CHARACTERIZATION OF BEHAVIOR OF HUMPBACK WHALES IN HAWAIIAN WATERS

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EXECUTIVE SUMMARY

Humpback whales make annual migrations to winter assembly areas in subtropical and tropical waters to mate and, after a year gestation, give birth. The main Hawaiian Islands are the largest such assembly area in North Pacific. Since the late 1970s humpback whale research in Hawaii has been at the forefront of the investigation of reproductive behavior patterns of this species. This report reviews available information and summarizes our current understanding of the behavior of humpback whales in Hawaii.

Humpback behavior patterns in Hawaii represent a continuum of reproductive activities that begin on late season feeding grounds and occur throughout the migration. In Hawaii, whales are found around all the main islands, with concentrations on shallow banks within the Four Island Group, Penguin Banks and to a lesser degree off the Kona coast and Kauai. It is apparent whales circulate freely throughout the islands, although questions remain as to if differential use of specific locations occurs. Cows with newborn calves are more likely to be found in shallow, inshore waters than the general population. Humpback whale abundance peaks in February-March, but whales are common from December through May and seen as early as September and as late as June. The arrival and departure of whales is segregated to some degree by age, sex and reproductive condition, with strong suggestions that, with the exceptions of some males, many whales are present for short periods relative to a five-six month long season.

Female reproductive cycles govern much of the humpback whale behavior in Hawaii. Humpback whales give birth on the average every two-three years, although postpartum estrus is common with annual birth occurring in some portion of the population. The sexual cycle peaks during the three-five winter months, with peak ovulation in January-February. Females are seasonally polyestrus, undergoing several cycles if pregnancy does not occur. Peak ovulation period coincides with most behavioral activity in Hawaii including the peak of singing, male competitive and aggressive behavior, and transience of individuals among groups. With a 50:50 sex ratio, and the average birth rate two-three years, many more mature males than fertilizable females are present in any one breeding season, leading to increased competition among males.

It is generally agreed that humpbacks follow a polygynous or promiscuous mating system. The former implies that males monopolize females in some way; in the latter they do not. Mating system hypotheses include dominance polygyny where males develop and maintain, through display and fighting, a hierarchy for access to females; and lek polygyny where males assemble and advertise to females through song. A further emerging hypothesis proposes formation of male coalitions and cooperation to access females. All these hypotheses require further testing.

Most male behavior patterns, interactions and associations are short-lived, lasting only minutes to hours, with the animals apparently orienting to any female in estrus.

Earlier studies emphasized male antagonism and avoidance of each other; more recent studies report non-agonistic male-male interactions. Male behavior patterns include singing; interaction with singers, at times forming all male pairs, trios or larger groups; and escorting or guarding females, defending or challenging the escort position with a variety of agonistic behavior including displays, sounds and physical clashes that may result in bloody wounds. There are some suggestions of cooperative and even care-giving behavior amongst some males.

Female behavior patterns are set in two contexts: mating or birth and newborn care. Some portion of females undergoes postpartum ovulation and are involved in both activities in one season. Little is known about female mating strategies and behavior; however, this likely includes maximizing contact with males, minimizing contact and potential competition with females, and accomplishing mating in as short time as possible for energetic considerations. Female behavior may include acceptance of the male escort, leading or being chased by multiple competitive males, and mating. Female-female associations are rare on the breeding grounds. A typical behavior flow begins with a female-male pair in apparent calm union; this pair joined by other males often leading to competitive groups; and eventually the group breaking up leaving a pair again, which may or may not include the original male. Female behavior may influence the selection of a mate through encouraging competition and accepting/rejecting copulation. It has been proposed that females select males based on song but there is no evidence to support this hypothesis.

Female humpbacks in Hawaii are involved in birth, nursing and protection of young. These cows with newborn often occupy shallow, inshore waters presumed to separate them from mating activity and harassment of males, more turbulent offshore conditions, and predators. Birth has not been observed, although circumstantial evidence indicates it peaks at the time of year whales are in Hawaii. With sightings as early as December, cows with newborn peak in numbers in February-March, and are usually the last groups seen in May and June. Cow/calf pairs usually maintain an active separation from each other. Cows with calves apparently travel and circulate through the region like other whales. Travel is the most cow/calf common behavior. When resting the cow often lies in a horizontal position at 30-70 feet below the surface with calf under her head or body. The calf surfaces every five to six minutes, circles, and dives back towards the cow, with the cow surfacing every 10-20 minutes. Suckling occurs when cow/calf is either stationary or traveling. Play is a common activity with the calf mimicking most adult actions and postures. Some sounds by the calf and between cow and calf have been documented, but relative to males they are quiet. It has been proposed that the single male escort is accepted by the cow as it may offer indirect protection from groups of males.

Juveniles, ranging from yearlings to four to five years old, make up a portion of the Hawaiian humpback population; little is known of their behavior patterns. They are found on the periphery of adult groups, in association with adult males including involvement in apparent sexual activity, in juvenile pairs, and alone. One observation reports a sub-adult attempting to feed in Hawaii.

We may have a greater understanding of humpback whale reproductive behavior than other whales; however, overall, our knowledge is still young and dynamic with many aspects at the hypothetical stage and others barely described. Streams of important investigation include the relationship of habitat and behavior, male and female reproductive strategies, and factors that affect birth and newborn success.

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INTRODUCTION

Humpback whales (*Megaptera novaengliae*) migrate between high latitude, summer feeding grounds, and subtropical or tropical winter assemblies for reproductive purposes (Scammon 1869, Kellogg 1928, Dawbin 1966). The Hawaiian Islands comprise the largest known reproductive assembly in the North Pacific Ocean. Currently, they are utilized by approximately four to six thousand whales (Calambokidis et al. 1997, Cerchio et al. 1998). The Hawaiian Islands seem to be the primary migratory destination for humpback whales from summer feeding grounds in British Columbia and Alaska, but it is also clear that the region is visited to some degree by whales from throughout the Pacific Basin (Winn et al.1981, Darling and Jurasz 1983, Payne and Guinee 1983, Darling and McSweeney 1985, Baker et al. 1986, Darling and Cerchio 1996, Calambokidis et al. 1997, Salden et al. 2000, B. Mate pers.comm. 2000). Humpback whales assemble in Hawaiian waters to mate, and following a year gestation, to give birth and nurse newborn calves (Chittleborough 1958, Herman and Antinoja 1977, Rice 1978).

The reasons humpback whales undergo this annual migratory cycle of many thousands of kilometers away from their feeding grounds are not well understood. The whales shift seasonally from a context of feeding, resting and net energy gain, to one of fasting, traveling, birthing, nursing, mating and significant energy expenditure (Scammon 1869, Nishiwaki 1966, Clapham 1999). Consistent environmental conditions across winter assemblies are warm water (19-25°C) and banks of relatively shallow depth (<200 m), which presumably offer significant survival benefits to the whales, perhaps especially mothers and newborn (Lockyer 1981). The winter assembly also serves the purpose of concentrating and mixing whales from seasonally separate feeding grounds, likely with important gene flow implications (Paslboll et al. 1995, Baker et al. 1998).

In Hawaii and during the breeding season, humpback whales presumably pursue theoretical mammalian objectives of maximizing reproductive success (Emlen and Oring 1977). Tenets typically include male strategies to maximize matings, and female strategies to select a “high quality” mate, while avoiding unwanted mating activity, particularly during newborn care (Jones and Swartz 1984, Taber and Thomas 1984, Smultaea 1994, Cartwright 1999). We expect male strategies to include seeking out and competing in some way for estrus females; and at the same time for females to engage in behavior to select, passively or aggressively, the most “fit” mates. As birth and newborn care are incompatible with mating behavior, females also behave to separate and protect young from male harassment, and prepare them for migration when they are just weeks old. Most humpback behavior patterns, communications and interactions observed in Hawaii are likely dedicated to one or more of these objectives.

Our understanding of humpback whale reproductive behavior has developed in two decidedly separate chapters. The first began in the 1930s, but primarily occurred through the 1950s and 60s. This involved the examination of thousands of whales, harvested by the whaling industry, to investigate the condition of reproductive organs, ovaries and testes, and status of the fetus (e.g., Chittlebourough 1958, Nishiwaki 1959, Dawbin 1966). While this work provided an invaluable framework for understanding reproductive cycles, virtually nothing was revealed of the actual reproductive behavior. The second chapter began in the mid-1970s with the development of the study of living whales in their natural habitat. From close surface and underwater observations and development of sighting and behavioral histories of specific whales identified by photographs of natural markings, the first descriptions of natural behavior patterns arose. Studies of humpback whales in Hawaii have been at the forefront of this second chapter of investigation into the reproductive behavior of this species.

The sea conditions in Hawaii, including calm lees protected from trade winds combined with warm, clear water, and easy access to high densities of whales make it a remarkable location to study whale behavior. Since the first trials to study individual living whales in the 1970s, there has been a steady stream of research, photography and film, resulting in many first-descriptions, new insights and hypotheses on humpback whale behavior. Several research programs initiated in the late 1970s and 1980s such as, the Center for Whale Studies (D. Glockner-Ferrari and M. Ferrari), University of Hawaii (L. Herman and graduate students), and Hawaii Whale Research Foundation (D. Salden) have continued through the present, with remarkable longitudinal data sets and ongoing contributions. Most current studies (11 Federal Permits in 2001) are multi-year programs moving through larger research questions in stages. When combined with similar studies in such regions as New England, the West Indies, Alaska, Mexico, Japan, and eastern Australia, this work has led to an unprecedented surge in the knowledge of humpback whale behavior and almost a complete revision of our understanding of these animals in the past two decades.

The purpose of this report is to review all the available information and characterize behavior patterns of humpback whales in Hawaiian waters.

MATERIALS AND METHODS

The information synthesized here comes from three sources listed below.

Humpback Whale Studies Conducted in Hawaii

These studies make up the majority of the content of this report, taken from over 50 references listed in Appendix 1. Papers published in technical journals and books were the primary source of information, followed by unpublished reports and graduate dissertations that contained otherwise unavailable information. Conference abstracts were

used when no other source of unique information was available. Personal communications were included when offered, especially when they updated published information.

These materials were reviewed, summarized, and then synthesized in an attempt to deliver the current state of knowledge on humpback whale behavior. A large amount of information is contained in these works, with much overlap in some areas, especially in the earlier whale studies out of Hawaii (1979-85). In cases where all relevant studies essentially agreed, generalized statements are made and all of the references that provide some information or discussion on the topic are included. In cases where differences in interpretations and alternate hypotheses have developed, the arguments are discussed, and questions that remain open noted. Finally, cases are noted where initial published speculation has since been proven incorrect or misleading.

Humpback Studies in Other Regions

In addition to information from studies based in Hawaii, applicable studies from other regions are presented, many of which have addressed similar or related research questions to Hawaii. For example, Alaskan studies have provided important related information on birth rates or singing behavior (e.g., Straley et al. 1998, McSweeney et al. 1989); in the North Atlantic studies off New England and the West Indies based on long term research programs and sighting histories, and the collaborative YONAH project that pooled photo-identification and genetic data from around the Atlantic rim (e.g., Mattilla et al. 1987, Clapham et al. 1992) have greatly enhanced our understanding of humpback reproductive behavior patterns observed in Hawaii. Australian studies have focused on humpback behavior during the migration to the breeding grounds, and have provided a critical perspective on reproductive behavior patterns including song (e.g., Brown and Corkeron 1995, Noad et al. 2000).

Humpback Studies Based on Whaling Data

Prior to studies on living whales, virtually all life history parameters were constructed from the examination of reproductive organs of a large series of specimens resulting from whaling operations. This information is invaluable in the description of reproductive cycles, and for providing a physiological context for behavioral observations. Included is information from studies in the North Pacific (Nishiwaki 1959-61, Tomlin 1967), Australia (Chittleborough 1958, 1965), New Zealand (Dawbin 1966), and Africa (Mathews 1938).

This is a report on behavior, however, the fields of population biology, physiology, ecology, and the subject of human disturbance of the whales are closely linked. Separating out the subject of behavior from these realms is at times difficult and

arbitrary. In addition to a description of specific behavior patterns in Hawaii, reference is made to migrations, local movements, habitat use, and physiological cycles. Not addressed are the issues of human impacts on whale behavior.

A variety of terms to describe social groups and behavior and specific actions or postures developed along with the early studies. These terms vary to some extent between research groups within Hawaii, and between Hawaii and other regions. In Appendix 2, terms are melded from three Hawaiian studies: Darling 1983, Glockner-Ferrari and Ferrari 1985, and Gabriele 1992 (whose terms were in turn based on Bauer 1986 and Helweg 1989), and these are used in this report. Where postures or actions were correlated with gender in the earlier reports the specific source of the correlation is referenced. Social groups are defined in Table 1 and include references to significant (first or largest) data sets confirming sex composition.

Table 1. Definition, typical behavior and sex composition of humpback social units.

Term	Definition	Typical Behavior	Sex Composition	Sex Reference
Cow/calf	Mother and calf of the year	Pair stationary (apparently resting), or traveling; with calf beside or in contact with cow; often inshore of other groups; do not normally mix with other cows/calves	Female and offspring	
Cow/yearling	Mother and year old calf from previous year	More common in early season, near weaning; many similarities to cow/calf behavior but more separation between cow and yearling	Female and offspring	
Cow/calf/yearling	Mother and calf of year with yearling still present	Rare; combination of the above	Female and offspring	
Subadults	juveniles - from recently weaned yearling to 4-5 years	Alone; in pair/trio with other juveniles; in association with adult male singing or in sexual activity; and following on periphery of adult groups	Male and Female	Darling 1983, Glockner-Ferrari and Ferrari 1985
Cow/calf and escort	Mother/calf and escorting male	Common; males stays close to female; if stationary, often below; if traveling, just to one side; escort will defend position against other males with agonistic behavior	Female- Male	Darling 1983, Glockner 1983, Darling et al. 1983, Baker and Herman 1984, Mobley and Herman 1985
Singer	Adult singing humpback song	Usually alone; but at times paired with male or female, or as escort; may be stationary or traveling; generally sings for 10-15 minutes between brief surfacings; sings until interacts with other whales	Male	Winn et al. 1978, Darling 1983, Glockner-Ferrari and Ferrari 1985, Darling and Berube 2001
Joiner	Non-singing males that join singer	Approach and join a singer; singing- joining interchangeable behavior	Male	Darling 1983, Darling and Berube 2001
Lone	Lone non-singing adult	Usually traveling steadily on one direction to eventually join other whales	Usually male; rarely female	Darling 1983, Gabriele 1992
Pair	Pair of adults	At least 3 common behavior patterns; traveling side by side steadily in one direction; milling with varied interactions including probable agonistic or mating; stationary, remaining submerged, close together and motionless for 15-20+ minutes at a time	Male-male or Male-female	Darling 1983, Clapham et al. 1992, Gabriele 1992
Competitive/surface active group	Larger group (3-20) of adults - may include juveniles on the periphery	Group usually moving rapidly, often at surface and in random directions, includes social sounds; interaction predominantly aggressive behavior between males (with possible male coalitions at work), following the female; most activity by principal escort defending its position from	Multiple males and one female; later in season typically female is cow with calf (exceptional, brief instances of two females)	Darling 1983, Glockner-Ferrari and Ferrari 1985, Clapham et al. 1992

		challengers or secondary escorts		

RESULTS

General Behavior – The Hawaiian Breeding and Nursery Grounds

Definition and Boundaries

The geographic boundaries of reproductive behavior are not readily defined, as the activities occurring in Hawaii are apparently a continuum of behavior beginning in the late season feeding grounds, occurring throughout the migration, as well as in the winter assembly (Glockner and Venus 1983, McSweeney et al. 1989, Clapham and Mattila 1990, Brown and Corkeron 1995, Craig and Herman 1997).

The Hawaiian regions utilized by the whales are well documented and have been consistent from the first surveys (Wolman and Jurasz 1977, Rice and Wolman 1978) to present (Mobley et al. 1999), shown in Figure 1. The whales are distributed throughout waters around the main Hawaiian Islands with highest densities on Penguin Banks and within the Four Island Group of Maui, Molokai, Lanai and Kahoolawe, and with lesser concentrations off the Kona coast, and around Kauai.

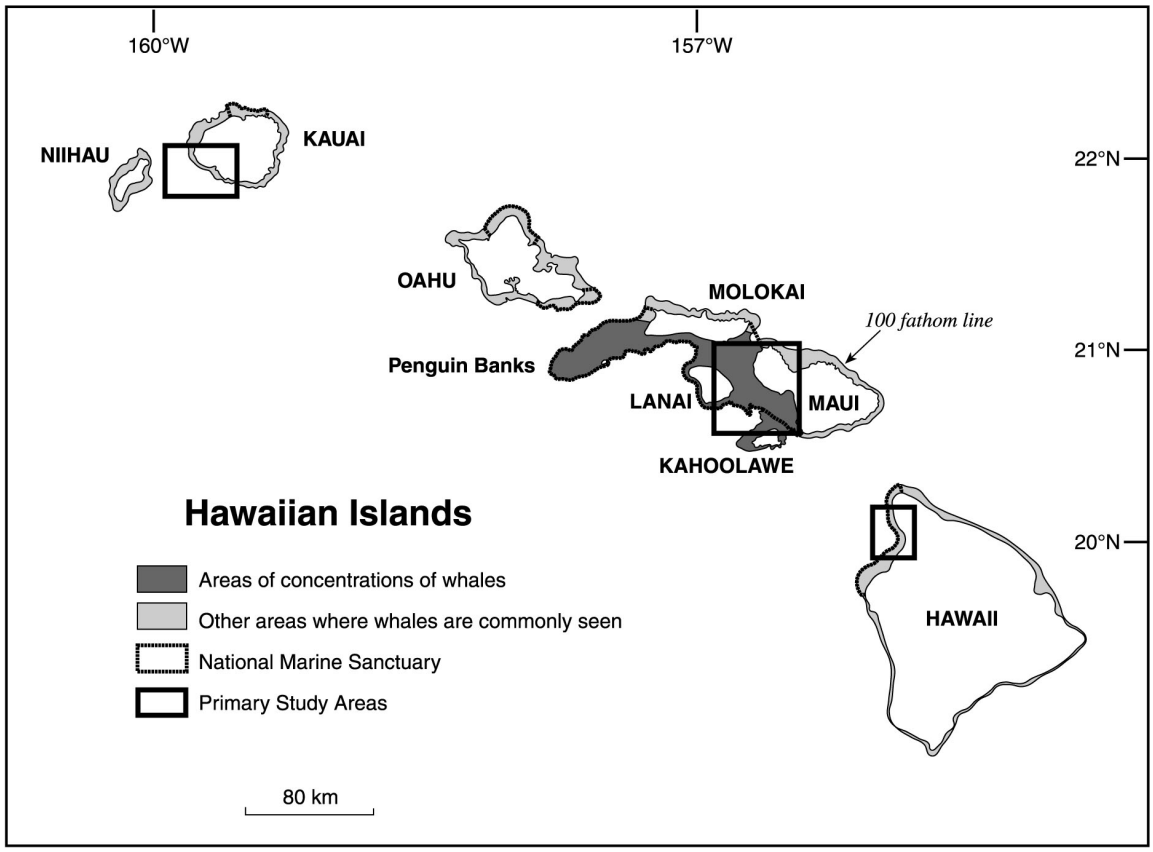

Figure 1. Hawaiian Island humpback whale distribution, primary study sites, and Hawaiian Island

Humpback Whale National Marine Sanctuary boundaries.

The highest densities of whales appear to correlate with shallow banks around or between islands. In Mobley et al.'s (1994) (cited in Frankel et al. 1995) surveys the majority of animals, 74% of all pods seen, were in waters less than 100 fathoms (182 m). However, deep inter-island channels are crossed regularly (e.g., Mate et al. 1997, Cerchio et al. 1998) and singing activity occurs in deeper waters surrounding the Hawaii banks (Frankel et al. 1995). Dive profiles indicate the humpbacks utilize the full three dimensions of the Hawaiian bank habitat, with both shallow as well as deep dives to 200 feet and apparently the ocean floor (Baird et al. 2000).

Most behavior studies have been conducted off: 1) west Maui in the Auau and Kalohi channels between Maui, Lanai and Molokai; 2) the Kona coast of Hawaii with most along the northwest Kohala coast; and 3) to a lesser degree, off the west and south shores of Kauai. These are all calm water lees from trade winds, and comprise a relatively small portion of the overall winter range (Figure 1).

Local Movements and Use Patterns

The potential circulation of all social classes of whales throughout the main Hawaiian Island chain, with animals not remaining in any one area for extended periods, appears to be the rule (e.g., Mate et al. 1997, Cerchio et al. 1998); however hypotheses of differential use of the region appear in the literature, and several questions remain open (e.g., Baker and Herman 1981, Mobley and Herman 1985, Craig and Herman 2001).

Based on northwesterly movement of highest whale densities, there was early, published speculation that whales entered the Hawaiian region at the southern end of the Big Island, and generally moved through the region southeast to northwest, eventually leaving from Kauai (Baker and Herman 1981). This was subsequently shown not to be a strict rule, with records of short-term movements of individually identified whales moving in the reverse direction from Maui to Hawaii (Darling and McSweeney 1985), Kauai to Hawaii (Cerchio et al. 1998), and satellite tagged whales moving seemingly at random throughout the islands (Mate et al. 1997).

Cerchio et al. (1998) reported 15 within one season resightings between Hawaii and Kauai with nine whales moving from Hawaii to Kauai and six moving the reverse direction, and concluded there was no directional trend between the islands. The shortest inter-island movement time was eight days. They suggested that males were significantly over represented in inter-island matches, and that animals actively engaged in courtship behaviors might be more wide ranging than others. The notion of free circulation, non-unidirectional movement around the islands was emphasized by a whale satellite-tagged by Mate et al. (1997) which, in 9.9 days, traveled at least 820 km (mean 80 km /day) through the coastal waters of five of the Hawaiian Islands: Kauai, Oahu, Molokai, Penquin Banks and the Kalohi Channel between Molokai, Maui and Lanai. These authors

also note that Kauai may be a northward migration departure point, and hence there remains some speculation that general abundance may shift northward as the season progresses (Mate et al. 1997).

The picture emerging is one of no social/behavioral boundaries within the main Hawaiian Islands, and high mobility throughout the islands by all social groups – possibly some more that others. However, speculation of differentiated use patterns of the overall area persists. Baker and Herman's (1981) suggestion of some degree of segregation between whales wintering off different islands, appears not to be the case. However, there are hints that behavior patterns and social groups may vary to some degree between some locations; these may be due to whale density differences rather than habitat or geographic preferences by specific whales (Mobley and Herman 1985, Smultea 1994, Frankel et al. 1995). Recently, Craig and Herman (2000) speculated that female distribution in Hawaiian waters may depend on reproductive status, with females more likely to be accompanied by calves off Maui than off the Hawaii. Overall, the question of whether predominant adult social groups and behavior patterns vary between locations within the main Hawaiian Islands remains open.

The clearest case of habitat preference is that cows with young calves are consistently found in shallower, more inshore waters than the majority of the population (e.g., Glockner-Ferrari and Ferrari 1985, Smultea 1994). However, attempts to define specific nursery areas or conditions have been confounded by the fact that cows with young calves are by no means confined to shallow waters or to one region within the islands. Cow/calf movement throughout the island chain occurs (Craig and Herman 1997, B. Mate pers. comm. 2001), and they are regularly sighted on Penguin Banks, some of the roughest offshore water in the area (Mobley et al. 1999, B. Mate pers. comm. 2001).

Presence and Individual Length of Stay

Humpback whales are abundant in Hawaii from mid-December through early April, with peak numbers in February and March (e.g., Herman and Antinoja 1977, Mobley et al. 1999). However, whales are regularly seen from November through May, and sightings have occurred as late as the end of June and as early as September (Glockner-Ferrari and Ferrari 1985, M. Jones pers. comm. 2001). Thus humpback whales may utilize Hawaiian waters during ten months of the year.

A figurative bell-shaped abundance curve of humpbacks in Hawaii, as shown in Figure 2, correlates with a variety of behavior studies. For example, Thompson and Friedl (1982) had song detections as early as November and as late as June which peaked between February and May. Au et al. (2000) noted the peak of singing activity was end of February to mid-March. Other studies indicate that the degree of transience in groups (Mobley and Herman 1985), amount of aggressive activity (Baker and Herman 1984) and number of competitive/mating groups (Darling 1983) all appear to have similar occurrence and peak times related directly to the density of whales in the area.

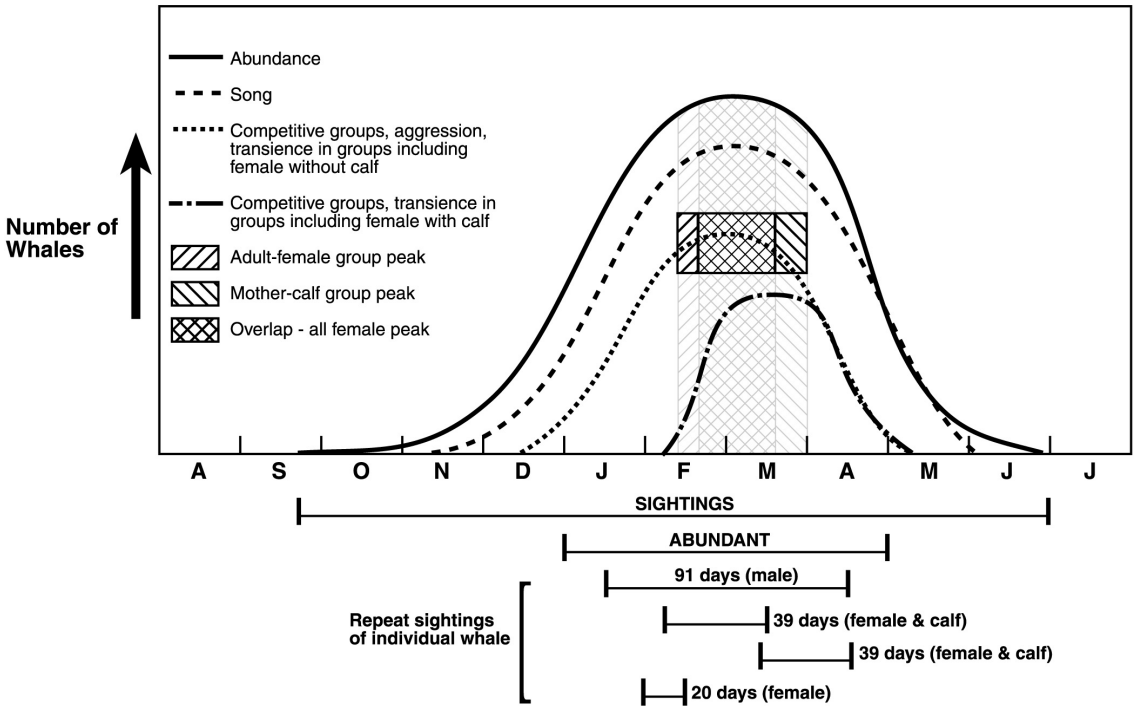

Figure 2. Timing of humpback whale social and behavioral events in Hawaii – figurative summary (after Thompson and Friedl 1982, Darling 1983, Baker and Herman 1984, Mobley and Herman 1985, Gabriele 1992, Mobley et al. 1999, Au et al. 2000).

The arrival and departure of whales in Hawaii is likely segregated to some degree by age, sex and reproductive condition. Studies based on whaled specimens indicate migratory order as follows: first in the procession are females with a yearling; followed by immature independent whales, resting females (whose ovaries and mammary glands showed no evidence of recent activity) and mature males; and finally females in late pregnancy. The departing migration is in the same order: mature females unaccompanied by calf (either newly pregnant or resting); then immature whales; mature males; and finally new mothers (Chittleborough 1958, 1965; Nishiwaki 1959, 1966; Dawbin 1966). This order appears corroborated to some extent by observations in Hawaii: juveniles are common early in the season; adult pairs (presumably male-female) without calf common in January and early February; the increase in numbers of cows with calves after February 1 and through March; and cows with newborn the last to depart (e.g., Baker and Herman 1981, Darling 1983, Glockner-Ferrari and Ferrari 1985, Mobley and Herman 1985, Gabriele 1992). At the peak of the season all age/sex/reproductive categories are present.

It is apparent that some portion of mature females do not make the entire migration each year, presumably due to high energy costs of migration and reproduction (Lockyer 1981). There is an ongoing discussion in the literature of the females "missing" from the breeding grounds, and it is generally agreed that far more males than females make the migrations (Chittleborough 1965, Dawbin 1966, Brown et al. 1995, Craig and

Herman 1997). Brown et al. (1995) noted a ratio of 2.4:1 males to females on the migration past East Australia. Craig and Herman (1997) assert that individual males undertake the migration to Hawaii more often than individual females, and suggest this is due to females taking a "resting year", and some females becoming pregnant enroute and returning to the feeding grounds. However, this question remains open as, for example, limited Alaska data on over-wintering whales does not indicate a preponderance of females (Straley 1999).

There are suggestions that most individual whales do not spend the whole season in Hawaii, and in fact are present for short periods relative to the overall humpback season. Darling (1983), from the results of a study from 1977-81 with 1,553 identifications of 922 individuals and 631 repeat sightings, reported that although whales were present over five months or more, 88 % of repeat sightings of individuals were within six weeks, and the majority two weeks. Although this is not conclusive due to the small study area in relation to the size of the Hawaiian range, it is highly suggestive. The construct is that individuals arrive, spend a period of several weeks in Hawaii then leave, just as other individuals arrive and so on.

The exception to this pattern appears to be that some males spend a significantly longer time in the region. In Darling's (1983) data all 17 whales of known sex recorded over a six week period were males. Whereas the longest reported repeat sightings of females have been: 39 days (two different cows with calves) (Darling 1983), 37 days (Mobley and Herman 1985), 48 days (Glockner and Venus 1983), and four-five weeks (Gabriele 1992), the longest repeat sightings of individual males have been 91 days (13 weeks) (Darling 1983) and eight-nine weeks (Gabriele 1992). This suggests that some males may be present from mid-Jan to mid April or essentially the entire peak season. Further, several examples suggest that some specific individuals stayed for a long period from year to year (Darling 1983). These longer term repeat sightings of males combined with a Darling and Morowitz (1984) theoretical calculation that suggests a small sub-population of whales (presumably these males) remain a longer period than average, led to speculation that these may be mature and perhaps dominant males that are maximizing mating opportunities. This has not been proven.

Reproductive Cycles

One key to humpback whale behavior patterns in Hawaii is the female reproductive cycle, particularly timing, recurrence and duration of estrus, and factors which may influence these in the short-term. Male mating strategies and behavior directly result from the distribution of estrus females in time and space, which in turn are governed by broader ecological factors (Emlen and Oring 1977). Our understanding of the humpback female reproductive cycle has developed from: 1) the examination of ovaries of a series of whaled specimens (Mathews 1938; Nishiwaki 1959, 1960, 1962; Chittleborough 1965; Dawbin 1966; Tomlin 1967); 2) birth histories of individual

females (Glockner-Ferrari and Ferrari 1985, Baker et al. 1987, Clapham and Mayo 1987, Straley et al. 1994); and 3) circumstantial evidence from male behavior patterns (e.g., Darling 1983, Baker and Herman 1984). Reproductive cycle information is summarized in Table 2, as it sets the context for much of the behavior in Hawaii.

Table 2. Reproductive cycle summary.

Age of maturity	4-6 years
Birth rate	Variable: average one calf every 2-3 years; annual birth potential
Gestation	11-11.5 months
Lactation	10 months
Timing of estrus	Peak 3-5 winter months; exceptions may occur throughout year
Timing of spermatogenesis	Peak during winter months
Recurrence of estrus	Seasonally polyestrus (if pregnancy does not result)
Duration of estrus	Unknown - one circumstantial observation of at least 6 days (Darling 1983)
Postpartum estrus	Common, but percentage of successful conceptions unclear
Operational sex ratio	2-3 males to 1 female

Sexual Maturity and Birth Rate

Most female humpback whales reach sexual maturity mean age of four-five years indicated by whaling studies (Chittleborough 1959, 1960, 1965; Nishiwaki 1959), and observations of two females of known age in the North Atlantic that attained sexual maturity at four and six years (Clapham and Mayo 1987). However, there is only limited information from the North Pacific, and early data from Alaska suggests that reproductive age may be eight or more years (Gabriele pers. comm. 2001). Thereafter, the average birth rate is every two to three years (2.38: Barlow and Clapham 1996 in North Atlantic, 2.26: Straley et al. 1994 from Alaska), however, there is significant variability in this cycle, and clear evidence of an annual birth potential (Mathews 1938, Chittleborough 1958, Darling 1983, Glockner and Venus 1983, Glockner-Ferrari and Ferrari 1985, Baker et al. 1987, Straley et al. 1994, Barlow and Clapham 1996). One of the most cited examples is a known cow that had four calves in four years and seven in 11 years (Glockner-Ferrari and Ferrari 1995). Straley et al. (1994) reports five females from Alaska that demonstrated successful annual reproduction.

Researchers have puzzled over the annual birth rate. On one hand, examination of ovaries of whaled animals suggests that only a small portion (one estimate in Chittleborough 1958: 8.5%) of females overall conceive annually, which, considering the significant energetic costs of simultaneous lactation and gestation seems logical. On the other hand, the near universal behavior of males accompanying and competing over cows with newborn calves (e.g., male escorts found in over 80% of cow calf encounters by Glockner-Ferrari and Ferrari 1985), backed up by the annual birth rate histories, strongly suggests a post-partum estrus is a common occurrence. This apparent incongruity may be explained by a significant difference between the numbers of postpartum ovulations versus successful postpartum conceptions referred to by the whaling data (Glockner-Ferrari and Ferrari 1985, Mobley and Herman 1985). Gabriele (1992) suggests that most

escorting of females with calves occurs after the other single (more reproductively promising) females leave Hawaii. Straley et al. (1994) suggests that that postpartum ovulation is a common event in female humpback whales, but that only a proportion of ovulating females can maintain pregnancies, dependent on the individual's current condition.

Timing, Recurrence and Duration of Estrus

Studies based on examination of a large series of specimens indicate humpback whales generally undergo a seasonal sexual cycle with its peak during three-five winter months (Mathews 1938; Nishiwaki 1959, 1960, 1962; Chittleborough 1965, Dawbin 1966). In the North Pacific, Nishiwaki (1959, 1960, 1962) determined the peak of ovulation occurs from the end of January to the end of February in western Pacific, Ryukyuan waters, coinciding well with the peak abundance and activity in Hawaii. To complicate this view however, some reports, also based on examination of ovaries, indicate successful pregnancies can occur well out of synchronization with the majority (Mathews 1938, Chittleborough 1954, Tomlin 1967). Tomlin (1967), by examining humpback fetuses in the North Pacific, suggested that successful mating can occur in 11 or 12 months of the year, with two apparent peaks, one in Feb-April and the other in September.

Mathews (1938) and Chittleborough (1965) conclude that females humpback are seasonally polyestrus. Mathews (1938) states that females frequently to not become pregnant at first ovulation of the sexual cycle and may experience several cycles before pregnancy occurs. Chittleborough (1965) suggests that there may be several sexual cycles terminating when conception is successful or when they migrate to feeding grounds. The duration of a particular estrus cycle is not known. Darling (1983) reports an observation of the same female leading competitive groups of males on both 1 and 6 February 1980, and this may indicate an estrus cycle extended over that time period.

The only direct insight into timing and duration of estrus for humpbacks in Hawaiian waters, and confirmation of whaling data now 40+ years old, are behavioral observations of extreme male interest in, and competition over, females. This behavior is mostly likely the result of female estrus. Darling (1983) plotted sightings of different male/female groups over five seasons, 1977-81, clumped into one-week periods represented in Figure 2. Presuming that male attention of a female in indicative, estrus occurred over at least six months from December to May, with the majority from mid-January to mid-April. A peak of multiple male (presumably single female) competitive groups without calves occurred through February and March, several weeks earlier than multiple males following females with calves, apparently undergoing postpartum estrus. Gabriele (1992) presents complimentary data, with the occurrence of male-female groups peaking 9 February to 19 March, followed by male-mother/calf groups peaking 19 February to 1 April, and notes the overlap from 19 February to 19 March when the most estrus females per male are present, with the lowest operational sex ratio. Overall this

correlates well with peak pod membership changes (Mobley and Herman 1985), aggressive encounters (Baker and Herman 1984), and singing activity (Au et al. 2000). And, as noted by Au et al. (2000), this behavioral information correlates well with peak ovulations estimated by whaling data.

Humpback social and behavioral patterns are closely linked to the female reproductive cycle. For example, with a sex ratio at birth of 50:50 (Chittleborough 1954, Glockner-Ferrari and Ferrari 1990), and if the majority of females follow a two or three year birth cycle, then there are many more sexually mature males than fertilizable females in any one season. This leads to increased competition between males (Emlen and Oring 1977, Gabriele 1992). The fact that females come into estrus over a five month (or longer) period suggests that males develop mating strategies over extended time periods, to "be there" for the next wave of females. Due to postpartum ovulation, males seek out and compete for access to estrus females with newborn calves, with potentially negative impacts on the calf (Cartwright 1999). Also, subclasses of recently weaned yearlings and juveniles less than four or five years old are likely to be engaged in different behavior patterns than the mature animals.

Mating Behavior

There remains no documented observation of humpback whale copulation in Hawaiian waters, yet the circumstantial evidence is sufficient to presume that it occurs. However, this leaves us guessing when and in which behavior pattern or social group mating actually occurs, what behavior precedes or follows, or if an individual animal mates once or many times during the season. This makes any discussion of mating behavior somewhat speculative.

Mammalian mating systems are generally divided into two broad categories: monogamous and polygamous. The former implies that a male and female form a pair bond and only mate with each other; the latter implies that individuals have multiple mating partners. Observations strongly suggest there is no permanent pair bond formed between specific male and female humpbacks, therefore monogamy is ruled out as the mating system. This contradicts Wilson's (1975) categorization of humpbacks in his overview of social organization, where he suggests they form family groups (this mistake was apparently the result of anecdotes from Slijper 1962).

There is general agreement that humpbacks, like most mammal species, are polygamous (Herman and Tavolga 1980, Baker and Herman 1984). More specifically, humpbacks are likely either polygynous, implying that a male monopolizes and mates with several females, or promiscuous where no apparent monopolizing of females occurs and both males and females mate several times with different individuals (Darling 1983; Mobley and Herman 1985; Clapham 1993, 1996; Gabriele 1992; Brown and Corkeron 1995). These suppositions are based on behavioral observations including: 1) short-term associations of males with different females (e.g., Darling 1983, Mobley and Herman

1985); 2) multiple males competing through overt fighting for access to single females (e.g., Tyack and Whitehead 1983, Baker and Herman 1984); 3) a male-biased operational sex ratio, i.e., a high ratio of sexually active males to fertilizable females (e.g., Emlen and Oring 1977, Gabriele 1992); and 4) male-male interactions involving the song (Darling 1983, Darling and Berube 2001).

The question of whether humpbacks are polygynous or promiscuous is significant and, apparently, remains open. Baker and Herman (1984) suggested they are promiscuous, with females associated serially and simultaneously with multiple males, and males associated serially with multiple females. Gabriele (1992) notes it seems doubtful that a single male could monopolize a female and prevent other males from mating with her. On the other hand, Brown and Corkeron (1995) point out that characteristically, in promiscuous systems: 1) males compete primarily through sperm competition; 2) behavior is characterized by male-male interactions that are not highly aggressive; and 3) males have relatively large testes and penises (as in gray and right whales). They note this description does not fit humpback whales, known for their striking male-male agonistic interactions around females, and relatively small testes and penises (Brownell and Ralls 1986). Thus Brown and Corkeron (1995) argue that it would seem unlikely that males would physically compete for access to a female, only to then engage in sperm competition as promiscuity suggests.

The key question to further understanding humpback behavior on the breeding ground is whether or not males attempt to monopolize females with strategies such as formations of territories, harems or dominance hierarchies common in land mammal mating systems. At this time, observations of individual behavior and mating success are not detailed enough to warrant conclusion on this question. However, several hypotheses have emerged and are summarized in Table 3.

Table 3. Mating system hypotheses.

Mating System	Characteristics	Accounts For	Problems
Dominance Polygyny	Males determine beforehand through displays and fights an order that determines which has priority access to estrus females; individuals must remember outcomes of previous encounters; relatively few dominant animals obtain most matings	Variable male-male interactions facilitated by song ranging from brief non-agonistic to agonistic; variable male competition over females; seems a functional system for estrus over 3-5 months	No conclusive documentation of dominance sorting; or proof of variable mating success; some say that male movements and impermanence of affiliations give this no time to develop or have utility (Frankel et al. 1995)
Lek Polygyny	Males assemble in mating area generally establishing display territories; offer no resources other than genes; display to females, offering opportunities for females to select mates; usually just a few males obtain most matings	Multiple males seasonally assembled; no resources other than genes; displaying through song (presumed directed at females as well as males)	No establishment of male spatial structuring, i.e., territories (although floating territories have been proposed Clapham 1996); no evidence that the song is directed at or attracts females
Male Cooperation	Males form coalitions to assist each other in obtaining matings (Note: this behavior could evolve in several different mating systems for non-dominant males)	Several observations of non-agonistic and/or apparently cooperative male unions in relation to estrus females; apparently used by other cetaceans	Rare among non-related males, hence with theoretical challenges

The hypotheses of dominance polygyny (e.g., Darling 1983, Mobley and Herman 1985, Clapham 1992, Brown and Cockeron 1995, Darling and Berube 2001) and lek formation (e.g., Herman and Tavolga 1980, Whitehead and Moore 1982, Mobley and Herman 1985, Clapham 1996, Cerchio 1996) have received about equal attention in the literature. The former predicts the development and maintenance of a male hierarchy for access to estrus females by fighting and display – potentially with the song the male-male display; the latter predicts males create territories (perhaps "floating," see Clapham 1996) and the song functions as a display to attract females to the most "fit" male. As Table 3 indicates both hypotheses account for some observations but both have detracting aspects, and neither has been tested conclusively.

A further emerging hypothesis suggests that some males may cooperate and even form coalitions to optimize mating opportunities. This idea is based on a few

observations of the apparent coordination or cooperation of some males in gaining access to a female in competitive groups in the West Indies (Clapham 1992 et al.), Australia (Brown and Corkeron 1995) and Hawaii (Darling and Berube 2001), and the speculation by the latter authors that such organization of males may be facilitated by the song. This is a substantially different view of the mating system, and may dominate discussion over the next few years.

All of these ideas remain highly speculative, and are very likely to be modified with further research. Ultimately, only genetic studies that deduce paternity and differential mating success of males will illuminate the mating system of humpback whales. Such studies are underway in the Socorro, Mexico breeding area (S. Cerchio pers. comm. 2001).

Male Behavior Patterns

Male humpbacks in Hawaii are found in lone behavior, in male-male associations and interactions, and in male-female associations and interactions. Male behavior patterns are: 1) singing; 2) interacting with singers or non-singing males – at times forming all male pairs, trios or larger groups; 3) escorting or guarding adult females; 4) defending, or challenging, the escort position with aggressive behavior; and 5) presumably mating.

Most male behavior patterns, interactions and associations are short-lived, lasting only minutes to hours, with the animals apparently orienting to any female in estrus while, reportedly, either avoiding each other (Tyack 1981,1983; Frankel et al. 1995), or involved in agonistic interactions (Tyack 1981, 1983; Tyack and Whitehead 1981; Darling 1983; Baker and Herman 1984; Mobley and Herman 1985). Male-female pairs (with or without calf) are the most stable groups lasting as much as a day or more (Darling 1983, Baker and Herman 1984, Glockner-Ferrari and Ferrari 1985, Mobley and Herman 1985, Gabriele 1992). Baker and Herman (1984) report one cow/yearling group that was escorted by the same male over two days. More recent studies have raised the possibility that some males may also form temporary non-agonistic or even cooperative unions (Clapham 1996, Brown and Cockeron 1995, Darling and Berube 2001).

Several researchers have speculated that males have two strategies to gain access to females: 1) singing to advertise to and/or attract them, and 2) fighting in competitive groups to gain access to them. It has been suggested that they alternate between these strategies (Tyack and Whitehead 1983, Frankel et al. 1995, Au et al. 2000). Although this speculation recurs in the literature, as discussed below, it is not proven and is being questioned by ongoing research.

Singing

Male humpback whales emit a complex series of loud sounds over and over known as their song (Payne and McVay 1971, Winn et al. 1973, Darling 1983, Glockner 1983, Darling and Berube 2001). Singing peaks strongly during the breeding season, but occurs during migrations to the breeding area and in late summer feeding grounds (Payne and McVay 1971, Winn and Winn 1978, Mattila et al. 1987, McSweeney et al. 1989, Clapham and Mattila 1990, Brown and Corkeron 1995, Au et al. 2000, C. Gabriele pers. comm. 2001). Singing is a ubiquitous feature of the breeding grounds, collectively introducing substantial noise into the environment (Au et al. 2000). Au et al. (2000) reports from studies off west Maui, that singing increased significantly at night, but note that Helweg and Herman (1994), recording off Kauai under different conditions and methodology, report no such diel rhythm.

Singers are most often lone adult whales, but may, in a minority of encounters, have an adult companion that is either male or female (at times with calf; that is, the escort is singing) (Darling 1983, Darling et al. 1983, Baker and Herman 1984, Glockner-Ferrari and Ferrari 1985, Frankel et al. 1995, Darling and Berube 2001). There have been a few observations of smaller, juvenile whales near a singer (Darling 1983, Glockner-Ferrari and Ferrari 1985). Singers may be stationary (or nearly so), with the tail approximately 7-15 m below the surface in a head down tail up posture as in Figure 3; or they may be traveling while singing (Tyack 1981, Darling 1983, Frankel et al. 1995, Darling and Berube 2001). It is not known at what age males begin singing, but the presumption is that it is related to sexual maturity (five to seven years). Glockner-Ferrari and Ferrari (1990) report one whale known to be ten years old that was observed singing.

Singing typically continues until the singer is either: 1) joined by other whale(s), usually a lone adult but occasionally a pair; or 2) the singer stops and swims off to join group that includes a female – either a competitive group composed of a female and several males, or cow/calf and escort thereby creating a competitive group (Tyack 1981, Darling 1983, Darling and Berube 2001). These interactions may occur after a singer has been singing for a few minutes or after many hours, this very likely dependent on density of whales and time of season. In the former case the pair most often split-up again quickly and travel in different directions, with often one or the other participant eventually beginning singing again. When a singer moves off to join a competitive group, documented as far away as 9 km distant (Tyack and Whitehead 1983), it is apparently attracted by the social sounds made in the group (Tyack 1983, Silber 1986, Mobley et al. 1988).

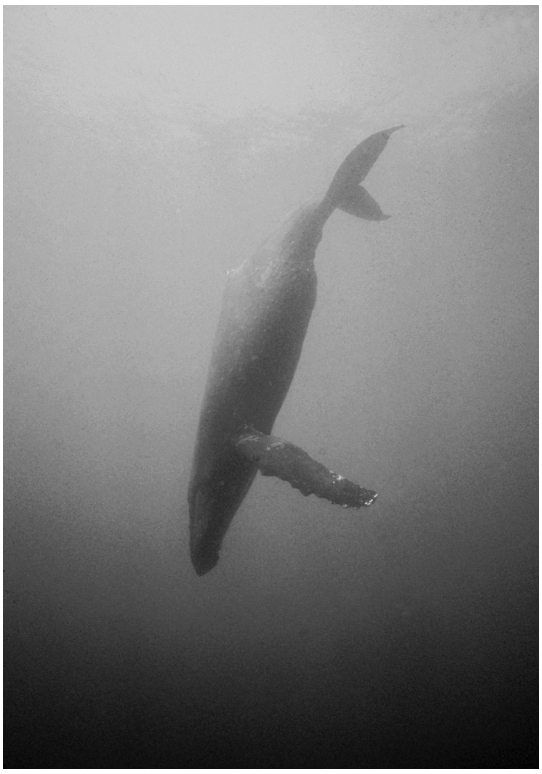

Figure 3. Singer. A common posture for a singer off Maui is motionless, head down and tail up with the fluke 7-15 m below the surface. Whales may also sing when they are traveling.

The song

The song varies from five-20 minutes in length. It has a hierarchical structure consisting of several different single sounds or "units" that compose a "phrase," which is then repeated a number of times in a "theme." Several different themes, often four to six, composed of different phrases, make up the song. The song is a continuous loop in that singers sing Themes 1, 2, 3, 4, 5, 6, then begin again at 1 and so on. The song session can continue for hours (Payne and McVay 1971). The most unique characteristic of the song is that it changes gradually in composition as it is being sung, but there is a tendency for all the whales in a population – which may range over ocean basins – to change collectively and sing essentially the same version at any one time (Winn et al. 1981, Payne et al. 1983, Payne and Guinee 1983, Cerchio et al. 2001). Humpback songs studied in Bermuda and Hawaii changed gradually, in a sense predictably, with the entire composition "turning over" in 4-5 years (Payne et al.1983, Payne and Payne 1985); but a recent study off eastern Australia showed potential for quicker change, with the whales adopting a song from western Australia in its entirety over just a two year period (Noad et al. 2000).

The function of the song has been, and continues to be, subject to much speculation. The speculation that has received the most discussion is that it is a sexual display by males to attract females and/or detract males (Winn and Winn 1978, Tyack

1981, Tyack and Whitehead 1983, Baker and Herman 1984, Helweg et al. 1992, Frankel et al. 1995 Clapham 1996, Au et al.2000). In this vein, Frankel et al. (1995) suggest the song is a male spacing mechanism. Within the idea that the song attracts females to the singer are the suggestions that it may provide some indication of fitness of the singer to the female (Chu and Harcout 1986, Chu 1988, Helweg et al. 1992), or that it attracts females in a lek mating system (Herman and Tavolga 1980, Mobley and Herman 1985, Clapham 1996). Alternatively, it has been proposed that the song is primarily a display between males, signaling status (Darling 1983), or otherwise involved in male social ordering (Darling and Berube 2001). Other proposed speculative functions of song include promoting synchrony of estrus in females (Baker and Herman 1984), a migratory beacon (Clapham and Mattila 1990), or sonar to locate females (Frazer and Mercado 2000).

Interactions with singers

Interacting with singers is a male behavior pattern. This may be the single most confusing topic in the humpback behavior literature. Substantial momentum has built up over 25 years of literature for the notion that males avoid singers, males invariably fight when in close proximity and the song serves to attract females for mating purposes (Tyack 1981, 1983; Tyack and Whitehead 1983; Baker and Herman 1984; Helweg et al. 1992; Frankel et al. 1995; Clapham 1996). Yet, there is increasing evidence that brief non-agonistic interactions between males are a common recurring pattern on the breeding grounds, and observations of females joining singers are extremely limited (Darling 1983, Brown and Corkeron 1995, Clapham 1996, Darling and Berube 2001).

The speculation that the function of the song was to attract females apparently arose in Winn and Winn (1978). Tyack (1981, 1983) concluded, with one example of a cow/calf joining a singer and playback experiments, that females joined singers, non-singers had a tendency to avoid singers, and the song signals male preparedness to fight. These views were tempered somewhat by Mobley et al. (1988) who reported playback experiments that indicated the song did not serve as an attractant for females, as measured by direct approach, although they suggest it may still serve as a basis for female choice. Helweg et al. (1992) proposed the song had two messages: for males to stay away and for females to join. Also, Frankel et al. (1995) suggest that, with 58 singers used in spatial analysis and the average distance between singers was 9.4 km, the song may serve to create and maintain distance between singers and between singers and other males. These authors also suggested that the song involves males advertizing the message to other singers to stay away, and otherwise may function as a basis for female choice.

In contrast, Darling and Berube (2001) report that lone males commonly join singers (76% or 32 of 42 observations) as illustrated in Figure 4, leading to brief interactions or longer term male groups. Of 22 lone whales that joined singers whose sex was determined, all were males. The joining or interacting male may approach slowly, circling several hundred meters away for a period of time, or may approach directly – like

a torpedo shooting under boat – and join the male singer. Singing usually, but not necessarily, stops with the joining. The interactions that occur vary from a close approach and departure with the two never surfacing together; to a brief simultaneous surfacing within a whale length from each other and splitting, to longer interactions that may include surface behavior, tail lobs, tail throws, breaches and flippering by one or both of the whales. In one in five such interactions the males did not split-up immediately and this led to pair or larger group formation (possibly related to dominance sorting or coalition formation), and in one case such a group joined a competitive group. Darling and Berube (2001) note that the wide range of behavior subsequent to joining, ranging from passive to agonistic, splitting to group formation, suggests a range of social relationships between the males. Thus, it appears the song facilitates interactions between males, the majority of which appear to be non-agonistic.

Figure 4. Singer and joiner. A singer is joined by a lone adult male. The singing usually stops when this occurs, and interaction is typically brief followed by a split. At times this interaction leads to formation of a male-male group.

Presuming all these observations are accurate, the best summary is that some males and some singers maintain distance from singers (Tyack 1981, 1983; Frankel et al. 1995), whereas others approach, join and interact with singers on regular basis (Darling and Berube 2001). This variability, or differential behavior of specific males towards each other, may be significant in terms of social organization. There remains extremely limited evidence that females are attracted to singers, but it is too early to rule out that some, as yet undiscovered, female-initiated interaction with singers occurs.

Escorting/Guarding a female

A common adult male behavior pattern on the breeding grounds is to pair with or "escort" a female; this is most readily recognized when the female has a calf, as shown in Figure 5. As many as 86% of cows with calves encountered in a season have been accompanied by an escort (Glockner-Ferrari 1985), and this is the most stable of known humpback social groups (beyond cow/calf) which may last for hours to days (Baker and Herman 1984, Mobley and Herman 1985). Stable pairs of adults, a predominant adult social group in January-February are likely often males "escorting" females without calf (Gabriele 1992). Although there was very early published speculation otherwise, there is now universal agreement that escorting is a male behavior pattern (Darling 1983, Darling et al.1983, Glockner 1983, Glockner and Venus 1983, Mobley and Herman 1985, Clapham et al. 1992).

Figure 5. Cow/calf and escort (aerial view). Females with young calves are commonly escorted by an adult male. This is one of the more stable social groups on the breeding grounds.

The escort male essentially "sticks" to the female. If the female is settled and resting, so is the escort; if traveling, the escort is usually within a whale length and within sight of the female. The escorts breathing and dive patterns generally follow those of the female. In a typical resting escort-female group where the cow is motionless, the escort will position itself just off to one side or below, also motionless. Escort males have been observed singing (Tyack 1981, Darling 1983, Darling et al. 1983, Glockner 1983, Frankel et al. 1995). A singing escort will surface in song themes it usually does not surface in, in order to follow the female, emphasizing its awareness of her location and behavior (JDD unpublished data).

Escorts are commonly joined by other male(s), whereby they become markedly agitated and this is usually followed by a variety of apparent agonistic behavior patterns. Generally the female and calf move during this male-male interaction with the escort attempting to maintain its position and, apparently, defend it against the challenger. This

interaction often melds into the typical active or competitive group described below (Tyack 1981, Tyack and Whitehead 1983, Darling et al. 1983, Baker and Herman 1984). An escort (often termed the principal escort when several males are present) may be displaced by other males; this observed both directly during competitive group interactions, and indirectly through short-term resightings of the cow and calf with different escorts. (Darling 1983, Tyack and Whitehead 1983, Baker and Herman 1984, Glockner-Ferrari and Ferrari 1985, Mobley and Herman 1985).

Several early published reports suggested the escort, then presumed female, played an allomaternal role in protecting the calf (Herman and Antinoja 1977, Herman and Tavolga 1980), however this is not the case. Even after determination that escorts were males there was speculation that they played a protective role to mother and calf. This was partially due to Chittleborough's (1953) description of a humpback escort defending a mother and calf in conflict with killer whales. Some observers interpreted the typical wariness of escorts to intruders, both whale and human alike, as protective of the cow/calf (Herman and Antinoja 1977, Glockner and Venus 1983).

Darling et al. (1983) suggested the escorts were primarily interested in mating with the female, and any defense behavior was to maintain its own position rather than protect cow and calf. Glockner and Venus (1983) agreed that a role of the escort was to mate with the female and noted one cow that had a calf four years in succession, was accompanied by an escort on each of seven sightings during the four years she was observed. Mobley and Herman (1985) suggested the escort affiliates with the cow long enough to: 1) detect if ovulating post-partum and if so remains there; 2) detect if non-ovulating and moves on; 3) detect if mated, and perhaps make an additional attempt; and 4) possibly guard against further mating, i.e., the duration of the affiliation may extend beyond courtship and mating if the male engages in post-copulatory "guarding" behavior against other males mating with the female.

Competitive/Agonistic behavior

Males clearly compete and fight with each other, most commonly over immediate access to a female (e.g., Darling 1983, Darling et al. 1983, Tyack and Whitehead 1983, Baker and Herman 1984, Glockner-Ferrari and Ferrari 1985, Clapham et al. 1992); but apparent agonistic behavior may also occur without a female present (Tyack 1981, Baker and Herman 1984, Clapham et al.1992, Darling and Berube 2001).

Displays and fights. Humpback whale agonistic behavior ranges from a variety of displays with no physical contact, to chases and blocking maneuvers, to physical contact including collisions and tail lashes or slaps to head and body resulting in bleeding wounds of head knobs, dorsal and tail (Darling 1983, Darling et al.1983, Tyack and Whitehead 1983, Baker and Herman 1984, Glockner-Ferrari and Ferrari 1985, Silber 1986). In one case in Maui a male died in one of these groups but no necropsy was performed to establish the cause of death (Pack et al. 1998).

There appear to be two general, but overlapping, types or degrees of combative behavior in these groups, with examples shown in Figure 6 and Appendix 2. There are non-contact behavior patterns including bubble-streaming; underwater blows; a posture with back arched and head above the surface (head lift); gulping air at the surface, resulting in extended throat pleats, and then releasing the air underwater; lunging and/or slapping the chin on the surface; clapping the jaws open and shut; and directing a tail lash at another animal without hitting it. These could be interpreted at displays of ferocity and/or preparedness to fight. These behavior patterns meld into blocking and chasing, which in turn lead to physical contact. All can occur at the same time in one group. Contact includes fierce collisions; tail lashes, including beating another animal's head with the tail; and rear body throws. These are violent, aggressive interactions (Darling 1983, Tyack and Whitehead 1983, Baker and Herman 1984, Silber 1986).

Figure 6. Examples of male agonistic displays. From left to right: 1) bubblestream - whale releases long streams of bubbles from its blowhole; 2) head lift - whale arches its back and swims with head out of the water, often gulping air and expanding throat; 3) rear body throw - whale throws its rear body out of the water (photos. J. Darling).

The whale's weapons are the tail, the whole body, and possibly the head. In one observation a whale turned head down and hit another whale on the tail stock with its head knobs. Fresh blood was noticed on the tail stock of the recipient. The combatants received apparently minor wounds consisting of bloody head knobs, dorsals and tail stocks. Some of the scars and scratches which are abundant on some whales, particularly males, may result from these encounters (Darling 1983, Baker and Herman 1984).

Competition for females. Competitive or "surface active" groups are the most striking of humpback behavior patterns on the breeding grounds, characterized by fast traveling whales and high-energy surface activity. These are composed of multiple males (two to 20), apparently competing for access to a female presumably in estrus, as shown in Figure 7 (Darling 1983, Darling et al. 1983, Tyack and Whitehead 1983, Baker and Herman 1984, Glockner-Ferrari and Ferrari 1985, Clapham et al.1992). It is not known if mating occurs in these groups, but seems a possibility as extended penises, and close rolling and contact have been observed (Darling 1983). On the other hand the movement of these groups is very fast, leading some to doubt mating can occur (C. Gabriele pers. comm. 2001).

Figure 7. Competitive group. Group of males following and competing for access to the single female (with calf).

Competitive groups are typically composed of a female (with or without calf), termed the nuclear animal by some authors, usually in the lead but at times in the center of multiple males (Darling 1983, Tyack and Whitehead 1983, Baker and Herman 1984, Clapham et al. 1992). There are several reported cases of two females present with multiple males but these appear to be exceptional (Glockner-Ferrari and Ferrari 1985, Clapham et al. 1992). The nearest whale to the female, the principal escort, is invariably the most agitated and active, clearly defending its position with bubble streams, high speed chases and blocks of incoming whales (Darling 1983, Tyack and Whitehead 1983, Baker and Herman 1984, Silber 1986). These groups are characterized by bursts of speed and changes in direction as the other whales, termed secondary escorts or challengers, apparently attempt to outmaneuver the principal escort, presumably to gain access to the female. Most of the interaction occurs with the principal escort and one or two of the challengers, with other animals following along on the periphery and apparently less involved. Tyack and Whitehead (1983) reported that occasionally the secondary escorts replaced the principal escorts but most often just left the group.

There is often a flow to the formation and dissolution of these groups. They begin with a male-female pair (calf may or may not be present) joined by one or more other males, with an ensuing chase and competition; this group moving rapidly about the area "picking up" additional males and losing males in the process (Darling 1983, Darling et al. 1983, Tyack and Whitehead 1983, Baker and Herman 1984, Glockner-Ferrrari and Ferrari 1985, Mobley and Herman 1985, Silber 1986). The activity level in the group ranges from great speed, 10+ knots, and exuberant lunges, blocks, charges, tail lashes to a slow quiet traveling of the group in an apparently stable formation (Darling 1983, Tyack and Whitehead 1983, Silber 1986, Clapham et al. 1992). A tentative conclusion is that there is a stable formation or arrangement of whales in these groups; it is only when an animal changes position, apparently coming closer to the female, that the activity increases (Darling 1983, Silber 1986). After a period of time ranging from minutes to many hours, the group breaks up, leaving a pair or pair with calf which may or may not include the same escort male. A study in the West Indies reported displacements of

principal escorts by other whales on average every 7.5 hours, and in seven of 10 instances the displaced escort left the group (Tyack and Whitehead 1983). Glockner-Ferrari and Ferrari (1985) reported that the occurrence of active groups leads to pair formation and, they speculated, eventually to mating.

Several investigators have suggested that levels of surface and agonistic activity are proportional to group size; the larger the group the more activity (Herman 1978, Tyack 1982, Tyack and Whitehead 1983). In contrast, Silber (1986) noted that surface activity rate and activity rate per individual was negatively correlated with group size, suggesting that a single whale was responsible for most of the displays as it threatened or clashed with other males, in an apparent attempt to preclude them from approaching the female. The majority of such activity was attributed to the principal escort.

Social sounds. A feature of larger, active, competitive groups are a wide range of loud, energetic, underwater vocalizations referred to as "social sounds" (Tyack 1983, Glockner-Ferrari and Ferrari 1985, Silber 1986, Mobley et al. 1988). Male humpbacks frequently interrupt such activities such as singing, and rapidly travel distances up to 9 km to join competitive groups (e.g., Tyack and Whitehead 1983, Silber 1986). Playback experiments indicate that the social sounds produced in these groups are the signal that elicits this behavior (Tyack 1983, Mobley et al. 1988).

Silber (1986) found that social sounds occurred almost exclusively in groups containing three or more whales and were rarely heard near single whales, pairs, or cow/calf groups. Group size changed frequently and a dramatic increase in vocalization rate resulted when a new whale entered a group. The vocalization rate was positively correlated with group size, suggesting that each group member contributed to overall sound production. Overlapping sounds, from two or more whales vocalizing simultaneously, were heard often leading to speculation that competing males emitted acoustic threats concurrently (Silber 1986).

Silber (1986) noted that some large groups exhibited very few vocalizations and little surface activity, and proposed that perhaps a temporary social dominance among males had been established and number of threats were reduced. The introduction of new whales may have upset a balance of social roles which resulted in an increase in the number of vocalizations. Silber (1986) further speculated that social sounds act to demonstrate aggression or agitation as adult males compete for temporary social dominance within the group, and proximity to the female.

All male group agonistic behavior. Agonistic behavior may also occur between groups of two or more males without a female present (Tyack 1981, Darling 1983, Baker and Herman 1984, Clapham et al. 1992, Darling and Berube 2001). This aspect of male interaction is far less clear than when in direct competition for a female. To date, observations involving just two males are generally in context of a singer and a male

which joins it (Darling and Berube, 2001). As discussed above, there is a range of behavior that occurs with this interaction, but the majority (22 of 26 interactions in Darling and Berube 2001) were non-antagonistic. In the other four cases, these authors reported higher energy behavior that included tail lobs, tail throws, breaching and flippering by either singer or joiner that could be agonistic in nature but did not develop into fights. Tyack (1981) recounts an apparently clear agonistic interaction between a singer and a joiner. Clapham et al. (1992) notes the all male groups they described in the West Indies could be due to residual aggression following the departure of a female, but adds this seems unlikely as most of the groups remained active for extended periods. These observations have led to speculation that dominance determination and maintenance may be occurring, a seeming necessity of the hypothesized dominance polygyny mating system, and reminiscent of land mammals with similar mating behavior (Darling 1983, Clapham et al. 1992, Darling and Berube 2001). However, the ongoing male relationships theoretically necessary for this type of behavior have not been elucidated (Frankel et al. 1995); our understanding of this behavior is very limited, and caution in interpretation is appropriate at this stage.

Cooperative male behavior

The most striking male-male patterns on the breeding grounds are of threats and competition (e.g., Tyack and Whitehead 1983, Baker and Herman 1984) combined with reports of male avoidance and spacing (Tyack 1981, 1983; Frankel et al.1995). In contrast, several observations suggest the potential for coordinated or cooperative behavior among some males, with possible formation of male coalitions to secure access to a female. Clapham et al. (1992) introduced this idea after observations of mutually non-antagonistic pairings between males in competitive groups involving a female in the West Indies, and Brown and Corkeron (1995) supported the notion with the observation in Australia of a male pair that moved between competitive groups engaged in agonistic displays with other animals, but not each other. Darling and Berube (2001) report an observation of males banding together around a singer before joining a competitive group, and speculated the song may facilitate this association. Much earlier, although not emphasized in their paper, Tyack and Whitehead (1983) noted examples of male pairs working as a non-agonistic unit in competitive groups in the West Indies. The working idea is that if less dominant animals join competitive groups together rather than alone, the odds of one of them outmaneuvering dominant males, and subsequently mating, may increase (Clapham et al. 1992, Brown and Corkeron 1995). To date the observations are limited and details of this behavior are not known.

Pack et al. (1998) describe the death of an adult male in a competitive group, including the prolonged post death association and contact by another adult male with the dead animal. One of the possible explanations offered was that this was a form of helping or epimeletic, altruistic-type behavior. This concept may fit with some form of extended association between individual males. Other hints of extended associations of adult whales (sexes unknown but likely males as no such associations of females have been

reported) within Hawaiian waters are given by Cerchio et al. (1998). These observations raise the possibility of a complexity in male interactions and behavior beyond initial descriptions, and if proven, may require re-interpretation of some observations.

Female Behavior Patterns

Female behavior patterns in Hawaii fall into two separate, and quite mutually exclusive, realms: 1) mating, and 2) birth and newborn care. For the majority of females on a two or three year birth cycle it is one or the other activity in any one year. Females that come to Hawaii are either late-lactating (with yearling), resting (neither pregnant or lactating), or late pregnant (Dawbin 1966, Gabriele 1992). For the first two categories of females the primary objective is presumably to mate, then return to feeding grounds. For the last category the objective is birth, protection of newborn, and preparation of the calf for return to the feeding grounds. As discussed above there is generally a substantial timing difference between the females: those there to mate are among the first to arrive and first to leave; those pregnant and birthing are the last to arrive and the last to leave. This translates into significant differences in time spent on feeding grounds: pregnant cows, 6.5 months; lactating cows, 4.5 months (Gabriele 1992). Female behavior varies dramatically with their objectives. On one hand selection of a mate may involve maximizing contact with males; whereas birth and newborn care involve minimizing contact with males (Gabriele 1992, Smultea 1994). As discussed earlier, an unknown portion of individual females undergo post-partum ovulation with mating activity occurring shortly after birth. For females that both give birth and mate a mid-season change in behavior must occur, but it is currently unclear if this is initiated by the female as a reproductive strategy, or simply the result of harassment by males.

Female mating strategies

Knowledge of humpback whale female mating strategies and behavior is very limited; in fact it may be the least known aspect of humpback whale behavior. Theoretically, just as males behave to maximize number of matings, females employ strategies to maximize their reproductive success (Emlen and Oring 1977). Gabriele (1992) suggests two potential female strategies: 1) accomplish mating while spending the least amount of time fasting on the breeding grounds for overall energetic considerations, and 2) when on breeding grounds maximize the number of males and minimize the number of females encountered. She notes that although overt physical competition for matings is apparently absent between female humpbacks, the mere presence of other estrus females during their own limited estrus constitutes competition for male attention.

Female associations on the breeding grounds are extremely rare (Baker 1985) and cows with calves at least generally appear to show active avoidance of each other (Herman and Antinoja 1977, Tyack 1981, Darling 1983, Glockner 1983, Tyack and Whitehead 1983, Baker and Herman 1984, Baker 1985, R. Cartwright pers.comm. 2001).

Tyack and Whitehead (1983) note that only twice was more than one cow with calf observed in any group at one time: once on Silver Bank two calves were seen together during the apparent accidental merging of two groups, which happened to be in same place at same time, but soon diverged; and once in Hawaii two calves were seen in a group of seven whales that was stable over an hour (no further details given). Darling (1983) reported one observation in Hawaii of two competitive groups each including a cow with calf that ran into each but soon separated. Between 1999-2001 off Maui, R. Cartwright (pers. comm. 2001) observed three incidences of short-duration multiple cow/calf groups, the longest interaction lasting 23 minutes. Glockner-Ferrari and Ferrari (1985) report one competitive group with two females, but felt one was a sub-adult. Clapham et al. (1992) in studies of the West Indies note only one case where a second female briefly joined and left a group that already contained a female. In Mobley et al.'s (1988) playback experiments, although the broadcast of feeding sounds (thought to be made by females) attracted the most whales, no female with calf ever approached them.

Female adult humpbacks in Hawaii are found alone with a calf (non-mating situation), in pairs with an adult male, and in larger competitive/active groups with multiple males. Females both without and with calf are found in these latter groups, although calf presence increases later in the season (Darling 1983, Gabriele 1992). Female mating behavior patterns include: 1) acceptance of a single male escort; 2) leading (or being chased by) groups of multiple competitive males; and 3) presumably mating. A proposed female behavior pattern, entirely speculative but commonly implied in the literature, is choice of males by their song. Lone adult females have been documented, but are a rare occurrence on the breeding grounds (Darling 1983, Gabriele 1992).

As mating has not been observed, it is a presumption that females identified in pairs and multiple male groups are involved in mating behavior. The following interactions have been observed within pairs or larger groups of adults suggesting mating or attempts at it: 1) females were followed or chased by males; 2) excited rolling and flippering in close proximity or contact with other whales; 3) female tail arching, or contorting of the tail stock into a "S" shape occurred suggesting presentation of the genital area; 4) "nosing" of female genital area by males, possibly checking reproductive condition; and 5) females rolling away from males, or extending the tail out of the water, apparently to put the genital area above the surface, suggesting avoidance actions (Darling 1983).

There are a number of examples of females observed with single or multiple male groups during one winter, re-identified with calf the following winter. Table 4 provides several of these examples from the literature. These observations, combined with the understood gestation period of 11-12 months (e.g., Chittleborough 1965), suggest the possibility that mating occurred in the pair or multiple male group.

Table 4. Behavior of females the year previous to giving birth

Darling (1983)	Eight examples of females identified as one of a pair of adults or in large groups of adults in the years they were not identified with a calf. In two cases the animal accompanying a female in a pair was a known male. Also, two cows which gave birth in consecutive years were accompanied by either a single escort or multiple males in the year before the consecutive birth.
Glockner-Ferrari and Ferrari (1985)	A whale that had a calf four years in succession was accompanied by an escort on each of the seven sightings during the four years it was observed.
Gabriele (1992)	In 13 of 16 cases where females identified with a calf had also been seen the previous season their behavioral characteristics were: typical pod size = 2; the other individual was very likely a male; and typical pod behavior was breathing and diving only.
Specific Examples (from Darling 1983)	
A. Examples of behavior patterns of a pair which included a female which gave birth the following year	E.g. 1. Cow #13 was identified on 3 March 1980 in a pair, and in the following season with a calf. The other member of the pair on this date was not sexed, but was seen in a group of five to seven adults earlier in the day suggesting it was far more likely a male than a female. This pair was milling with significant surface activity including flippering, breaching, rolling belly up, and one animal swimming upside down close to the surface just prior to blowing. The behavior patterns were not correlated with a specific animal. E.g. 2. Cow #17 was identified twice in a pair, 30 January and 18 February 1980, the year before it was seen with a calf. The partner on each occasion was different. On 30 January it was a known male. The only behavior noted was that the male lifted its head above the water when it was swimming beside the female. The male had a raw, bloody area on its peduncle, probably the result of an aggressive interaction between it an other males over access to the female.
B. Examples of behavior in a larger group which included a female that gave birth the following year	E.g. 1. Cow #15 was identified in a group of 4+ adults the year before it was identified with a calf. The behavior of this group included flippering and rolling, along with a variety of apparently aggressive interactions including head lifts, chin slaps, jaw claps, tail lashes and bubble streams. Specific behavior patterns were not correlated with individuals. E.g. 2. Cow #18 was identified in large groups on 1 and 6 February 1980, the year before it was found with a calf. On 1 February it was first seen with a group of 4+ adults and later in a group of 8+ adults (probably the same core group with additional animals). The behavior patterns noted were flippering, head lifts, jaw claps, tail lobs and underwater blows. This example also indicates that a female may be close enough to estrus over a period of six days to attract males.

Pair - Female with male

Pairs of adult humpbacks are a common social group in Hawaii and other winter assembly areas. Studies have shown these may be either a female and male (as is functionally the case in cow/calf and escort groups) or two males (Darling 1983, Clapham et al.1992, Darling and Berube 2001). Female-male pairs are relatively (in comparison to larger groups or male pairs) stable, often maintaining a calm, exclusive union for hours to a day or longer (Darling 1983, Baker and Herman 1984, Glockner-Ferrari and Ferrari 1985, Mobley and Herman 1985, Gabriele 1992). Instances of conclusive sexing of both individuals when a calf is not involved, combined with extended behavioral observations, are limited, however general patterns that are likely female-male follow.

Female-male pairs have been observed traveling, however, the most common behavior pattern has been of the pair stationary as shown in Figure 8, making near-synchronized long dives of 20-30 minutes or more (Darling 1983, Gabriele 1992). These long dives separated only by three to four blows at the surface have caused this behavior to be referred to by some researchers as "breathholding" and the whales as "breathholders" (e.g., Darling 1983). Underwater observations indicated that these pairs dive to approximately 50-100 ft, and stop, remaining virtually motionless. Often one whale was in a more horizontal position, and the other a more vertical, head down, position. Beyond this, there was notably little overt or obvious interaction or activity between the whales (Gabriele 1992, Darling unpublished notes). In a few observations one of the whales was singing (Darling, unpublished notes). Gabriele (1992) noted that breaching, flipper slapping, head lunging, underwater blows and fluke slaps occurred in these groups, but infrequently. The behavior is markedly similar, and likely identical, to an escort with cow and calf – minus the calf. These pairs tend to persist until another adult (male) joins, potentially leading to formation of a larger competitive group, and may result after a larger group has broken up (Glockner-Ferrari and Ferrari 1985). The development or instigation of these pairs is not understood, but apparently they are mutually acceptable as there is no obvious escape behavior. The most likely explanation is of a female approaching estrus and accepting the male attention, or alternatively, having mated, allowing a guard against unwanted attention (Mobley and Herman 1985).

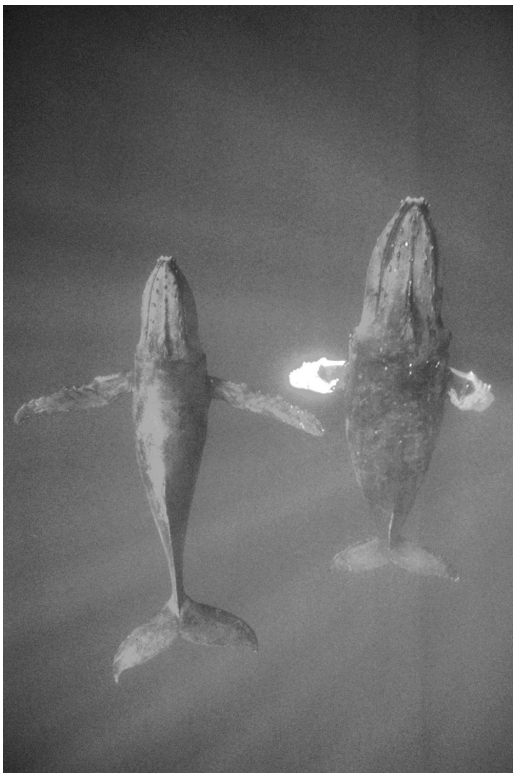

Figure 8. Female-male pair. Often the pair of adults lie motionless approximately 5-15 m below the surface for periods of 15-30 minutes or longer. They usually surface together for three to four blows, then immediately return to this sub-surface position. This is presumed to be primarily a female-male pair behavior, but sex determination data is limited. These are commonly referred to as " breathholders."

Females in competitive groups

During the breeding season an adult female (with or without calf) is, with few exceptions, the center or focus of competitive groups of two to 20 or more males, with all the attendant competitive and aggressive activity described above (Darling 1983, Darling et al. 1983, Tyack and Whitehead 1983, Baker and Herman 1984, Glockner-Ferrari and Ferrari 1985, Clapham et al. 1992).

It is likely that the competitive groups are ultimately a test of male fitness, with the most "fit" gaining access to the female. Following this presumption is the speculation that the female, by moving rapidly in front of the group and leading it over substantial distances: 1) avoids unwanted matings, and/or 2) attracts as many males as possible thereby increasing the level of competition in the group and ultimately gaining a more fit mate (Tyack and Whitehead 1983).

As noted above, there is consistent evidence that singers may stop singing and join competitive groups as they move within range, and that social sounds made in these groups are the signal that attracts the incoming males (Tyack 1981, Darling 1983, Tyack and Whitehead 1983, Baker and Herman 1984, Glockner-Ferrari and Ferrari 1985,

Mobley and Herman 1985, Silber 1986, Mobley et al. 1988, Darling and Berube 2001). If females were trying to attract males it would seem to make sense for them to be making the social sounds. However, currently there is no evidence that females make sounds in these groups, and observations suggest it is primarily, if not solely males, doing so (Silber 1986). This raises several questions, including whether or not the purpose of females leading these groups is really to attract additional males as speculated.

Female humpback whales have appeared to influence selection of mates in several other ways, such as avoiding unwanted mating by moving genital region from the water (Darling 1983), or behaving aggressively towards a sub-adult male (Clapham et al. 1992). Glockner-Ferrari and Ferrari (1985) report seven occasions where the female led males to shoreline or to vessels, resulting in change of escort or retreat of males; Mattila et al. (1988) suggests females lead groups into areas with many coral heads in the Silver Banks with the same objective. Baker and Herman (1984) report that fluke slaps, inverted fluke slaps, flipper slaps, and breaches were most commonly associated with the behavior of the lead animal in competitive groups and suggest these are a response of the female to the aggression and advances of the competitors.

Females choosing males via song?

There has been substantial speculation that females exercise choice of mates though listening to their song (e.g., Winn and Winn 1978, Tyack 1981, Herman and Mobley 1985, Chu 1986, Chu and Harcourt 1988, Helweg et al. 1992, Frankel et al. 1995), and such female choice may be the driving force behind song change (Tyack 1981). However, there is no evidence for this, and only very limited data suggests females may actively join singers.

Two studies have reported, collectively, three instances of known females joining singers (Tyack 1981, Medrano et al. 1994). Tyack (1981) gives one example of a female with calf that joined a singer, and Medrano et al. (1994) report two observations of females joining singers. One of these involved a cow and calf that joined a singer, and the other a pair of adults that approached a singer, one of which, later genetically determined to be a female, joined it. In addition, there have been several cases where females approached the experimental playback of songs, although as noted by Mobley et al. (1988), these were the exception. These observations have subsequently been discussed widely (e.g., Baker and Herman 1984, Mobley et al. 1988, Frankel et al. 1995, Clapham 1996, Au et al. 2000) in the context of the song as advertisement to females. As mentioned above, some researchers have speculated that males have two alternative strategies for gaining access to females: 1) singing and 2) joining a larger competitive group (e.g., Tyack and Whitehead 1983, Frankel et al. 1995, Helweg et al. 1992, Au et al. 2000). From a female perspective this suggests they may select males through song or by encouraging aggressive contests.

Selection of males by females via the song may be the best known unproven hypothesis regarding the breeding behavior of humpbacks. Considering the evidence building that the song is primarily a signal between males (Darling and Berube 2001), the failure of song playback experiments to regularly attract females (Mobley et al.1988), and very few actual observations of females joining singers, some clear behavioral evidence that female choice of singers actually occurs is needed to retain a "female attraction" hypothesis. This is a significant issue in terms of characterization of humpback behavior in Hawaii – both male and female.

In acknowledgment of the lack of evidence that song attracts females, several researchers have proposed that the response of females need not be an approach to the singer, but instead an "invitation" for the male to approach her (Helweg et al. 1992). Mobely et al. (1988) suggest a female may indicate her preference for a particular singer and hence a particular song by whether she allows the pursuing singer to join her, or perhaps a return vocalization (that has not been heard or listened for). They suggest then that although the song may not serve to bring females directly to singer, it may still serve as a basis for female selection. Another suggestion is that the song may simply allow females to locate and evaluate singers, and females may lead a competitive group toward the loudest deepest song she hears, inviting the singer to compete (C. Gabriele pers. comm. 2001).

Birth and Young

The context for behavior patterns of late pregnant or recent postpartum females is maintenance of circumstances that are optimal for rest, nursing and protection of young, including avoidance of sexually active males. Females with young, as shown in Figure 9, may separate themselves from mating activity spatially, utilizing inshore shallow areas (e.g., Smultea 1994, Mobley et al. 1995), and perhaps temporally, seeking this refuge when courting or aggression increases, daily or seasonally (Smultea 1994). Also, there is speculation that some births occur prior to the peak of the mating season, and postpartum ovulation occurs some weeks after birth, further providing some degree of space between birth and mating activities (Glockner and Venus 1983, Mobley and Herman 1985, Glockner-Ferrari and Ferrari 1990).

Figure 9. Cow with young calf. Cows with newborn young are commonly sighted through the winter often in shallower or more inshore waters than the adult population.

In a study of habitat use on the Kona coast of Hawaii, Smultea (1994) concluded that humpback groups containing a calf occurred in significantly more shallow water and nearer to shore than did groups without a calf during afternoon hours and, late in the season, throughout the day, apparently coinciding with increased male activity. She concluded that adults without a calf may use deep water to facilitate breeding behavior while maternal females may use shallower water to avoid harassment and injury to calves from sexually active males, turbulent offshore conditions or predators. This is consistent with other observations of humpbacks (e.g., Whitehead and Moore 1982, Glockner-Ferrari and Ferrari 1985), as well as gray and right whales (Jones and Swartz 1984, Payne 1986). It is thought that conspecific encounters could result in premature social interactions with the calf, increased energy expenditure, interruption of nursing bouts, mistaken imprinting or nursing attempts, potential separation of calves from cows and even injury to calves (Jones and Swartz 1984, Thomas and Taber 1984, Smultea 1994).

Little is known of the impact of predation on the behavior of humpback whales in Hawaii. Potential predators in the area include false killer whales (*Pseudorca crassidens*) pygmy killer whales (*Feresa attenuata*), killer whales (*Orcinus orca*) and sharks, particularly tiger sharks (*Galeocerdo cuvier*). Killer whales are rarely seen in Hawaiian waters, however they are certainly a predator in cooler seas (Chittleborough 1953, Steiger and Calambokidis 1995). Predation by false and pygmy killer whales could well be a factor in behavior, especially considering an anecdote by a fisherman of false killer whales attacking a calf off the island of Hawaii (Darling 1990 p.52). Whether this is a rare or common occurrence is unknown. Tiger sharks are clearly a significant predator in the Hawaiian breeding area, with observations of them following apparently sick calves (F. Nicklin pers. comm., 2000), and attacking living but entangled adults (M. Jones pers. comm. 2001). However, whether they actively pursue healthy calves is not known. There

are suggestions that shallow water may confound echolocation abilities of odontocetes, and otherwise minimize the vulnerability of calves from below (Wursig and Wursig 1980; Thomas and Taber 1984).

Birth

A most striking non-observation in Hawaii is a birth. During tens of thousands of observation hours through the whale watching industry, as well as multiple researchers present over 25 years, a birth has not been documented. This may reflect just how critical separation of birth from activity in the region is. This separation may be accomplished seasonally (before Hawaii), spatially (simply away from all activity), or perhaps by occurring nocturnally.

At the same time there is little question that birth occurs during the winter season. Extensive examination of dead whales indicate peak ovulation (with gestation of 11-12 months), term fetuses and birth coincide with winter months (e.g., Chittleborough 1958, Nishiwaki 1959). Direct evidence from Hawaii includes observations of: 1) tiny calves with folded dorsal fins and crease marks clearly within days if not hours of birth (e.g., Darling 1983, Glockner-Ferrari and Ferrari 1985, Cartwright 1999); 2) on 11 January 1994 a humpback placenta was found within 15 minutes of a young calf appearing with a female (Silvers and Salden 1997); and 3) one sighting of a female without calf on 31 January 1981 and with a calf on 16 February 1981, 17 days later, apparently indicated a birth occurred (Darling 1983).

Newborn behavior

The earliest published record of a cow with young calf in Hawaii is 24 December (Craig and Herman 1997), however whale-watch sightings of newborn calves are reported prior to that date (M. Jones pers. comm. 2001). Past studies suggested cows with newborn were relatively rare through January (e.g., two pairs in five seasons, Darling 1983) until early February (Baker and Herman 1984, Glockner-Ferrari and Ferrari 1985), but there is little current information on cow/calf abundance in the early winter season. After 1 February the numbers of cows with calves increase markedly. They are commonly sighted, and are the last groups present in late May and June (Glockner-Ferrari and Ferrari 1985, Gabriele 1992). Although density of cow/calf pairs can be high in mid-season, they generally maintain an active separation from each other.

Cows with newborns apparently travel and circulate though the island chain as do other social groups. Day to day resights of specific cows with calves in one location are not common (Darling 1983, Glockner-Ferrari and Ferrari 1985, Craig and Herman 1997). Mate et al. (1997) satellite-tagged a cow with calf that soon after began the northward migration traveling 150 km per day. In subsequent tagging of cows earlier in the season he found extensive movement between at least the Maui and Penguin Banks regions (B.

Mate pers. comm. 2001). The purpose, or cause, of this steady movement is not known; perhaps it is part of the swimming regimen preparing the calf for migration, or possibly the result of the cow being pursued or harassed by males. Cartwright (1999) found that travel was by far the most common activity of cows with calves occurring 55% of observation time, and increasing with single or multiple escorts. Rest was the next most common activity, occurring in 12% of observation time.

A commonly observed cow/calf behavior pattern is resting. As described by Glockner-Ferrari and Ferrari (1985), the cow lies in a horizontal position at a depth ranging from approximately 10-20 m below the surface. The calf usually positions itself above the mother's head or directly below the chin as in Figure 10. The calf rises slowly to the surface by itself every two to six minutes to blow three or four times while swimming in circular pattern (Glockner and Venus 1983). The calf then descends to its mother (which may surface every 10-20 minutes). Often the calf will twirl its body and swim upside down. Physical contact frequently occurs between the mother and calf.

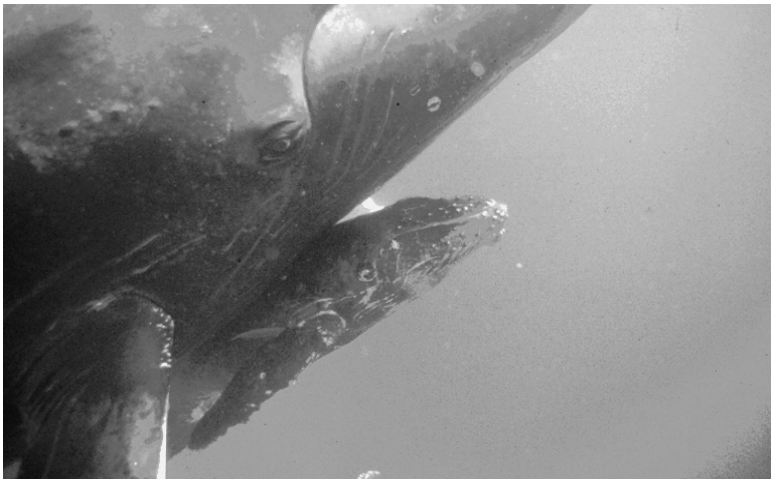

Figure 10. Cow with young calf resting. A typical resting position is with the calf under the cow's head, often in contact with its mother.

The calves nurse throughout their first winter, the process of weaning beginning between six and 10 months of age (Clapham 1996), and culminating in separation after the first feeding season. Glockner-Ferrari and Ferrari (1985) describe suckling occurring while the cow was lying stationary in a horizontal position at a depth of 30-50 ft. The calf positioned itself below the cow at approximately 30 degree angle to the midline of her body, the tip of its mouth touching her mammary slit. In one case they observed the calf's jaws opening and closing. After the calf stopped suckling the cow and calf slowly moved on. On another occasion they observed suckling while the animals were traveling (Glockner-Ferrari and Ferrari 1985).

Play by the calf, perhaps in the form of mimicry, seems an important element of newborn behavior in Hawaii. Glockner-Ferrari and Ferrari (1985) note that on many occasions they observed the calves imitate the behavior of their mothers by repeating the behavior immediately after the mother has performed it, including breaching, tail throwing, tail slapping, and flippering. In 1983 these authors observed calves imitate the behavior of the escort, performing head lunging, throat expansion, chin slapping and bubble streaming. Cartwright (1999) describes calf surface behaviors, including flippering, spyhops (head rise), twirling (roll), tail slaps (lob), tail swishes (lash), peduncle (tail) throws, head lunges, full breaches and half breaches (belly flop), all activities seen in adults (terms in parentheses are those given in Appendix 2).

Although generally not vocal, at least compared to singers or competitive groups, calves do occasionally produce sounds, with at least a single grunt type vocalization (Glockner-Ferrari and Ferrari 1985, F. Nicklin pers. comm. 2000). Glockner-Ferrari and Ferrari (1985) note one occasion when they heard loud continuous vocalizations but were unable to determine if sounds were being emitted by the calf, mother or both.

Acceptance of escort by cow with calf

As described previously the cow/calf and escort trio, as illustrated in Figure 11, is a commonly observed social group in Hawaiian waters and has a relatively high level of stability versus other groups (Glockner-Ferrari and Ferrari 1985, Mobley and Herman 1985). The behavior of mothers and calves is often influenced by the presence and behavior of the escort, and the presence of pursuing males (Glockner-Ferrari and Ferrari 1985, Cartwright 1999).

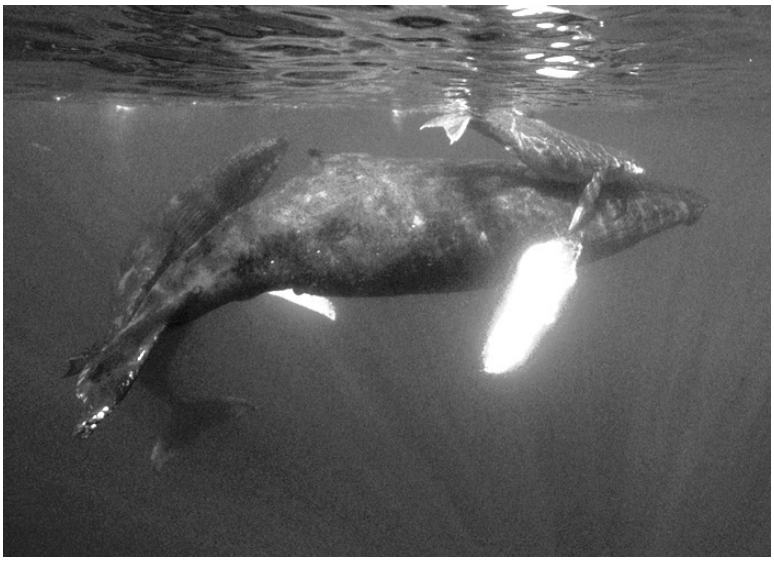

Figure 11. Cow/calf and escort. The stability of these groups suggests the cow accepts the male escort, possible gaining some protection from harassment by other males.

Cartwright (1999) studied the impact of single and multiple escorts on cow/calf behavior. She determined that as escorts join the mother/calf pair the energy demands of the behavioral regime increase, although much more so in the case of multiple escorts versus single escorts. Cartwright (1999) noted that the stability of the mother/calf and escort group indicates that this association is a choice made by both the mother and escort, and suggested that, as there is some energetic cost to this association for the mother due to changes in the time budget, there must be some benefit (as per Krebs and Davies 1996). The mother may associate with single escort as a trade off; the single escort raises the energy expenditure of the group to some degree, however multiple escorts have the potential for a far greater negative impact. By associating with a single escort the mother may avoid or minimize the impact of harassment by groups of other males (Cartwright 1999).

Juvenile behavior

A segment of the Hawaii whale population is juvenile, including recently weaned yearlings and whales up to four to five years old and sexual maturity. There are few studies and limited information on behavior of these younger whales, in part because they can be difficult to detect or identify reliably.

Some yearlings make their first winter migration to Hawaii with their mothers, then separate, and older juveniles are also present to some degree, at least earlier in the season (Dawbin 1966, Glockner-Ferrari 1985, Gabriele 1992). Glockner-Ferrari and Ferrari (1985) documented three whales as both calves and yearlings. One calf was reseen as a yearling still with its mother and reseen as a two year old with two other whales neither its mother, indicating some juveniles return to Hawaii. However, as Craig and Herman (1997) note, there is evidence that not all juveniles make the entire migration.

Sub-adults, generally defined by visual size estimations, are often noted on the periphery of other social groups including cow/calf pairs, adult pairs and larger groups of adults – following the action but not intimately involved (e.g., Glockner-Ferrari and Ferrari (1985), Darling and Berube 2001). Glockner-Ferrari and Ferrari (1985) report sub-adults: 1) in active groups; 2) with adult males; 3) accompanying each other (in pair); and 4) alone (one of the lone sub-adults a female). These authors note two occasions where yearling-sized whales were with an adult male and engaged in apparent sexual activity; in one interaction observed for three hours they were, “rubbing against each other twirling and swimming upside down and rolling together caressing each other with their flippers.” At one point the penis of the sub-adult was extended and rubbed against the genital slit of the adult. Glockner-Ferrari and Ferrari (1985) also report an instance where a sub-adult with a male was the apparent object of a fight between adult males. Darling (1983) reports a much smaller animal, presumed to be yearling or older juvenile, staying around an adult singer.

Other reported behavior attributed to sub-adults in Hawaii includes an apparent feeding lunge through mackerel (Salden 1989), and there is some speculation that many of the whales that approach boats and divers, and swim for extended periods in close proximity to them, are sub-adults (JDD).

DISCUSSION

More is known more about humpback whale social organization and behavior than any of the other great whales, due in large part to concentrations of humpback whales in nearshore and relatively calm locations worldwide; this offering accessibility to researchers. It is important, however, to remain aware that overall our knowledge is still very young, with many of the topics discussed the result of just one or two papers; many the result of the authors' first impressions and insights; many at the hypothetical stage and with a high proportion of speculation. This is a progress report only – a collection of often incomplete observations, with some ideas of what they might mean.

Any attempt to outline what we do not know about humpback behavior would make for a longer report than this one. Not only has research to date raised as many questions as answers, there are entire realms barely addressed, with examples including predation, behavior at night, or age-related changes in behavior. And, there is the reality that neither birth or copulation has been documented. When this finally occurs it may cause us to revisit many of the tentative conclusions to date. There are several major streams of investigation into humpback behavior in Hawaii, some with beginnings in the early studies in the 1970s, that, as they are pursued, will contribute enormously to our understanding of the animals.

The fundamental question, What qualities attract humpbacks to Hawaii?, has not been adequately addressed. It is apparent that the warm water and shallow banks are a consistent feature across humpback breeding areas, however there are strong suggestions that mating and birth (or at least behavior associated with mating and young calves) occur enroute, in colder, deeper water. We do not know if the whales are seeking out this physical habitat, if the assembly is primarily social, the specific location not important, or if this entire migratory cycle is simply the optimal physiological/energetic pattern considering food seasonality. There is a notion that females seek out Hawaii assembly conditions for calving, and this governs the behavior or males that follow for mating purposes. This may indeed be the case, however it is apparent that most females do not give birth the same year they mate, so the question remains as to why they (and the males) make the journey. On the other hand if, as proposed, a female strategy is to maximize contact with males over as little time as possible, perhaps the males set up in Hawaii knowing the females will come. Understanding the critical attributes of the habitat and behavioral dynamics of the assembly is crucial in defining meaningful conservation strategies.

One continuing stream of questioning is whether humpback whale social organization patterns and behavior vary with different geographic locations and the associated habitat within the main Hawaiian Islands. Initially it was proposed that some level of segregation of whales between islands existed. As this is apparently not the case, the question then shifted to whether the proportion of specific social groups and related behavior patterns vary between islands/locations. Although growing evidence indicates individual movements are characterized by rapid, un-directional circulation throughout the islands, there remain questions of differential use of locations. Although it is clear cows with young calves are more likely to occupy shallow inshore areas than other social groups, the purpose and importance of this behavior is entirely speculative. The fundamental question is whether there is a direct relationship between habitat type and behavior, or if habitat availability correlates with density of whales, which in turn determines behavior patterns.

Humpback whale reproductive strategies and the related behavior of males and females remain the focal subject of studies in Hawaii. Male behavior patterns are hypothesized, but far from established. The stream of thought has gone the full spectrum, from males acting independently perhaps within a dominance order, and either avoiding each other or fighting over females, to the possible existence of non-agonistic groups that may cooperate in mating. Males are in continual contact through the song, whose function is still not clear. There are hints of coherence of groups of males over time, and care-giving behavior between males – even after death. The existence of variable relationships between individual males through a dominance order or otherwise, and how these are established and maintained, remains to be explored. Differential mating success between males, as implied by mating system hypotheses can only be determined genetically and such studies are not yet underway in Hawaii. The key to characterization of mating behavior is the ongoing testing of predictions of the hypotheses of dominance polygyny, lekking, or cooperative behavior and either accepting or rejecting these ideas.

Female mating strategies, a key to characterizing overall behavior in Hawaii, are one of the least understood aspects of humpback behavior. How females choose, or otherwise influence the selection of a mate is not known. Proposals that females choose males on the basis of the song advertisement have not been proven. There is no indication that females are attracted to singers, however it is possible the females may both react to and potentially control the song in some, as yet undiscovered, way. The ideas that female strategies include selective migratory behavior to breeding grounds, and maximizing contact with males in as short as time as possible seem logical but require testing. It remains unclear if the postpartum mating that occurs is a female strategy to maximize reproductive success, or the result of harassment of males in a one-sided sex ratio.

Cows and calves have been the focus of studies in Hawaii since the late 1970s, with major contributions in describing general behavior and individual reproductive histories. However, behavior patterns at birth, and the factors that affect its success and the survivorship of newborn have not been defined. It is likely birth and the nurturing of newborn are one of the primary reasons humpback whales are in Hawaii, yet we have

little idea of their habitat or social requirements. As cows with calves occupy the most inshore, shallow waters in Hawaii, their interaction with human activities and pollution can be significant – yet we do not know enough about natural patterns to adequately identify what the impacts may be.

These are all substantial realms of inquiry, each with many specific topics and questions that need to be addressed to conclusively characterize the behavior of humpback whales. Hawaii will be one of the key locations in the world where this occurs, due to its calm lees, warm waters, density of whales, and accessibility.

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All included in Appendix 1

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APPENDIX 1

HAWAIIAN HUMPBACK BEHAVIOR AND RELATED LITERATURE

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APPENDIX 2

Actions and Postures of Humpbacks in Hawaii

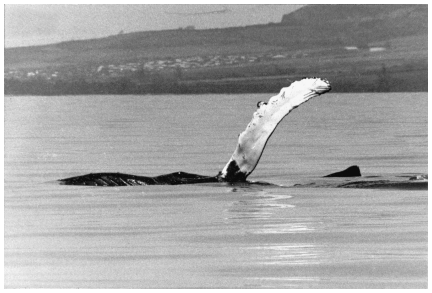
The following terms are derived from Darling 1983, Glockner-Ferrari and Ferrari 1985, and Gabriele 1992 (adapted from Bauer1986 and Helweg 1989). Alternative terms used to for same behavior are in parentheses. Glockner-Ferrari and Ferrari (1985) proposed the gender of whales that performed some activities; this is noted by an asterisk. Examples are given in Figure 12.

Displays/Actions of General Population (or not known if sex/age specific)	
Side fluke (half fluke, lateral fluke display)	Whale is at the water's surface with one fluke blade extended above the surface; indicative of whale swimming on side
Inverted posture (belly-up)	Whale turns ventral side to surface
Roll	The whale rolls ventral side or belly-up, at times slapping flippers on surface as it rolls all the way over
Head rise (spy hop)	Whale raises its head vertically out of the water while stationary with flippers outstretched, and without open mouth or extended throat pleats
Tail extension	Whale raises its tail slowly into the air, usually high enough that the genital area is above the surface, and holds it there for a time
Tail arch	The whale curves its tail stock and fluke into an "S" shape on horizontal plane and holds it here while swimming forward
Flippering (flipper slap)	The whale raises a flipper into the air and slaps it down on the surface of the water, once or many (20+) times in succession. Males and females*
Tail lob (lob tail, fluke slap)	Whale extends flukes above the water's surface and slaps them down on the surface of the water. This can occur "right way up" with the whale slapping the ventral surface of its flukes on the surface, or the reverse, with the whale belly-up slapping the dorsal surface of its flukes on the surface; occurs once or many (37+) times in succession. Males and females*
Rear body throw (tail throw, peduncle slap)	The whale throws the rear portion of its body from the water such that the edge of its flukes strike the water forcefully. Males and females *
Belly-flop (half breach)	The whale leaps partially out of the water and lands on its belly
Breach	The whale leaps from the water, spinning in the air before re-entry, once or many (35+) times in succession. At times two associated whales breach simultaneously (double breach). Males and females*

Displays/Actions Mostly Occurring in Competitive Groups/Situations (males)	
Tail lash (fluke swish)	One whale lashes its tail, often towards another; can occur with flukes on a horizontal or vertical plane; within striking distance or not
Head lunge	The whale lunges forward with most of its head coming out of the water. Often principal escort or challenger*
Underwater blow	The whale releases a blast of air from its blowhole below the surface of the water, usually just prior to surfacing
Bubble stream (bubble trail)	The submerged whale releases a controlled stream of bubbles from its blowhole, leaving a long line or wall of bubbles behind it. Males*
Bubbling	Large bubbles emitted from mouth. Escort or dominant male*
Air gulp (throat inflation)	The whale gulps air on the surface, and thereby extends its throat pleats, then releases the air underwater; purpose may be to enlarge throat for display or collect air to release underwater. Escort or dominant male*
Head slap (chin slap)	Whale lunges/leaps partially out of the water and strikes the ventral side of its head forcefully on the surface
Head lift (S-shaped posture)	The whale travels with its back arched and head above the surface
Jaw clap	The whale opens and closes its jaws, clapping them together, at times audibly
Chasing (tail chasing)	One whale rapidly chases another; one may throw its tail upward above the surface, with the chaser lunging and slapping its head against the water immediately behind the first whale. Males*
Charge	One whale charges at another, often bubble-streaming in the process
Block	One whale blocks the path of another with its body
Strike	One whale intentionally strikes another with its flukes, whether underwater or on the surface
Collision	Two whales collide, apparently intentionally
Trumpeting	A whale vocalizes on the surface with a prolonged low trumpet-like or foghorn-like sound emitted from the blowhole

Figure 12. Examples of humpback whale actions and postures.

Breach



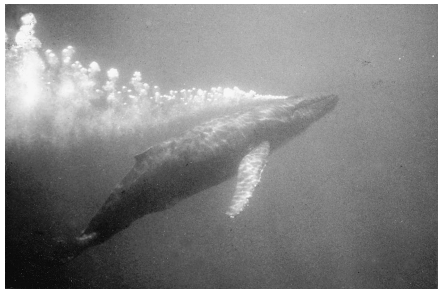
Flippering

Tail Lob (reverse)

Tail Arch

Tail Extension

Belly Flop



Bubble Stream

Head Lift

Rear Body Throw