow an unescorted female with a calf an increased opportunity to join with a single male escort that may provide protection against other potentially aggressive males (e.g., Wrangham 1979; Wrangham and Rubenstein 1986; Mesnick 1997; Cartwright and Sullivan 2009). Whether or not mothers of older calves are more receptive to the presence of an escort is unknown, but calves were observed circling at the surface in each of the three unescorted female-calf groups that either approached or remained neutral to playback trials, and circling by calves may be an indicator of older calves (Cartwright and Sullivan 2009b). Third, not unlike females without calves, some females with calves may be approaching SAGs in an effort to maximize mating opportunities during periods of estrus. Whaling studies have shown that at least some females with calves enter post-partum estrus (Chittleborough 1958, 1965), and re-sightings of the same females with a different calf in two or more consecutive summers indicate that annual reproduction can be
successful, especially for larger, older females that are more likely to be able to sustain consecutive pregnancies (Straley et al. 1994).

Results of this study indicate that female reproductive class is a critical factor in determining how females respond and interact with males during the breeding season. Overall, females with calves avoided playback recordings of social sounds produced by male humpbacks in surface-active groups (SAGs) on the Hawaiian breeding grounds, while females without calves responded neutrally or positively. Significant differences between females with and without calves were found in each of the five response variables measured, including general response (avoid, neutral, approach), distance moved, speed traveled, behavior (i.e., change from rest to travel), and respiration patterns (i.e., response times and downtimes). Although sample sizes were relatively small within groups, the strict sampling protocol combined with the consistency of responses, and the replication of these responses under natural conditions (this study; Chapter 2), suggest that the results of this study are indicative of how females respond and interact with multiple males on the Hawaiian breeding grounds. Whether or not females with calves actively avoid males, at least to this degree, in less concentrated areas than found off the West coast of Maui, is unknown. Future studies aimed at deciphering the meaning and function of social sounds produced by individual males in aggressive contexts on breeding grounds will allow more detailed playback studies to be conducted to determine if social sounds produced by different individuals and/or groups elicit different responses from females. In conclusion, this study suggests that male-female interactions during the breeding season are likely a reflection of a combination of factors, beginning with female reproductive class, but also including possible costs and benefits of specific male escorts, stage of the reproductive cycle, age-class and body condition.
LITERATURE CITED


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CHAPTER 5

SUMMARY AND SYNTHESIS

For nearly thirty years researchers have debated the type of mating system that best characterizes and describes humpback whales (*Megaptera novaeangliae*) (Herman and Tavolga 1980; Darling 1983; Brown and Corkeron 1995; Clapham 1996; Cerchio et al. 2005; Darling et al. 2006). Initially researchers suggested that the humpback whale mating system was a form of polygyny, where males compete for females through displays and fights, with the dominant males securing the majority of matings (e.g., dominance polygyny: Darling 1983; Brown and Corkeron 1995; lek: Mobley and Herman 1985; Cerchio 2003; floating lek: Clapham 1996). Recent genetic and behavioral studies have raised questions as to whether this is the appropriate context within which to view humpback whale behavior (Valsecchi et al., 2002; Cerchio et al., 2005; Darling et al. 2006). One of the critical gaps hindering our understanding of humpback whale behavior is our lack of knowledge about the role the reproductively active female plays within the breeding system. Virtually nothing is known about the timing and length of female estrus cycles (Clapham 1996), and little is known about how females interact with males on breeding grounds (Darling et al. 2006; Cartwright and Sullivan 2009), including whether females actively choose or select mates based on specific male attributes as is often found in polygynous mammals (e.g., Andersson 1994).

A formidable challenge in describing and understanding female behavior has been the difficulty of sexing individuals in the field when a calf is not present (e.g., Gabriele 1992; Craig et al. 2002). In previous studies focused on female behavior, female no-calf groups often included females in multiple male groups, which made direct comparisons with escorted mother-calf groups (i.e., female with calf and a single male) challenging, especially because the presence of multiple males has since been found to affect the behavior and movement of females (Cartwright and Sullivan 2009). Although genetic studies now indicate that the majority of pairs on breeding grounds are male-female (Brown and Corkeron 1995;
Pomilla and Rosenbaum 2006; Cypriano-Souza et al. 2010), male-male pairs are also found on humpback breeding grounds (Darling 1983; Clapham et al. 1992), which further complicates descriptions of female behavior as the behavioral differences between male-female pairs and male-male pairs have not yet been discerned in the literature. Consequently, although pairs of whales are one of the most prevalent social groups on winter breeding grounds (Pomilla and Rosenbaum 2006; Cypriano-Souza et al. 2010), the social role and function of these pairs has not been systematically studied, and little is known about sex-specific behavior within these groups. One of the primary goals of this study was to determine the sex of the individuals within pairs in order to compare and describe the similarities and differences in behavior between females with and without calves on the breeding grounds.

The overall purpose of this study was to address these gaps by examining the role of the reproductively active female humpback on the winter breeding grounds to determine if female behavioral interactions with males differed based on female reproductive class (i.e., presence or absence of a calf). Female humpbacks migrate to winter breeding grounds for two reasons, mating and calving. Until now however, whether or not these purposes are distinct and represent potentially different or even conflicting reproductive objectives has been unclear. Theoretically, mature females without calves migrate to breeding grounds to maximize mating opportunities, while late pregnant females migrate primarily to give birth and/or to raise calves in warmer waters. Gabriele (1992) hypothesized that females without calves should maximize associations with males on breeding grounds to ensure conception occurs as early in the breeding season as possible to facilitate an early return to feeding grounds in order to maximize feeding opportunities in higher latitudes. In contrast, the energetic demands of lactation during the prolonged fasting periods characteristic of the breeding grounds (Lockyer 1981, 1984) and potential consequences of annual reproduction for lifetime reproductive success (Chittleborough 1955) coupled with low rates of successful annual reproduction (Chittleborough 1958; Glockner-Ferrari and Ferrari 1990; Clapham and Mayo 1990; Straley et al. 1994; Mikhalev 2000 cited by Noad and Cato 2007) suggest that the majority of females with calves may try to avoid mating in successive years.

Based on these observations, I hypothesized that female humpbacks may behave differently around males during the breeding season based on female reproductive class. I investigated how
females with calves (female-calf) and females without calves (female no-calf) interacted with males by comparing time budgets, associations, and movement patterns. I examined how relative body size (based on results of fluke photogrammetry), age-class (sighting histories based on photo-identification) and male behavior influenced the range and variability evident in female behavior and movement patterns within male-female groups. I also conducted experimental playbacks of recorded sounds typically produced by males within multiple male groups associated with male-male competition on humpback breeding grounds (e.g., Darling 1983; Tyack and Whitehead 1983; Silber 1986) with females with and without calves. Although mature females are rarely alone on breeding grounds and hence difficult to find and follow, unescorted mother-calf pairs gave us a baseline comparison of female-calf behavior without a male in each of these studies.

Does Female Reproductive Class Affect Female Time Budgets, Male-Female Associations, and Movement Patterns?

Female reproductive class (i.e., presence or absence of a calf) influenced and characterized some, but not all aspects, of female behavior, association, activity and movement patterns. Female reproductive class affected the length of time spent on breeding grounds, the likelihood of being pursued by multiple males, the extent of time spent resting and traveling, and the degree of short-term movement and specific behaviors (e.g., socializing, active behaviors). While female reproductive class did not affect the overall prevalence of associations with males, it did affect how females responded to males. Unescorted mother-calf groups had time budgets that were more similar to male-female pairs than escorted mother-calf groups. Male-female pairs (females without calves) were characterized by extensive resting periods, whereas the majority of escorted mother-calf groups divided their time between periods of rest and travel. Indeed, the amount of time devoted to resting was significantly higher in females without calves than escorted female-calf groups, and female-calf groups escorted by males traveled significantly further distances and at greater speeds than male-female pairs. Of the three social groups involving females that I followed during this study, male-female pairs traveled the least and escorted mother-calf groups the most. Because time budgets of escorted mother-calf groups were significantly different from both unescorted mother-calf groups and male-female pairs, our data strongly suggest that the presence of a newborn calf is a significant factor in male-female interactions during the breeding season.
Do Females with Calves Attempt to Avoid Males During the Breeding Season?

In mammals, female avoidance of males may include fleeing, hiding, and/or struggling (Mesnick 1997). Specific behaviors associated with female avoidance include females moving away, changing direction, engaging in avoidance behaviors (e.g., elephant seals, *Mirounga leonine*: Galimberti et al. 2000: flipping sand backwards at males, swinging hindlimbs side to side), or approaching other animals (e.g., Sumatran orangutans, *Pongo pygmaeus abelii*: Fox 2002). In this study, female humpbacks that actively avoided and/or fled from males were consistent with female avoidance responses to males in other species (elephant seals, *Mirounga leonine*: Galimberti et al. 2000a; Grevy’s zebra, *Equus grevyi*: Sundaresan et al. 2007; Muller et al. 2007). Avoidance was the primary response from female humpbacks confronted with a lone aggressive male in this study (Chapter 3), and female humpbacks typically responded to lone males engaged in chasing bouts with behavior patterns associated with male avoidance in the literature (e.g., Tyack 1981; Mobley and Herman 1985; Glockner-Ferrari and Ferrari 1985). For example, females actively avoiding males engaged in behaviors typically associated with aggression or avoidance including head lunges, tail throws, and peduncle throws (e.g., Tyack 1981; Baker and Herman 1984; Craig et al. 2002), approaching nearby boats (Glockner-Ferrari and Ferrari 1985), and/or swimming at high speeds over comparatively long distances, often in a circular direction.

Three different lines of evidence from this study, collected in both natural and experimental conditions, suggest that humpback females with calves avoid males more often than females without calves during the winter breeding season. First, while only 2% of groups including females without calves avoided their male companion (2/89), nearly 30% of females with calves avoided the male escort that accompanied them (Chapter 2). Second, females with calves were significantly more likely to be pursued and chased by males than females without calves (Chapter 3). Female humpbacks that were chased actively avoided and/or fled from chasing males. In these situations, females typically swam over twice as far and over twice as fast as females not chased. Thirdly, females with calves were significantly more likely to avoid playback recordings of sounds produced by male humpbacks when in surface-active groups on breeding grounds than females without calves. While nearly three-quarters of female-calf groups moved away from the male sounds, nearly three-quarters of female no-calf groups responded
neutrally or positively. In response to playbacks, females with calves traveled significantly further distances and at significantly higher speeds than females without calves. The degree and consistency of the reaction of females with calves to playbacks of male sounds suggests that like other mammals (e.g., *African lions, Panthera leo*: McComb et al. 1993; baboons: *Papio cynocephalus ursinus*: Kitchen et al. 2003) female humpbacks may use acoustic cues to avoid interactions with multiple males during the breeding season. Indeed, if lack of movement is indicative of male tolerance and movement indicative of male avoidance, then females without calves rarely avoided interactions with males while females with calves frequently avoided males.

**Variability in Male-Female Interactions During the Breeding Season**

Despite clear differences between female-calf and female no-calf groups on breeding grounds, one of the most striking findings to come from this comparative study was the variability in behavior and movement patterns I found within the different female groups, especially those involving a male (male-female pairs and escorted mother-calf groups). For example, in a two-hour period movement in escorted mother-calf pairs ranged from 1.3 km to 12.2km and in male-female pairs from <1km to 8.2km; similar findings were reported for speed of travel. I also found variability in how female groups responded to playback recordings of sounds produced by males. Despite widespread avoidance of social sounds by females with calves and neutral responses by females without calves, a small number of females within each social group responded in unexpected ways. Five playback trials led to females, both with and without calves, actively changing direction toward or decreasing distance to the playback vessel (i.e., approaching) during the playback trial. This range in behavior suggests that female behavior during the breeding season may be the result of a number of factors, beginning with female reproductive class, but also including the possible costs and benefits associated with specific male escorts, the stage of the female estrus cycle, age-class, body size and condition.
Body Size, Age-Class and Male Behavior Affect Male-Female Interactions

Individuals within male-female groups on humpback breeding grounds varied in terms of size and/or age-class, and these variables, coupled with female reproductive class, significantly influenced female behavior and movement patterns and presence of aggression by lone males toward females (Chapter 3). Using fluke photogrammetry techniques (Calambokidis et al. 2001), I found that individuals within male-female groups showed considerable variation in relative fluke size, suggesting that different sized (aged) whales may occupy the same social roles and may contribute to the substantial variability in behavior and movement patterns observed within social groups containing females on the breeding grounds (Chapter 2, Chapter 4).

Similar to other mammals (elephants, *Loxodonta africana*: Poole 1989; Equids: Rubenstein 1986; elephant seals, *Mirounga leonine*: Galimberti 2000; orangutans, *Pongo pygmaeus abelii*: Fox 2002), I also found a relationship between the size of males (as estimated by fluke size estimates) and females and male behavior; males that chased females had smaller fluke sizes than males that did not chase females. Although the fluke size of males ranged up to 4.52m, the largest escort that I measured chasing a female with a calf was 3.83m. Not all small males chased females, however, suggesting that like other mammals (Gross 1996) individual male humpbacks may choose between different tactics when pursuing and/or interacting with a female. For example, one male chased two different mothers in two different years, suggesting that some males may use certain tactics if successful (see Cerchio et al. 2005).

I also found a relationship between female size and chasing. The mean fluke size for mothers that were chased was significantly smaller than mother’s not chased, and three of the four smallest mothers measured were chased. Although the fluke size of females ranged up to 4.61m, none of the fluke sizes of females involved in chasing events was larger than 4.1m, similar to the pattern I found in male fluke size and chasing events. Although sample sizes were limited, females with smaller flukes (< 4m) were significantly more likely to be chased by males than females with larger flukes, suggesting that males may be targeting smaller and/or younger females that might not have the experience, reserves and/or endurance to outlast or defend against chasing males.
Implications for Male and Female Reproductive Strategies

Animal societies, and the mating systems that comprise them, are a result of the relationships between individuals (Emlen and Oring 1977; Rubenstein and Wrangham 1986; Rubenstein 1994), and the outcomes of the reproductive strategies employed by individuals to acquire and obtain mates (Emlen and Oring 1977; Clutton-Brock 1989). Studies of mating systems across a wide array of taxa have shown that there is a great degree of variation and flexibility within and between species (see review Clutton-Brock 1989) based on how individuals adjust to different ecological and social pressures and to individual variation in needs and abilities (Rubenstein 1994). The mating system of humpback whales (Megaptera novaeangliae) appears to be no exception. Although humpbacks migrate for the purposes of reproduction, the individuals on the breeding grounds represent different age classes (sub-adult/adult) and reproductive classes (e.g., with or without calf), and have different body sizes and condition. Individuals within social roles (e.g., escort to mother-calf, female in male-female pair) range from small to large, experienced to inexperienced, and immature to mature. Male interactions range from agonistic and competitive (e.g., Tyack and Whitehead 1983) to non-agonistic and coordinated (e.g., Darling et al. 2006; this study), and in this study I found that male-female interactions range from apparently tolerant and passive to intolerant and aggressive. This wide range in physical, social characteristics and physiological states present in both sexes undoubtedly leads to substantial variability, and potential conflict, in how any two individuals, both of the same or different sex, interact with each other.

Humpback whale mothers, not unlike other female mammals with offspring, may be in conflict with breeding males that stand to maximize reproductive success by increasing access to receptive females (Trivers 1972; Smuts and Smuts 1993). Nearly a quarter of mother-calf pairs on breeding grounds were actively and at times aggressively pursued by smaller and/or younger lone males, suggesting that some form of male harassment, at least by a subset of the population, may not be uncommon for lactating females. In other mammals, lactating females have also been found to experience higher rates of harassment from males than non-lactating females (primates: Smuts 1985; orangutans, Pongo pygmaeus abelli: Fox 2002; Grevy’s zebra, Equus grevyi: Sundaresan et al. 2007). Aggressive behavior by males, although not uncommon for females with calves, was not observed in
groups containing mature females without calves. As such, mature females without calves that migrate specifically for mating purposes may still be choosing males, either directly or indirectly, based on specific male attributes such as male body size, strength and fitness, and those attributes may be intertwined with the presence of male harassment.

Even if only some males in the population are using harassment as a reproductive tactic to gain access to mates, protection can become a valuable resource that other males use to attract females (Mesnick 1997). Female preference for larger, older and potentially more dominant males may lead to selection for increased size, strength and fighting ability in males and may be the primary criterion of female choice in mating systems where females seek out alliances with males as a form of protection from more aggressive males (Mesnick 1997). The significant variability I found in female activity, movement and behavior patterns around lone males suggests that females are tolerant and accepting of males that do not act or behave aggressively and that might be older and/or of larger size. Female avoidance and repulsive behaviors were typically associated with aggressive male behavior, which was related to relative body size and age-class. Indeed, the relative size and age data I was able to collect suggests that size and/or age may be a critical component to female preference patterns in humpback whales. Body size and age-class have previously been implicated in female choice (Spitz et al. 2002) and male mate choice (Pack et al. 2009) patterns in humpback whales. For example, primary escorts in multiple male groups, where females may discriminate between males based on size, age, strength, and/or fitness, are reportedly larger in body size than males in other social roles on breeding grounds (e.g., escorts to female-calf pairs).

Rubenstein (1994) has argued that the best option for a reproductively active female may be to associate with males that simultaneously keep other males away while not altering her time budget and activity pattern. Our results suggest that this scenario may be one of the most important factors governing male-female interactions during the winter breeding season. While outright rejection of males was relatively infrequent, especially for mature females without calves, on several occasions I did observe females approach other male groups, which led to male-male competition and at times to the focal male
being lost or displaced, suggesting that female humpbacks may solicit male competition to lose or displace an unwanted escort.

**Directions For Future Research**

Collectively, the data from this study strongly suggest that male-female interactions during the breeding season are a reflection of a combination of factors, beginning with female reproductive class, but also including possible costs and benefits of specific male escorts, stage of the reproductive cycle, male and female body size (age-class), and possibly female body condition. Clearly, the most critical gap and limiting factor in all studies of humpback reproductive behavior is our current lack of knowledge about the female estrus cycle. Separating male behavior from female behavior is a formidable challenge for behavioral studies, and our results suggest that there is significant flexibility governing male-female interactions during the breeding season. Developing a more complete understanding of male-female relationships and interactions during the breeding season depends upon our ability to isolate and consider the influence of other variables, including how female estrus cycles influence these interactions. Comparisons with other breeding populations that vary in terms of oceanographic and ecological conditions, population density, migration and reproductive patterns will also help illuminate how these factors contribute to and affect female behavior and male-female interactions during the breeding season. These potential differences both within and between populations suggest that there is considerable complexity in the factors governing reproductive behavior in humpback whales, and that caution should be used when comparing behavioral patterns or generalizing results between populations.

In the meantime, future studies aimed at investigating how male-female interactions are affected by male behavior, male and female body size, and age-class (calf and adults), may help explain the substantial variability I observed between males and females and increase our understanding of how female choice operates in breeding populations of humpback whales. Size data from this study and others (e.g., Spitz et al. 2002) are still limited and as such it is impossible to make conclusions about how body size of males and females characterizes and influences the mate choice patterns in humpback whales; however, data from studies using different photogrammetric methods is beginning to accumulate and taken together suggests that this is a fruitful direction for future research. This study confirms that
fluke photogrammetry (Calambokidis et al. 2001) is a useful and cost effective tool for examining the influence of relative body size (see Sousa-Lima and Groch 2010) on the variability in behavior found within male and female social roles on breeding grounds.

Results of this study suggest that some level of female choice may be occurring in humpback whale populations. For the last 30 years, most studies have suggested that the songs of male humpbacks may provide females with a mechanism of choice (see review Darling et al. 2006), but to date, there is still no empirical evidence that female humpbacks use the male song to choose males. Indeed, all evidence to date shows that other lone males, not females, are attracted to singers (Darling and Berube 2001; Darling et al. 2006; Smith et al. 2008). In contrast to observations of males competing for females on breeding grounds, interactions between singers and other lone males (joiners) are typically brief and markedly non-agonistic (Darling and Berube 2001; Darling et al. 2006). Recently, Smith et al. (2008) stated that singers often escort female-calf groups and proposed an intersexual function for humpback song. However, in this latter study only 17.5% (20/114) of the singers sampled escorted females, and these data were biased toward the location of male singers and did not necessarily reflect the overall number of females present in the area.

In our study focused on females, I found that singers accompanied even fewer females. Although I sampled 551 groups of females on breeding grounds, singing was only heard in six of the 194 male-female pairs (3.1%) and in 17 of the 188 (9.0%) escorted mother-calf groups encountered. Despite the relatively low occurrence of male singer-female associations found in both studies, both studies found that singers were significantly more likely to accompany females with calves than females without calves. Why male singers would accompany female-calf groups and not female no-calf groups is an interesting and intriguing question for future studies. If singing were a reproductive display necessary for male-female interactions during courtship as proposed by Smith et al. (1999) I would expect to find both a higher frequency of associations between singing males and females, and for singing males to be equally (if not more) likely to accompany females without calves that migrate for the purposes of mating. This study demonstrated that female reproductive class is an important factor in male-female interactions, and may suggest that males sing around females with calves more due to the female’s reluctance or
disinterest in mating than due to courtship. Considering male singing leads to the attraction and joining of other males one might speculate that singing around females may be initiating or 'inviting' others males for assistance around an otherwise reluctant female. Darling et al. (2006) provided evidence that singer-jointer interactions may lead directly to apparently cooperative and coordinated behavior around female-calf pairs, and hypothesized that the song is a real time measure of association between individuals, possibly providing a means of mutual assistance in mating.

Instead of male song as the primary mechanism of female choice, our study suggests that male body size and age-class may be critical parameters of female preference ripe for future investigation. Results of our playback study suggest that females listen and respond to acoustic cues in their environment other than humpback song, principally social sounds produced by males in situations associated with male-competition. Other female mammals have been found to use various aspects of male vocalizations produced during aggressive encounters (like the social sounds used here) to discriminate between male competitive ability, physical condition, body size, and/or mating success (e.g., rates of display: McComb 1991; formant frequencies: Charlton et al. 2007; amplitude: Wyman et al. 2008). Studies of the function of individual social sounds produced in surface-active groups on breeding grounds are virtually non-existent and thus whether or not female humpbacks are using social sounds as possible cues to male fitness or body condition is unknown. It is speculative but feasible that like other mammals, sounds produced in agonistic encounters might contain cues to a male’s body size or fitness that could be important to females. Indeed these sounds might prove to be more variable, and unlike humpback songs, may differ more between individuals thereby providing females with more individual acoustic cues than songs to discriminate between.

Finally, the frequency of females with calves that were chased and pursued by males was surprising and warrants further study to determine the extent and consequences of this behavior within the social organization of breeding humpbacks. Male aggression has been correlated with populations with higher densities (see review Knell 2009). The density of the population around the Hawaiian Islands (Calambokidis et al. 2008), especially around Maui which hosts one of the most concentrated aggregations within the Hawaiian Islands (Mobley et al. 1999), may influence the degree and frequency of
male aggression toward females I report here. Smaller and more diffuse populations may not be
subjected to the same degree of harassment. Some evidence that this may be the case comes from
smaller sub-populations of humpback whales scattered around the South Pacific Islands where the
frequency of males escorting female-calf groups decreases from between 69-85% reported in Hawaii
(Darling 1983; Glockner and Venus 1983; Glockner-Ferrari and Ferrari 1985; Craig et al. 2002) to 0% in
the southern Cook Islands (Hauser et al. 2000). As such, future studies may be aimed at determining
whether or not this is a function of the dense aggregation in the Hawaiian Islands (Calambokidis et al.
2008) or even Maui (Mobley et al. 1999), or a more universal and defining characteristic of the mating
system of humpbacks worldwide.
LITERATURE CITED


Herman, L. M., Tavolga, W. N. (1980). The communications system of cetaceans. In L. M. Herman (Ed.), *Cetacean Behavior, mechanisms, and functions* (pp. 149-209). New York: John Wiley and Sons.


McComb, K. P., Anne; Packer, Craig; Grinnell, Jon (1993). Female lions can identify potentially infanticidal males from their roars. Proceedings of the Royal Society of London Series B Biological Sciences, 252 (1333), 59-64.


APPENDICES
### Appendix A

**Ethogram**

<table>
<thead>
<tr>
<th>BEHAVIOR</th>
<th>DESCRIPTION</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Active Behavior</strong></td>
<td>Displays at or above the water surface that involve a whale slapping or waving a body part on or near the surface of the water (e.g., tail slaps, breaches, head slaps, etc).</td>
</tr>
<tr>
<td><strong>Agonistic Behavior</strong></td>
<td>Aggressive behaviors that include body strikes, threats (e.g., inflated head lunges, jaw claps).</td>
</tr>
<tr>
<td><strong>Breath-holding or Breath-holders</strong></td>
<td>Behavior where a male-female pair will remain submerged for 15-25 min at a time, surface and move only to breathe before diving and repeating the whole process again.</td>
</tr>
<tr>
<td><strong>Calf Circling</strong></td>
<td>Intervals where the calf surfaces alone and takes a series of three or more blows while moving in a circular path at the surface (see Glockner and Venus 1983).</td>
</tr>
<tr>
<td><strong>Male Circling</strong></td>
<td>In male-female pairs, a behavior where the male surfaces alone and makes a circle above the resting and submerged female before the pair surfaces together, often several minutes later.</td>
</tr>
<tr>
<td><strong>Downtime</strong></td>
<td>Length of time between the onset of a terminal dive and the first blow in the surface interval.</td>
</tr>
<tr>
<td><strong>Group</strong></td>
<td>Whales within 2-3 body lengths of each other or that are engaged in similar travel and behavior patterns while at the surface.</td>
</tr>
<tr>
<td><strong>Resting</strong></td>
<td>Frequent floating at surface or remaining in one location while submerged, moving only when at the surface and to breathe. A calf circling is a sign of resting in female-calf groups.</td>
</tr>
<tr>
<td><strong>Socializing</strong></td>
<td>Situations where one or more individuals approach the research vessel, often staying at or near the surface for extended periods of time. During these interactions, the female often rolled upside down at or near the surface, and/or engaged in other surface behaviors (e.g., head rises, flippering).</td>
</tr>
<tr>
<td><strong>Surface Interval or Surface Bout</strong></td>
<td>The amount of time at the surface between the first breath and the terminal dive.</td>
</tr>
<tr>
<td><strong>Traveling</strong></td>
<td>Directional movement that results in a change in location between subsequent surface and dive locations (Thomas and Taber 1983).</td>
</tr>
</tbody>
</table>
APPENDIX B

Summary of within season re-sights between 2003-2008.

<table>
<thead>
<tr>
<th>No.</th>
<th>Group Type 1</th>
<th>Role 1</th>
<th>Sex</th>
<th>No. Days</th>
<th>Group Type 2</th>
<th>Role 2</th>
<th>Same Male-Female(^1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Singer</td>
<td>Singer</td>
<td>Male</td>
<td>45</td>
<td>Singer</td>
<td>Singer</td>
<td>NA</td>
</tr>
<tr>
<td>2</td>
<td>SAG(^2)</td>
<td>Primary Escort</td>
<td>Male</td>
<td>43</td>
<td>SAG</td>
<td>Challenger</td>
<td>NA</td>
</tr>
<tr>
<td>3</td>
<td>Pair</td>
<td>Male in Pair</td>
<td>Male</td>
<td>3</td>
<td>MCE</td>
<td>Escort</td>
<td>NA</td>
</tr>
<tr>
<td>4</td>
<td>MCE(^2)</td>
<td>Mom</td>
<td>Female</td>
<td>33</td>
<td>MCE</td>
<td>Mom</td>
<td>NO</td>
</tr>
<tr>
<td>5</td>
<td>SAG</td>
<td>Challenger</td>
<td>Male</td>
<td>15</td>
<td>Lone</td>
<td>Single</td>
<td>NA</td>
</tr>
<tr>
<td>6</td>
<td>MCE</td>
<td>Mom</td>
<td>Female</td>
<td>17</td>
<td>MCE</td>
<td>Mom</td>
<td>Unknown</td>
</tr>
<tr>
<td>7</td>
<td>Singer</td>
<td>Singer</td>
<td>Male</td>
<td>19</td>
<td>Singer</td>
<td>Singer</td>
<td>NA</td>
</tr>
<tr>
<td>8</td>
<td>MCE</td>
<td>Mom</td>
<td>Female</td>
<td>21</td>
<td>MCE</td>
<td>Mom</td>
<td>NO</td>
</tr>
<tr>
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<td>MCE</td>
<td>Mom</td>
<td>Female</td>
<td>4</td>
<td>MCE</td>
<td>Mom</td>
<td>NO</td>
</tr>
<tr>
<td>10</td>
<td>MCE</td>
<td>Escort</td>
<td>Male</td>
<td>9</td>
<td>MCE</td>
<td>Escort</td>
<td>Unknown</td>
</tr>
<tr>
<td>11</td>
<td>Lone</td>
<td>Single</td>
<td>Male</td>
<td>13</td>
<td>SAG</td>
<td>Secondary Escort</td>
<td>NA</td>
</tr>
<tr>
<td>12</td>
<td>MC</td>
<td>Mom</td>
<td>Female</td>
<td>8</td>
<td>MC</td>
<td>Mom</td>
<td>NA</td>
</tr>
<tr>
<td>13</td>
<td>Singer</td>
<td>Singer</td>
<td>Male</td>
<td>41</td>
<td>MCE</td>
<td>Escort</td>
<td>NA</td>
</tr>
<tr>
<td>14</td>
<td>Singer</td>
<td>Singer</td>
<td>Male</td>
<td>5</td>
<td>MCE</td>
<td>Escort</td>
<td>NA</td>
</tr>
<tr>
<td>15</td>
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<td>Presumed Male Pair</td>
<td>Unknown</td>
<td>7</td>
<td>Pair (with sub-adult)</td>
<td>Presumed Male</td>
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</tr>
</tbody>
</table>

\(^1\) Same Male-Female: NA = Not applicable; YES = Identification photographs indicate same male and female photographed twice together; NO = Photographs available but indicate different male and female sighted together; Unknown = Data not available (e.g., one individual was not identified on one of the sightings).

\(^2\) SAG = Surface Active Group

\(^3\) MCE = Escorted Mother-Calf Group
<table>
<thead>
<tr>
<th>No.</th>
<th>Group Type 1</th>
<th>Role 1</th>
<th>Sex</th>
<th>No. Days</th>
<th>Group Type 2</th>
<th>Role 2</th>
<th>Same Male-Female¹</th>
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</thead>
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<td>33</td>
<td>SAG</td>
<td>Secondary Escort</td>
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<tr>
<td>17</td>
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<td>Challenger</td>
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<td>MCE/SAG-calf</td>
<td>Escort or Challenger</td>
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<tr>
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<td>Female</td>
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<td>SAG</td>
<td>Nuclear Animal</td>
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<tr>
<td>19</td>
<td>MCE</td>
<td>Mom</td>
<td>Female</td>
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<td>Pair</td>
<td>Male in Pair</td>
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<td>Challenger</td>
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<td>Escort</td>
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<td>Pair</td>
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<td>Pair</td>
<td>Male in Pair</td>
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<tr>
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<td>43</td>
<td>MCE</td>
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<tr>
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<td>Pair</td>
<td>Female in Pair</td>
<td>Female</td>
<td>2</td>
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<td>NO</td>
</tr>
<tr>
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<td>MCE</td>
<td>Mom</td>
<td>Female</td>
<td>21</td>
<td>MCE</td>
<td>Mom</td>
<td>NO</td>
</tr>
<tr>
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<td>Mom</td>
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<tr>
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<td>Primary Escort</td>
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</tr>
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<td>Singer</td>
<td>Singer</td>
<td>NO</td>
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<td>Escort</td>
<td>YES</td>
</tr>
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<td>Male</td>
<td>3</td>
<td>Pair</td>
<td>Male in Pair</td>
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<td>MCE</td>
<td>Mom</td>
<td>Female</td>
<td>7</td>
<td>MCE</td>
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<td>SAG</td>
<td>Challenger</td>
<td>NO</td>
</tr>
</tbody>
</table>