

MALE HUMPBACK WHALE DIES IN COMPETITIVE GROUP

Aggressive behavior between male humpback whales (*Megaptera novaeangliae*) in various winter grounds has been well documented (Darling *et al.* 1983, Tyack and Whitehead 1983, Baker and Herman 1984, Glockner-Ferrari and Ferrari 1985, Mattila *et al.* 1989, Clapham *et al.* 1992, Medrano *et al.* 1994). Typically, aggression occurs within “competitive groups” composed of multiple males apparently vying for proximity to a lone female with or without a calf (Tyack and Whitehead 1983, Baker and Herman 1984, Glockner-Ferrari and Ferrari 1985). Although male-male aggression within competitive groups can on occasion escalate to severe body strikes, which may result in raw, bloody dorsal fins or rostral tubercles (Herman and Tavolga 1980, Darling *et al.* 1983, Baker and Herman 1984), there are no previous reports of humpback whale fatalities associated with such aggression.

On 9 February 1996, we observed a dead adult male humpback whale in waters off Lahaina, Maui, Hawaii. It had been a member of a competitive group of at least four whales approximately 1 h 40 min earlier, and evidence presented here suggests it died during the ongoing competitive activities. Three whales from this competitive group remained with the dead whale and directed a variety of behaviors toward it. One of these three, later identified as a male, remained with the dead whale for over four hours. Here, we summarize the events preceding and following the death of the whale and describe more fully the behaviors of the other whales toward it.

Initial observations of the competitive group are based on a surface videotape obtained by a passenger aboard the whale-watch vessel *Lin Wa II*. This vessel located the competitive group at approximately 1300 about 2 km offshore of Lahaina, traveling NW at approximately 5 kn (9.0 km/h). *Lin Wa II* passengers and crew observed the group for over two hours.

Table 1 consists of an analysis of the surface videotape. Although the videotape had no chronometer recording and had been stopped and restarted several times during videography, it was still possible to extract a reasonably accurate chronology of events. This chronology was broken down into four parts based on changes in the activities of the group of whales, as summarized in Table 1. The distance from the whale-watch boat to the whales was approximately 150 m in Parts 1 through 3 and about 50 m or less in Part 4. In Part 1 the angle of the video camera relative to the whales did not permit a clear view of the ventral surfaces of their tail flukes. In Parts 2, 3, and 4, the camera angle was more favorable. Three whales, arbitrarily labeled here as A, B, and C, could be discriminated from one another by the distinctive patterns of black-and-white coloration on the ventral surfaces of their tail flukes (Katona *et al.* 1979). Although there was sufficient information on the surface video to discriminate among these whales, there was not enough de-

Table 1. Chronology of events surrounding death of humpback whale in competitive group in Maui as recorded on surface videotape from whale-watch vessel. Counter times are from Hi-8 video player.

| Part | Counter start—end | Events |
|------|-------------------|--|
| 1 | 0'00"—2'31" | Competitive group of four humpback whales travel rapidly at surface, blow, dive, surface asynchronously, chase each other, and perform inflated head lunges ^a ($n = 5$). Additionally, video captures single peduncle slap ^b performed by lead whale in direction of trailing whale. There is no evidence of dead whale, and angle of boat relative to whales makes identifying them from ventral surface of tail flukes impossible. |
| 2 | 2'32"—15'49" | Whale (hereafter referred to as Whale D) surfaces dorsal first, does not blow, rolls onto left side, and remains motionless. Second whale performs head rise ^c next to it. Over next 13 min several whales mill in loose circle around Whale D, surface asynchronously, and perform head rises ($n = 8$), head lunges both with and without jaws slightly open ($n = 8$), and underwater blows ($n = 1$) near it, as well as fluke-down dives with steep peduncle arches. ^d On 10 occasions whale positioned at side or below Whale D observed waving one or both pectoral fins over whale D. Distance from camera to whales (approximately 150 m) does not allow for identification of individuals performing pectoral fin behaviors. On occasion, Whale D appears to sink below surface. Other whales either submerge or arch their backs, possibly pushing against whale D. Each time Whale D resurfaces, peduncle appears first followed by dorsal fin. Whale D never seen blowing, although other whales observed to blow frequently. |
| 3 | 15'50"—31'22" | Whale D remains motionless on left side at surface. Distance between camera and whales decreases to approximately 50 m. Whales A, B, and C repeatedly surface next to Whale D. Head lunges have decreased in frequency ($n = 2$). On 12 occasions (4 initiated by Whale A and 2 by Whale C) whale individually performs "pectoral-grasp" behavior toward Whale D. It extends pectoral fins about Whale D's body from either dorsal or ventral side and then strokes pectoral fin across Whale D's abdomen. Also, on 10 occasions whale lifts its head obliquely from surface and then either submerges (small head rise), or carefully places head on Whale D's abdomen and then slides head toward water. Additionally, whales perform prolonged and controlled underwater blows ^e next to Whale D, lasting at least 5 sec ($n = 5$). |
| 4 | 31'23"—47'54" | Approximately 30 cm of whale penis is seen above surface as Whale C performs pectoral-grasp behavior on Whale D. Whale A performs 14 additional pectoral-grasp behaviors on Whale D. Head lunges now occur rarely ($n = 1$) while other behaviors continue to be offered frequently, including head rises or lifts ($n = 10$), tonal inhalations (wheezing sounds performed during inhalation) ($n = 7$), and underwater blows ($n = 7$). |

^a Head of whale is thrust forward out of water, typically with throat area inflated and enlarged.

^b Whale's caudal peduncle and flukes are raised high in air and then flung sideways toward water surface with great force.

^c Head of whale rises vertically out of water, rostrum pointing skyward.

^d Whale arches peduncle and performs dive in which undersides of tail flukes not visible above surface.

^e Whale exhales just below surface.

tailed information for matching the flukes against past photographs. The flukes of the dead whale (whale D) were submerged in these parts and thus not recorded on the surface video. However, during our own subsequent observations we did obtain highly detailed fluke photographs of whales D and A.

During Part 1 of the surface video, the whales engaged in behaviors typical of a competitive group, such as frequent head lunges with throat pleats inflated (Tyack and Whitehead 1983, Baker and Herman 1984). During Part 2, an apparently dead whale appeared at the surface (whale D). Other whales from the group milled about this whale, frequently lifting their heads slightly out of the water and waving their pectoral fins over the motionless animal. Throughout Parts 3 and 4, whale D was never observed to issue a blow, though other whales from the group were clearly observed blowing. The frequency of head lunges during Parts 3 and 4 ($n = 3$ during 32.1 min of videotape) decreased dramatically from that observed during Parts 1 and 2 ($n = 13$ during 15.8 min of videotape). Additionally, during Parts 3 and 4, whales A and C contacted whale D with their pectoral fins and heads in a manner not observed in competitive groups (see Table 1). In Part 4, a penis of one of the three live whales was seen protruding above the water's surface for several seconds near whale D's tail stock (peduncle) while whale C stroked its pectoral fin across whale D's abdomen.

During Part 4, the captain of the *Lin Wa II* placed a radio call for assistance from any research vessels in the area. At approximately 1441, research teams from the Hawaii Whale Research Foundation (HWRF), the Hawaiian Center for Whale Research (HCWR),¹ and the Center for Whale Studies (CWS) began arriving in the vicinity of the dead whale. Its location at that time was 20°51.3'N, 156°41.4'W. Initial surface observations revealed whales A, B, C, and D present. However, whales B and C departed within 1–2 min.

Divers using snorkel gear were able to observe at close range (<1 m) all surface areas of whale D's body including its ventral side. Underwater visibility was approximately 20–25 m. Whale D was lying on its left side, its body bowed in an inverted "U" position with its midsection and its extended right pectoral fin visible at the surface.² It appeared to be an adult based on its size (approximately 13 m). Its mouth was open at an angle of approximately 45°. The baleen plates were visible and appeared intact. No foreign matter was observed in its mouth. The blowholes were shut tightly and the right eye was half open and unclouded. The left pectoral fin extended downwards at a 30° angle to the mid-line of the body. There was no evidence of decomposition, fractures, contusions, or open wounds. There was extensive scarring on the lower and upper jaw, around the right eye and blowhole, along the peduncle region, on the left side, and on the dorsal side of the tail flukes. A wound on the ventral side of the right blade of the flukes appeared new, as it was pink in color. No external bleeding was observed. The absence of a hemispheric lobe caudal to the genital slit, the relative distance between the genital slit and the anus, and the lack of mammary slits indicated that the whale was a male (True 1904, Glockner 1983). A sample of skin was obtained for DNA analysis.

Throughout our observations, whale A remained near whale D. Whale A was also approximately 13 m long. It bled from many of its rostral tubercles, a condition, as was noted earlier, sometimes observed in humpback whales involved in high levels of aggressive competition. Close-range observation of the ventral surface of whale A when it performed a pectoral-grasp behavior on whale D (see below) or turned ventral side up, allowed us to identify it as a male, using the same sex-identifying features noted for whale D.

On numerous occasions whale A swam toward whale D from below, approached its dorsal side, and positioned itself either alongside whale D's back or ventral-side-up under its left side, head-to-head and tail-to-tail (see Fig. 1). Whale A then grasped whale D with its pectoral fins (as in Table 1, Part 3), and either raised the ventral surface of its peduncle region toward the water's surface, or pressed this region against whale D's peduncle, on or near its genital area. Occasionally during this behavior, whale A's genital slit opened and pulsed (*i.e.*, the outer folds quivered), although whale A's penis was not observed.³ Whale A then broke contact with whale D. Typically, whale A performed several bouts of the pectoral-grasp behavior before diving to approximately 15 m where it could be seen resting in a vertical position with its rostrum pointing toward the surface. During two separate periods of 6 min 18 sec and then 4 min 16 sec, six and five distinct bouts of the behavior occurred. Based on these 11 bouts, a mean duration of 14.6 sec for the pectoral-grasp behavior was calculated from the time whale A first raised its pectoral fins about whale D's midsection to its first break of contact with whale D (range = 6.9 sec to 21.9 sec). Between bouts whale A remained near whale D's dorsal side at or just below the surface (mean duration = 52.0 sec, range = 8.8 sec to 87.1 sec). Occasionally, bouts of the pectoral-grasp behavior by whale A were preceded by whale A orienting its rostrum 1 m or less below whale D's genital area. On at least three occasions, when whale A was positioned between whale D's dorsal side and a diver filming, it lashed its tail laterally in the direction of the diver.

In addition to the pectoral-grasp behavior, whale A continued to place its head on whale D's abdomen and produce tonal inhalations (see description in Table 1, Part 4). From 1511 to 1637, the length of time whale A spent at or just below the surface in close proximity to whale D before diving increased from approximately 1 min to 49 min. Over the course of our observations no other whales approached either whales D or A, although two whales were seen traveling approximately 100 m from the site. Observations of whales D and A continued to approximately 1830.

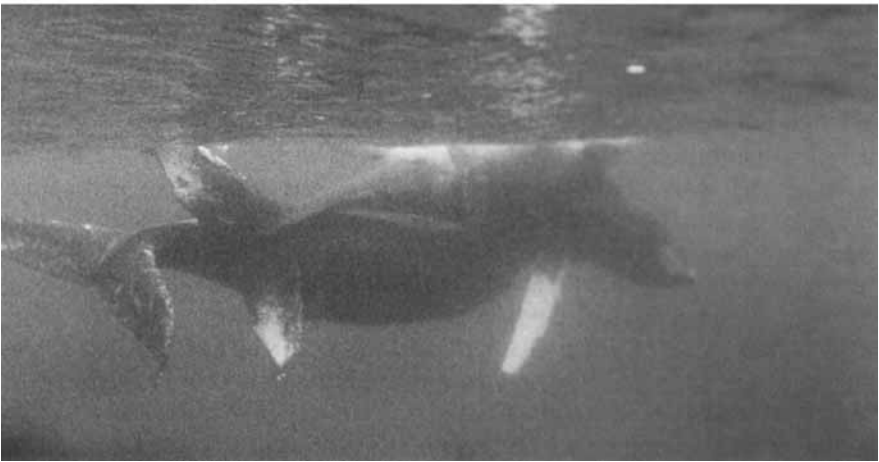
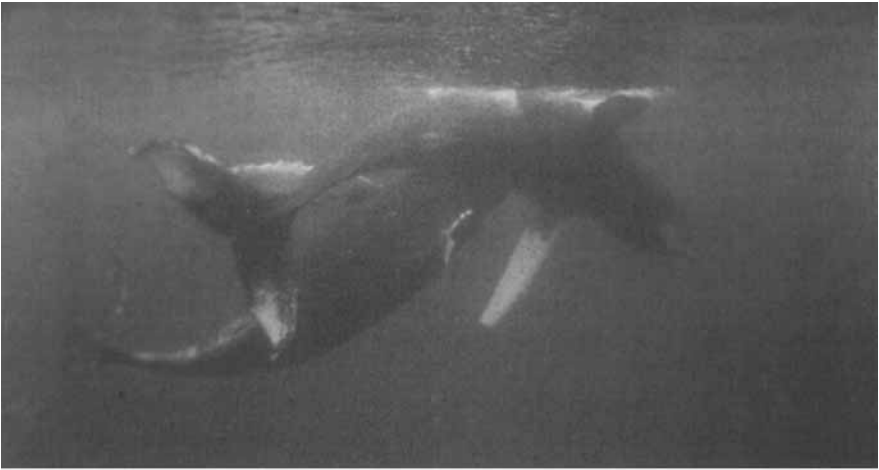
Still photographs of the tail flukes of whales D and A were matched against the various fluke catalogs maintained by the authors (*e.g.*, see Perry *et al.* 1988) and the fluke catalog of the National Marine Mammal Laboratory (NMML). Table 2 reveals one match to whale A from Maui in 1996, and six matches to whale D: four from southeast Alaska in 1991 (Fig. 2) and 1994, and two from Maui in 1992 and 1994. During the 1994 Maui sighting, whale D was a primary escort in a competitive group and was observed head lunging, blocking, and chasing the "challenger," as well as creating underwater bubble trails.

Previous studies (Glockner 1983, Glockner-Ferrari and Ferrari 1985, Clapham *et al.* 1992) have revealed that escorts in competitive groups are males, almost without exception. In none of these earlier sightings of whales A and D were the two seen together. At the earliest sighting of whale D, in October 1991 in southeast Alaska, it was judged to be an adult, based on its general appearance and size. Although yearlings may often be identified in the field by their relatively smaller size, at somewhat later stages in their development they cannot be readily distinguished in size from adults. Therefore, assuming at the time of its first sighting in October 1991 that whale D was at least 1.5 yr old, at the time of its death in February 1996 it would have been at least 6 yr old, and therefore in all probability sexually mature (Chittleborough 1955, Clapham 1992).

On 13 February the carcass of a whale was sighted several kilometers off Olowalu Point, Maui (20°47.9'N, 156°41.2'W), approximately 6.3 km south of the location of whale D 4 d earlier. It was estimated to be 13 m long and floated on its left side, its vertebrae, ribs, skull, and mandible plainly visible. Most of its skin, blubber, and muscle tissue were missing, as well as its entire ventral pleat region and tail flukes. Its intestines and stomach floated at the surface, still attached to its body. They appeared distended, possibly gas-filled from decomposition (see Tomilin 1967). At least six 4-m tiger sharks (*Galeocerdo cuvieri*) fed on the carcass. In 4.5 h of observation no other whales were observed to swim within 200 m of the carcass. Subsequent comparison of DNA sequences extracted from a skin sample of the carcass with those of the specimen obtained from whale D provided compelling evidence that the carcass was whale D.⁴

The death of a humpback whale during competitive, agonistic encounters is a most unusual event not previously reported. The dramatic change in whale behaviors from Part 1 to Parts 2, 3, and 4 of the surface video footage (see Table 1) suggests that whale D died either during Part 1 or between Parts 1 and 2. Part 1 of the surface videotape provided no evidence of a dead whale. The activities of the whales were consistent with those of a typical competitive group (Tyack and Whitehead 1983, Baker and Herman 1984, Glockner-Ferrari and Ferrari 1985). During Part 2 there was a significant change in group behavior, and a whale could be seen lying motionless at the surface, not breathing. Although the other whales in the group continued to perform occasional head lunges (as they had in Part 1), they also milled about the motionless whale and performed small head rises near it. The frequency of head lunges decreased and other behaviors not observed in Part 1 began to emerge, including the pectoral-grasp behavior, the tonal inhalations, and the behavior of a whale resting its head on the abdomen of the motionless whale. Whether or how the prior aggressive behaviors performed by the whales in this competitive group contributed to whale D's death is unknown.

The behaviors of the other whales toward whale D may have involved sexual components, helping behavior, or dominance displays, alone or in combination. Arousal evidenced by a visible penis during a bout of the pectoral-grasp behavior (see Table 1, Part 4), and the underwater observations of a pulsating



genital slit (whale A) while performing this same behavior suggest a sexual component. Observations of sexual behavior directed by a live male toward a dead male have been reported previously in other species. For example, Dickerman (1960) observed a male ground squirrel (*Citellus tridecemlineatus*) curl its body around the posterior end of a dead male squirrel that lay in a position resembling that commonly adopted by females during copulation. Dickerman concluded that the curled position of the dead ground squirrel acted as a "sign stimulus" to "release the copulatory drive in the male" (p. 403). In the present case, we do not know whether the position of whale D acted to elicit a sexual response in the other male humpback whale. Indeed, there are no reported observations by researchers of copulation between male and female humpback whales. Early descriptions of humpback whales copulating while rising vertically out of the water (as reported in Slijper 1962, Tomilin 1967) are of dubious authenticity. However, there have been several observations of an adult male humpback being contacted by the penis of either a subadult male (Glockner-Ferrari and Ferrari 1985) or another adult male (CWS, unpublished data; HCWR, unpublished data; HWRF, unpublished data). In several of these instances, the male initiating penile contact approached the adult male from the dorsal side.

The pectoral-grasp behavior appears similar to the behavior of an adult humpback whale toward a right whale (*Balaena glacialis*) observed by Herman *et al.* (1980) during an aerial survey over Hawaiian waters. The humpback approached the right whale's genital area from below, lay with its ventral surface against the right whale's right side, and wrapped its pectoral fin around the back of the whale "as though caressing it" (Herman *et al.* 1980, p. 273). The authors stated that the observed behaviors "gave the strong impression that the humpback whale was engaging in courtship behavior" (p. 274). The pectoral-grasp behavior observed in the present case may have had similar sexual motivations.

Alternatively, however, the pectoral-grasp behavior might have been a form of helping, or epimeletic behavior, an attempt to support whale D at the surface. Tomilin (1967) reported four instances of an adult humpback whale on the North Pacific summer grounds "standing by" (after Caldwell and Caldwell 1966) a harpooned adult humpback. Zenkovitch (1956) reported a humpback whale supporting an injured humpback under the surface for 40 min before being harpooned itself by whalers (from Slijper 1962, p. 195). There have been many subsequent reports of helping behavior by cetaceans,

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Figure 1. Sequence of still photographs taken from 16-mm film (CWS) of whale A (male humpback whale) performing "pectoral-grasp" behavior toward whale D (dead male humpback whale floating at surface). From top to bottom: whale A oriented ventral-side up approaching whale D from below with raised pectoral fins; whale A underneath whale D extending pectoral fins about whale D's mid-section; whale A wrapping pectoral fins around whale D's mid-section with peduncle raised upwards toward whale D's tail.

Table 2. Previous sightings of Whales D (dead whale) and A.

| Whale | Date | Location | Context | Source |
|-------|--------------|---|---|--------|
| D | 11 Oct. 1991 | SE Alaska (Sitka Sound) | Sighted as adult lunge-feeding with 15-20 humpbacks using bubble-net technique (Jurasz and Jurasz 1979) | JMS |
| D | 18 Oct. 1991 | SE Alaska (Sitka Sound) | Feeding subsurface with three humpbacks | JMS |
| D | 30 Oct. 1991 | SE Alaska (Salisbury Sound) | Sighted with at least five humpbacks | JMS |
| D | 16 Jan. 1992 | Maui, Hawaii (2 mi offshore of Launiupoko Park) | Sighted in competitive group of three humpbacks | HWRF |
| D | 11 Feb. 1994 | Maui, Hawaii (5 mi offshore of Puamana) | Sighted as primary escort (Tyack and Whitehead 1983), in competitive group of five humpbacks. | HWRF |
| D | 11 Dec. 1994 | SE Alaska (Sitka Sound) | Feeding with one humpback | JMS |
| A | 26 Jan. 1996 | Maui, Hawaii (0.5 mi offshore of Olowalu) | Sighted as escort in competitive group of female humpback, its calf, and six other humpbacks. | HCWR |

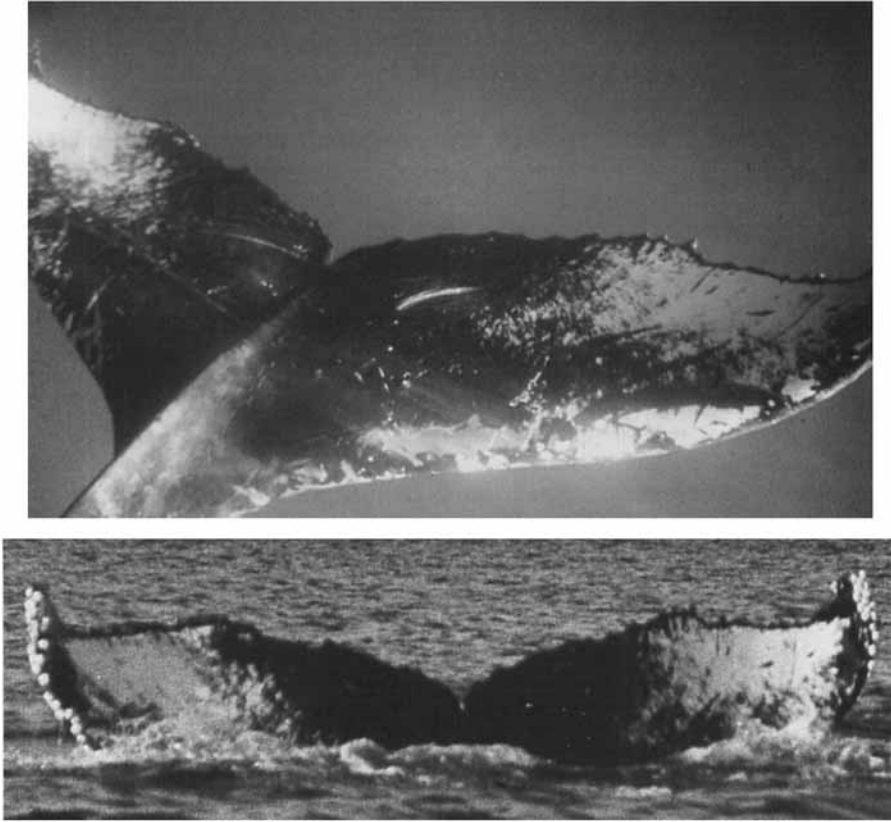


Figure 2. Photographs of ventral surface of whale D's tail flukes. From top to bottom: 9 February 1996 approximately 90 min post-mortem in waters off Lahaina, Maui (HWRF); and 11 October 1991 in Sitka Sound, SE Alaska at whale D's first sighting (JMS).

primarily odontocetes, toward other cetaceans in distress (*e.g.*, Conner and Norris 1982, Cockcroft and Sauer 1990, Lodi 1992, Harzen and dos Santos 1992, Felix 1994, Fertl and Schiro 1994). In the current incident, the behavior of whales A and C positioning themselves individually against or underneath whale D with their pectoral fins extended about whale D's abdominal region could be construed as tending to support whale D at the surface. However, the data showing that whale A spent, on average, more time between bouts of the pectoral-grasp behavior than actually performing this behavior, and the observation that whale D floated at the surface unsupported, potentially complicates any interpretation of the behavior as epimeletic. In evolutionary terms, the existence of helping behavior between adult male humpbacks is problematic unless one can show reciprocity or that some advantage accrues to the helper (*e.g.*, Conner and Norris 1982, Trivers 1985). Traditionally, adult male humpback whales have been cast as competitors on the winter grounds (Tyack and Whitehead 1983, Baker and Herman 1984), associating with each other

for several hours at most (Mobley and Herman 1985). However, Clapham *et al.* (1992) and Brown and Corkeron (1995) have presented evidence suggesting that some pairs of adult male humpbacks form coalitions for a period of time either en route to or on the winter grounds. Unfortunately, the relationship between whales A and D prior to whale D's death is unknown, although as mentioned earlier they were not seen together during any of the previous seven sightings.

A third possible interpretation is that the pectoral-grasp behavior was a dominance display. Joubert (1991) hypothesized that dominance sorting might have played a role in his observations of several young bull elephants mounting a dying 50-yr-old male elephant, although a sexual component seems plausible as well. In bottlenosed dolphins, as well as other mammalian species, dominance relations are often established or asserted through sexual displays (see Östman 1991). It is not known whether male humpback whales develop dominance relations on the winter grounds. Occasional observations of all-male competitive groups may suggest some dominance sorting (Clapham *et al.* 1992). However, competitive groups are relatively short-lived transient associations (Tyack and Whitehead 1983, Mobley and Herman 1985). Thus, although the escort positioned closest to the adult female in a competitive group might be regarded as dominant with respect to the other males of the group (Tyack and Whitehead 1983, Glockner-Ferrari and Ferrari 1985), it is not clear if such dominance would have any sustained value (see Frankel *et al.* 1995).

It is also possible that components of all three types of behavior were present simultaneously or sequentially as the motivations of whale A (or the other whales) shifted. Brown (1962) observed a captive male pilot whale copulating with a dead female pilot whale while transporting her to and from the surface. Also, as mentioned earlier, dominance and sexual behavior are commonly reported as co-occurring in many mammalian species (see Östman 1991).

In conclusion, the current observation appears to be the first documented instance of a male humpback whale dying while with a competitive group. Although bloody tubercles, raw dorsal fins, and related wounds have been reported previously from whales engaged in competition (*e.g.*, Herman and Tavolga 1980, Tyack and Whitehead 1983, Baker and Herman 1984), the death of a member of a competitive group underscores the potentially high costs of physical engagement during competition between male humpback whales on the winter grounds. The interpretation of the behaviors of the live whales toward the dead whale remains problematic but may offer a new perspective on social relations among male humpbacks on the winter grounds.

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¹ The Hawaiian Center for Whale Research is the name under which the Kewalo Basin Marine Mammal Laboratory's humpback whale research program now operates.

² Historical accounts of whaling for humpbacks and other rorquals state that they sink when killed (Slijper 1962, Tomilin 1967). Whale D, however, floated unsupported. Observations of live humpback whales "resting" at or near the surface without moving are common in Hawaiian waters and are possibly explained by air in the lungs.

³ On two occasions when whale A was near but not in contact with whale D, its genital slit was also observed to be open.

⁴ A portion of the mitochondrial control region and a portion of an actin intron (two variable regions in humpbacks) were sequenced from both skin specimens at Harvard University by Dr. Frank Cipriano. They yielded respectively 463 and 244 base pairs of overlapping sequences. Both the control region sequences and the actin intron sequences from the two specimens were identical in the regions of overlap, providing strong evidence that both specimens were from the same whale.

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THE NORTHERN ELEPHANT SEAL IN OREGON: A PUPPING RANGE EXTENSION AND ONSHORE OCCURRENCE

The northern elephant seal, *Mirounga angustirostris*, has undergone a phenomenal population growth in the past 100 yr, recovering from a population that numbered tens or perhaps low hundreds at the turn of the century to an estimated 127,000 individuals in 1991 (Stewart *et al.* 1994). Northern ele-