Maternal Behaviour of Humpback Whales in Southeast Alaska

by

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ABSTRACT

In this study, I characterize the maternal care patterns of humpback whales in southeast Alaska. Through a study of proximity behaviour, I show that humpbacks behave similarly to terrestrial ungulate 'followers': the cow and calf are rarely more than several body lengths apart; proximity between the cow and calf is greatest during periods of travel relative to other behaviours; and, proximity is greatest when the dive behaviour of the pair is synchronized. Unlike that observed in typical follower species, however, proximity is not found to decrease significantly as the pair's association lengthens. To account for this, I argue that the length of the observation period was insufficient to detect such a trend since maternal pairs remain together for several months after the last observations. In addition, I analyze the diving behaviour of the maternal pair to examine the potential negative consequences for the female associated with the follower tactic in humpbacks. The results suggest that several behavioural modifications are made by the cow and calf in an effort to minimize the duration of separation between the two. Ultimately, I argue that behaviour observed in humpback whales is commensurate in function with following behaviour in terrestrial ungulate followers. Humpbacks are migratory, and as in many migratory species, following behaviour provides a mechanism whereby the

maternal dyad can maintain close proximity during periods of travel. Moreover, as with many follower species, humpbacks can rely upon their large size as a means of defence against offspring predation. Finally, although obvious differences exist between the habitats in which humpbacks and ungulate followers reside, arguably both are open habitats that lack the cover necessary to allow for offspring concealment.

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Introduction

This study investigates the parental care behaviour of humpback whales (*Megaptera novaeangliae*) on a foraging ground in southeast Alaska. In general terms, parental care refers to the suite of behaviours observed in organisms that are directed towards the rearing of their offspring. These can include readily observable behaviours such as provisioning young (e.g., LoVullo *et al.* 1992, Farmer 2000) and providing them with protection from predation (e.g., Pooley 1962, Duellman & Trueb 1986). However, they can also include less recognizable behaviours, such as those involved with the transmission of learned behaviours between parent and offspring (e.g., Altmann 1963, Chesler 1969, Bergerud & Noland 1970, Galef & Clark 1971, Neuringer & Neuringer 1974, Edwards 1975, Stirling & Latour 1978). In all cases, however, the behaviours associated with parental care serve to increase the offspring's survivorship.

With reference to the mysticete whales, whaling data have provided us with a considerable understanding of the physiological responses that are involved with reproduction (e.g., Chittleborough 1958). There is, however, a paucity of data on the behaviour of these animals associated with the rearing of their young. Considering that many mysticetes, including humpbacks, have been heavily exploited in the past, and that their recovery rests largely on the survival of their offspring, any information we can obtain regarding the behaviour of mother-calf pairs will assist in their recovery. Ultimately, however, through examining an unstudied species such as a humpback whale, this study aims to contribute to a better understanding of the patterns and functions of parental care found in nature.

What follows is a brief review of parental care in various vertebrate taxa. Examples are used to illustrate the diversity of care strategies that are adopted by various organisms. Although the review draws examples from several vertebrate classes, there is a focus on mammalian parental care. This leads into a discussion of the specific questions to be addressed in this thesis and how they fit into the existing framework of parental care. Finally, a brief review of the literature on humpback whale life history with an emphasis on the northeastern Pacific population is presented.

Literature Review of Parental Care Behaviour in Vertebrates

Various parental care tactics have arisen independently in a wide variety of vertebrates. About 20% of the approximately 420 families of Osteichthian fish exhibit some form of parental care including nest maintenance, providing eggs with oxygenated water and protecting both eggs and offspring from predation (Helfman *et al.* 1997). Among amphibians, parental care is present in most families of caecilians and caudates, and approximately 60% of anuran families (Wells 1981, Duellman & Trueb 1986). Most reptiles do not practice parental care (Rosenblatt 2003), although it is observed among crocodilians and some Squamates (Pooley 1962, Rosenblatt 2003). Extensive parental care, however, is central to the biology of endotherms and is considered to be a key innovation in these organisms (Farmer 2000).

Differences in both the frequency of occurrence and extent of parental care among vertebrates generally reflect their contrasting life histories. R-selected species, as are many ectotherms, devote a considerable amount of energy towards the production of many offspring. These offspring are generally precocial and, although they often feed on different organisms than their parents, are typically capable of foraging independently at birth (e.g., Cott 1961, Clark & Gibbons 1969, Dodson 1975). In contrast, k-selected species, such as most endotherms, produce relatively few and typically altricial offspring. For example, Carrier & Auriemma (1992) have suggested that limitations in wing development of juvenile birds prevent them from flying, and as a consequence, they are unable to forage on their own. Similarly, juvenile mammals are typically born without the morphological features necessary to process the food upon which the adults forage (see Pond 1977). Therefore, in these organisms parental provisioning is necessary to allow offspring to develop until they can independently acquire and process their own food.

While the r- and k- selection dichotomy provides a broad framework from which to view contrasting parental care tactics, it provides little information regarding either the extent or source of variability inherent within tactics. For example, while a universal trait among mammals is their ability to produce milk to nourish their young, there is considerable variation between species in the duration of lactation. For instance, pine voles (*Microtus pinetorum*) lactate for approximately 21 days (Lochmiller *et al.* 1982), racoons (*Procyon lotor*) for approximately 70 days (Stuewer 1943) and polar bears (*Ursus maritimus*) for approximately 130 weeks (Berta & Sumich 1999 and references therein). These examples suggest that the lactational period is positively correlated with the size of an organism. This, however, is not always the case; closely related species of similar size can differ widely in the duration of lactation. Female Antarctic fur seals (*Arctocephalus gazella*) and Galapagos fur seals (*A. galapagoensis*) are nearly identical in weight (approximately 40kg); however, the lactational periods of the two range from under 120 days in the Antarctic fur seal (McCann & Croxall 1986) to approximately 730 days in the Galapagos fur seal (Trillmich 1979). Clearly then, size is not the sole determinant of lactational period. Alternatively, with regard to the previous example it has been suggested that Antarctic fur seals benefit from an abundant food source and, as a consequence, can produce greater quantities of milk in a shorter period than Galapagos fur seals inhabiting relatively nutrient poor tropical waters (Gentry *et al.* 1986, Trillmich 1990). Therefore, while demonstrating that a conserved feature of mammalian parental care such as lactation can show considerable variation, this example also suggests that ecological factors (e.g., prey availability) play a key role in determining the nature of the parental care strategy that a species employs.

Another example where ecological factors influence the way in which a species cares for its offspring is illustrated by the terrestrial ungulates. Among these animals, two general strategies exist that are presumed to reflect the need for the female to protect her offspring from predation. In one, the 'hider strategy', the offspring remain concealed at a distance from their mother during their first few weeks of life (Lent 1974). During this period, juveniles tend to minimize activity and contact between the pair is typically limited to brief nursing bouts. These species, such as pronghorn (*Antilocapra americana,* Autenrieth & Fichter 1975) and Thomson's gazelle (*Gazella thomsoni*, Fitzgibbon 1990), rely upon cryptic colouration and lack of scent gland development, and are frequently found in areas where suitable cover exists to allow the juvenile to remain concealed from predators (Jarman 1974). Alternatively, some juvenile ungulates, referred to as 'followers', accompany their mother soon after parturition and are rarely more than several body lengths from her until they separate permanently (Lent 1974). These species, including bison (*Bison bison*, Green 1992) and reindeer (*Rangifer tarandus*, Espmark 1971), tend to inhabit areas with limited cover and low vegetative profiles and may have highly developed social systems that presumably allow for increased vigilance (Jarman 1974). Thus, the habitat in which an animal lives appears to determine the strategy it employs to raise its young.

These examples serve to illustrate that although united by a common theme, that of provisioning their young, endotherms can differ widely in their approach to rearing offspring. Moreover, they suggest that ecological factors, such as habitat structure and prey availability, can often be better predictors than phylogeny alone of the parental care tactics a given species adopts. The second example, that of the hider/follower dichotomy in ungulates, further illustrates that parental care can be extended to include other necessary benefits to the offspring. For example, protection from predation is often a key component of a given care strategy. What may not be initially clear, however, is that there are typically costs to the parents associated with providing care for their offspring.

Among mammals, the costs of parental care necessarily include the direct costs of maternity associated with gestation and lactation that all females incur. There can be additional costs, however, associated with the post-partum rearing of offspring that are independent of these physiological costs. For example, terrestrial carnivores frequently utilize solitary (e.g., leopard, *Panthera pardus,* Seidensticker 1977; Florida panther, *Felis concolor coryi,* Maehr *et al.* 1989) or communal (e.g., spotted hyena, *Crocuta crocuta,* Hofer & East 1993) dens, in which their offspring are left unattended until they are able to accompany the female on foraging trips. Presumably, such an approach has arisen as a means for the female to continue to hunt without the need to remain vigilant for potential predators and without the direct interference of having her offspring accompanying her on foraging bouts. As a result, however, the female must frequently return to the den to nurse, which almost certainly represents a cost in terms of reduced foraging effort and/or efficiency. In another study, Ginsberg (1989) has shown that water restrictions during lactation force female Grevy's zebra (*Equus grevyi*) to forsake feeding opportunities and to inhabit areas of lower vegetative biomass than their non-lactating conspecifics. A similar pattern has been observed in lactating feral asses (*Equus asinus,* Moehlman 1974) and

Nubian ibex (*Capra ibex*, Maltz & Sholnik 1984) in desert environments as well. Clearly then, attending to offspring can have consequences to the parent.

Given the costs associated with raising offspring, it should come as no surprise that organisms have adopted various tactics to cope with or offset these costs. For example, foraging sperm whales (*Physeter macrocephalus*) typically dive to depths and for durations that appear to be beyond the limits of their offspring (Best 1979, Gordon 1987, Papastavrou *et al.* 1989). Therefore, without any behavioural adjustment, juveniles would be left unattended at the surface and consequently at a higher risk of predation. Whitehead (1996) has shown that lactating females continue to dive as they would if they were unaccompanied by a calf. The problem of separation that ensues, however, is solved by the adoption of alloparental care; other conspecifics typically remain at the surface to accompany the calf during the period of separation from its mother (Whitehead 1996). Grevy's zebras appear to benefit from alloparental care as well (Becker & Ginsberg 1990). Juveniles are often grouped into "kindergartens" (Klingel 1974), in this case guarded by a single male, while their mothers travel to watering holes where the risk of predation is high. Therefore, in these examples, social behaviour seems to function in part to reduce the costs to the parents associated with raising their young.

Reductions in the costs to the parent associated with their offspring's development can result from the behaviour of the offspring as well. For example, the young of several species have been shown to supplement their diet with solid food prior to weaning; this has been observed in bats (*Myotis lucifugus,* Fenton 1969), grey kangaroo (*Macropus canguru,* Poole & Pilton 1964), small rodents (Lackey 1967), jackrabbits (*Lepus californicus,* Sparks 1968) and hyenas (Kruuk 1972). Therefore, whereas the young may not yet have developed sufficiently to survive independently, the early onset of adult-like behaviour (i.e., foraging behaviour) can lessen the overall energetic demands imposed upon their mother by decreasing their dependence on her energy reserves.

The preceding discussion demonstrates that organisms vary considerably in both the nature and extent of parental care behaviour that they exhibit. Moreover, it illustrates that parental care can function as a means not only to allow for offspring provisioning, but also to provide other benefits to the young such as protection from predation. In addition, it illustrates some of the costs associated with parental care tactics and how these costs can be offset. Finally, the discussion serves to introduce two general issues that are addressed in this study with regard to humpback whales. These are as follows:

1. **What maternal care strategy do humpback whales employ in raising their offspring?**

There is a paucity of data related to the specific strategy that female humpback whales employ in raising their offspring. At least two previous studies have suggested that mysticetes adopt a follower approach to caring for their young. Taber & Thomas (1982) demonstrated that, similar to typical follower species, southern right whale (*Eubalaena australis*) calves remain close to their mother at all times. In another study, Smultea (1994) noted that humpback whale (*Megaptera novaeangliae*) cow-calf pairs maintain close proximity throughout their stay on their sub-tropical breeding grounds. These observations, however, were limited to the period during which the animals occupy breeding grounds. As with several mysticetes, both right and humpback whales divide their time between sub-tropical breeding grounds and high-latitude foraging grounds. While on the typically prey-deficient breeding grounds they rarely feed (Chittleborough 1965, Dawbin 1966). Consequently cow-calf pairs spend much of their time exhibiting other non-foraging behaviours such as resting and nursing. Little dedicated work, however, has been conducted to examine the associative behaviour of female mysticetes and their calves once they arrive on the foraging grounds. Because the female's behaviour necessarily changes when on these grounds, shifts in the associative behaviour of the dyad can be expected as well. In order to elucidate this, I examine the associative behaviour of female humpback whales and their calves on a foraging ground in southeast Alaska. Three hypotheses relating to this behaviour that are derived from earlier studies on similar behaviour in other taxa are tested.

Hypothesis 1: Cow-calf proximity is greater during travelling bouts than during foraging bouts.

Hypothesis 2: Cow-calf proximity decreases as the dyad's association lengthens.

Hypothesis 3: Cow-calf proximity is greatest when the behaviour of the dyad is synchronized.

2. What are the negative consequences to the female associated with this strategy, and are there behavioural responses evident in either member of the maternal dyad that could function to offset these consequences?

Several indirect lines of evidence suggest that juvenile humpbacks have a reduced capacity to dive relative to adults. Ultimately, the duration for which a diving animal can remain submerged is related to three physiological factors: its oxygen storage capacity, the rate at which it utilizes stored oxygen, and its anaerobic capacity (Schreer & Kovacs 1997). Oxygen storage capacity, which is a function of blood volume, is linearly related to body mass in mammals; consequently, larger animals have a proportionately greater storage capacity (Schreer & Kovacs 1997). Since the rate at which an animal utilizes stored oxygen (i.e., its metabolic rate) increases 0.75 times as fast as body mass (Kleiber 1961), the relative rate of stored oxygen depletion is less in larger animals relative to their smaller counterparts. In addition, the ability to function anaerobically, which is necessitated by long duration dives, correlates positively with an animal's size (Hochachka & Somero 1984). Therefore, larger animals can be expected to be better equipped to dive for longer durations. This leads to two preliminary hypotheses:

Hypothesis 4: Females dive for longer durations than their offspring.

Hypothesis 5: Calf dive durations increase across the season as the calf increases in size.

Presumably following behaviour has appeared in terrestrial ungulates as a response, in part, to predation (Lent 1974, Estes 1976); by maintaining close proximity, the juvenile follower benefits from maternal vigilance and defence as a means of predator avoidance and protection (Lent 1974, Estes 1976). If, however, calves exhibit a reduced capacity to dive as predicted above, then cow-calf separation may occur whenever long duration dive are necessary for the female. In these instances, the benefits of proximity will be lost. Therefore, to minimize this separation, the female can reduce the duration of her dives whenever the calf remains at the surface.

Hypothesis 6: Females dive for shorter durations when the calf does not follow.

Alternatively, a decrease in the frequency with which the calf remains at the surface during the cow's dive, and an increase in the frequency with which the calf synchronizes its behaviour with the cow, would serve to minimize the separation that occurs between the pair. Therefore, as the calf becomes more adept at diving across the season, both of these can be expected to occur.

Hypothesis 7: Calves synchronize their dives increasingly often as the season progresses.

Hypothesis 8: Calves dive increasingly often as the season progresses.

In addition to addressing these issues, the thesis will examine several other behaviours associated with parental care in humpbacks, including the female's time budgeting behaviour and the behaviour of the maternal dyad in the presence of a third whale. To set the stage, I first provide a review of the literature on northeastern Pacific humpback whale life history.

Literature Review of Northeastern Pacific Humpback Whale Life History

Typical of the large mysticetes, the humpback whale is a migratory species; individuals alternate between low-latitude breeding grounds in the winter and high-latitude foraging grounds in the summer (Nishiwaki 1966, Rice 1974). There are three primary breeding regions where North Pacific humpbacks assemble: (1) in the eastern North Pacific along the west coast of Baja California and mainland Mexico, and near the offshore Revillagigedo Islands; (2) in the central North Pacific around the main Hawaiian Islands; and (3) in the western North Pacific near the Ogasawara, Ryukyu, and Mariana Islands (Nishiwaki 1959, Rice 1978, Calambokidis *et al.* 2001). Interchange between these wintering regions has been observed (Calambokidis *et al.* 2001) but the rarity of such observations in conjunction with genetic evidence (Baker *et al.* 1990, 1994) suggests that it occurs infrequently.

Humpbacks begin to arrive on the wintering grounds in November (Norris & Reeves 1978). Examination of thousands of humpbacks caught by whalers on these grounds indicated that their stomachs are consistently empty of prey organisms (Chittleborough 1965, Dawbin 1966). Furthermore, despite the countless hours spent observing humpbacks on the wintering grounds, there are few observations of feeding (Baraff *et al.* 1991, Gendron & Urban 1993). It is therefore believed that during the winter the animals subsist upon the large reserves of fat stored in their blubber (Brodie 1975). Instead of foraging, individuals participate in mating and reproductive behaviours. Clapham (1996) has described the humpback mating system as a "floating lek". As in a true lek, individual males display their readiness to mate, in this case through the use of their long and complex vocalizations (Winn & Winn 1978, Tyack 1981). The term "floating lek" is used, however, since the system lacks the rigid spatial structure of a true lek.

Females become sexually mature at approximately 5 years of age (Lockyer 1984, Clapham & Mayo 1987a, Clapham 1992) and calve, on average, every two to three years thereafter (Baker *et al.* 1987, Clapham & Mayo 1987b). Gestation lasts approximately 11.5 months (Lockyer 1984). It has been suggested that the peak of calving occurs on the northern hemisphere breeding grounds in February (Herman *et al.* 1980, Balcomb & Nichols 1982, Whitehead 1982). Calves are typically 4-4.5m in length at birth (Chittleborough 1958, Clapham *et al.* 1999).

The number of whales on the wintering grounds is highest in February and then begins to decline as animals commence migration to the high latitude feeding grounds (Norris & Reeves 1978). Several authors have noted that the migration is segregated by sex and reproductive class (Chittleborough 1965, Dawbin 1966). Newly pregnant females are typically among the first to leave, presumably to benefit from a longer feeding season. Conversely, cow-calf pairs remain on the wintering grounds the longest, likely so the calf can gain sufficient strength to complete the journey to the feeding grounds.

Humpbacks in the north Pacific migrate to foraging grounds along the rim of the Pacific Ocean from California to the Aleutian Islands and the Russian far east. Research has shown that individuals assemble into geographically isolated feeding herds (Baker *et al.* 1986, Perry *et al.* 1990, Calambokidis *et al.* 2001). These include: the continuous coast of California, Oregon and Washington, which is believed to be the destination of humpbacks wintering in Mexican waters (Baker *et al.* 1986, Calambokidis *et al.* 2001), and northern British Columbia, southeast Alaska, Prince William Sound, the Kodiak Islands, and the Aleutian archipelago, whose population is composed almost entirely of Hawaiian migrants (Darling & McSweeney 1985, Baker *et al.* 1985, 1986, 1992, Calambokidis *et al.* 2001). There is some evidence to suggest that the latter feeding herd is actually comprised of several isolated herds with relatively little interchange between them (Calambokidis *et al.* 2001). Although there is a lack of sufficient evidence regarding the destination of humpbacks wintering in Japanese waters, solitary individuals have been sighted off both the Kodiak Islands and the coast of British Columbia (Calambokidis *et al.* 2001).

On the feeding grounds, humpback whales exhibit a diverse assemblage of feeding behaviours. They are observed feeding at depth (Dolphin 1988), lunge feeding at the surface (Jurasz & Jurasz 1979), or using their appendages to corral, stun or concentrate prey (Jurasz & Jurasz 1979, Weinrich *et al.* 1992). Humpbacks employ these foraging tactics to feed upon a number of different prey species. Several studies have suggested that in southeast Alaska euphausiids contribute most to the diet of individuals (Dolphin 1987a, 1988, Krieger 1990). Krieger (1990) has gone so far as to suggest that at the time of his investigations the overall distribution of most whales in southeast Alaska was related to euphausiid distribution. The euphausiid species most frequently reported in association with feeding whales there are: *Thysannoessa raschi* (Krieger & Wing 1984, 1986, Dolphin 1987a, 1988, Krieger 1990), *T. longipes* (Bryant *et al.* 1981), and *Euphausia pacifica* (Jurasz & Jurasz 1979, Bryant *et al.* 1981, Krieger & Wing 1984, 1986, Dolphin 1987a, Krieger 1990). Humpbacks also frequently consume schooling fish, including Pacific herring (*Clupea pallisii*) (Jurasz & Jurasz 1979, Baker *et al.* 1985, Krieger 1990, Straley 1990, Baker *et al.* 1992), capelin (*Mallotus villosus*) (Jurasz & Jurasz 1979, Krieger 1990, Baker *et al.* 1992), sandlance (*Ammodytes hexapterus*) (Jurasz & Jurasz 1979, Baker *et al.* 1992) and walleye pollock (*Theragra chalcogramma*) (Krieger 1990).

Individuals typically forage alone or in loose ephemeral groups (Weinrich 1991), although long-term stable associations have been noted (Weinrich 1991, Baker & Herman 1984, Sharpe 2001). Females with calves are considerably less social than other individuals. Clapham & Mayo (1987b) have indicated that cow-calf pairs were associated with other whales in only 23.3% of sightings whereas the same mature females in years without calves were associated with other whales in 72.5% of sightings.

The process of weaning commences on the feeding grounds. Van Lennep & van Ultrecht (1953, *in* Clapham & Mayo 1987b) have suggested that this process is gradual, with a transition period that includes both nursing and feeding on prey items. Calves are typically observed feeding for the first time in late July and August (Clapham & Mayo 1987b). Given that the height of parturition occurs in February, these calves are on average 5-6 months of age. The contribution that independently acquired food makes to the calves' diet, however, is unknown. The occasional observations of calves blowing bubble clouds in conjunction with their mother's feeding suggest that at least some behaviours may be learned by mimicry early in the weaning process (Clapham & Mayo 1987b). Gabrielle *et al.* (2001) have suggested that calves appear to become progressively more independent as weaning continues, until eventually the two animals separate. It is generally believed that the calves are fully weaned and separation occurs by the end of their first year (Chittleborough 1958, Baker *et al.* 1987). Separation usually occurs in tropical or subtropical waters before or during the early part of the calf's second winter (Baker *et al.* 1987, Clapham & Mayo 1987b, 1990); however, some mothers and calves have been observed to separate on the feeding grounds in late autumn (Clapham & Mayo 1987b, 1990, Baraff & Weinrich 1993). Calves typically attain body lengths of 8-10m at independence (Clapham *et al.* 1999).

That weaning occurs in humpback whales during their return migration to, or upon arriving at, their breeding grounds between 10.5 to 12 months after parturition is somewhat unusual among mysticetes. Other members of the family Balaenopteridae demonstrate considerably shorter weaning periods. For example, female blue whales (*Balaenoptera musculus*) wean their offspring after 7 months, as do fin whales (*B. physalis*), and perhaps sei whales (*B. borealis*) (Lockyer 1984). Bryde's whale (*B. edeni*) females wean their offspring after approximately 6 months (Lockyer 1984), whereas Minke whales (*B. acutorostrata*) do so between 4 and 6 months after parturition (Best 1982). The single member of the family Eschrictidae, the Gray whale (*Eschrichtius robustus*), appears to wean its offspring in under 7 months as well (Rice & Wolman 1971). The reasons for these differences, however, are unknown.

Several studies have noted that calves demonstrate some degree of post-weaning site fidelity (Baker *et al.* 1987, Clapham & Mayo 1987b, 1990, Weinrich 1998). For example, Weinrich (1998) demonstrated that calves sighted with their mothers on Stellwagen Bank, a 32km-long narrow bank in the Atlantic, were significantly more likely to return there than to a similar feeding area only several kilometres away. It should be noted, however, that although yearlings and their mothers are often found within a few kilometres of each other, they typically do not associate with one another (Baker *et al.* 1987).

Methods

I observed humpback whale mother-calf pairs in Frederick Sound and Chatham Strait, southeast Alaska between the months of June and September, 2001 and 2002 (Figure 1). These connected bodies of water represent a summer foraging ground for humpbacks in the North Pacific. I made all observations from one of three research platforms: a 50ft wooden vessel, or either a 20ft or 12ft rigid hulled inflatable. A total of 154 hours of observations on 42 different cow-calf pairs are used in this analysis. The duration of individual observations ranged from 25min to 8h03min with a mean of 3h44min.

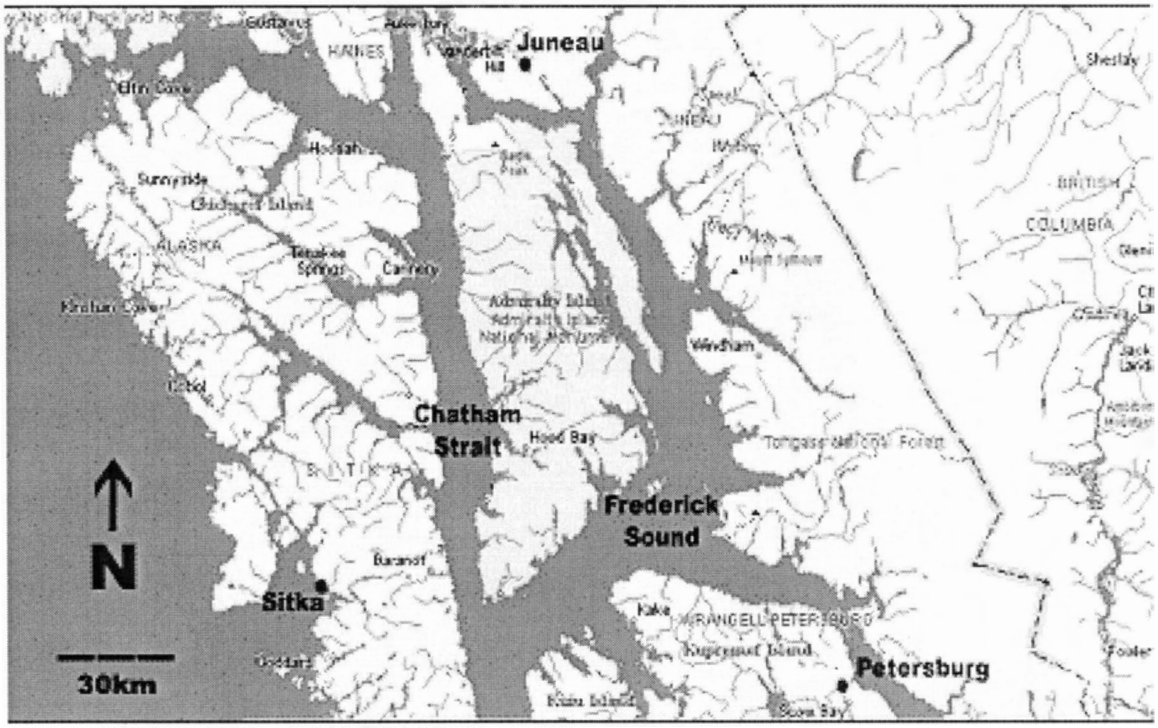

Figure 1. Map of southeast Alaska. Study area includes Chatham Strait and Frederick Sound and is located approximately between latitudes 57°00′N and 58°00′N, and longitudes 133°30′W and 135°00′W.

At the beginning of each observation day, I conducted a search until a mother-calf pair was encountered. These pairs are easily recognized by their close association, the marked size difference between the two (the calf is typically one third to one half the length of its mother; Clapham & Mayo 1987b), and the difference in the size of their blows. In addition, I approached single animals to determine whether they were calves that had separated from their mothers. Upon confirming that either a calf or a pair had been found, I positioned the boat at least 50m from the animals and made an attempt to adjust speed to match that of the whales. At that time, I commenced focal pair continuous sampling observations (Altmann 1974).

Unique fluke pigmentation, shape, and scarring allowed individual animals to be identified throughout and across encounters (Katona & Whitehead 1981). In instances where several animals were encountered together, I used the shape of the dorsal fin to identify individuals during surfacings when the flukes were not visible. Whenever the same individuals were encountered on more than one day within a single seasonal period (see SEASON below), the resulting data were pooled and treated as a single encounter. On two occasions, the same pair was observed in two different seasonal periods; these were treated as independent encounters. I recorded all encounters on either a Sony Digital-8 or miniDV digital video camera for later analysis; a time code is included on all recordings. To assist with later data transcription, I dictated field observations into the camera's microphone. These included: surfacing events, the identity of the individual that was being observed (i.e., mother, calf, or other); the orientation of each individual based upon compass headings and estimated to the nearest 22.5 degrees; the proximity of individuals to one another estimated in terms of cow body lengths between dorsal fins; and, any observable surface phenomena such as the appearance of bubble rings, surface foraging lunges, or aerial behaviour. Encounters were terminated after 8 hours of observations, or when necessary as a result of inclement weather, loss of light, or loss of the cow-calf pair. All observations occurred between 0800h and 2200h.

Upon reviewing the video tapes, I determined the time of each surfacing event. Since this was determined from the time code on the video at the moment when the blow appeared in the frame in conjunction with the dictated verification of the event made by myself in the field, surface time measurement error is considered to be negligible. In instances where I could not confidently identify an individual as being either the mother or calf, I coded the data as unknown and removed them from analysis. I reviewed each encounter at least twice to verify all observations.

To determine if patterns in mother-offspring behaviour varied temporally, encounters were subsequently divided into three observation periods (SEASON):

1) observations before July 15; 2) observations between July 15 and August 14; and 3) observations after August 14. The earliest observation occurred on June 9, 2002 whereas the latest occurred on September 14, 2002. Although humpbacks typically arrive on the feeding grounds sooner than the first recorded observation and remain several months after the last, extrinsic factors (primarily inclement weather) prevented observation outside of the study period.

For the sake of behavioural classification, I divided observations into individual cow dive cycles. A complete dive cycle, following that described by Dolphin (1987b), consisted of a surface interval with one or more ventilations and a corresponding dive (see Figure 2); a dive is defined here as any period between surfacings where the animal was submerged for 90s or more. Dive cycles in which the identity of the individual (i.e., mother, calf or other) could not be determined during the first or last surfacings within a cycle were omitted from analysis.

To determine whether patterns in mother-offspring behaviour varied with the behaviour of the female (BEHAVIOUR), I then classified the cycles into one of two categories based upon both the directional behaviour of the cow during surfacing events and her behaviour at the end of each dive cycle. To be classified as behavioural state 1 an animal had to travel on a relatively straight course with deviations of no more than 22.5 degrees between: i) the first and last surfacings of a dive cycle (i.e., within a surface interval); ii) the last surfacing of the current cycle and the first surfacing of the subsequent cycle (i.e., at the beginning and end of a dive); and iii) the first surfacing of the current cycle and the last surfacing of the subsequent cycle (i.e., across two consecutive dive cycles). In addition, the animal could not be observed to terminal dive (i.e., raise its flukes) during a dive cycle. Animals classified under behavioural state 1 maintained a straight course for an extended period; for the sake of discussion, I termed this behaviour "travelling". Animals exhibiting behavioural state 2 were typically erratic and rarely maintained a straight course; this behaviour was termed "foraging". The recognition that occasional deviations occurred during otherwise prolonged behavioural states led to the inclusion of another condition. For a change of state to occur, the new state had to persist for at least two dive cycles and/or 12min (the approximate average duration of two cycles). Two exceptions to this classification scheme exist. Both direct and/or indirect observations of feeding, such as surface lunging or the appearance of bubble rings or nets (see Jurasz & Jurasz 1979, Hain *et al.* 1982) at the surface in the vicinity of a whale resulted in classification as behavioural state 3, which I termed "surface foraging". Similarly, observations of animals remaining motionless at the surface for a period of 10min or more resulted in their behaviour being classified as behavioural state 4, termed "resting".

For the proximity analysis, I estimated the distance between the female and calf in terms of the female's body length (BL) whenever both animals were visible at the surface. In each case, I attempted to estimate the distance between the dorsal fins of each animal. Whenever the female and calf were estimated to be greater than 3 body lengths from one another, distances were scored as being either less than or greater than 50m. If I could not determine the identity of either animal (i.e., mother, calf or other) or the distance between the individuals could not be confidently estimated, the data were omitted from analysis. Since I conducted all observations, estimations of distances are believed to be consistent across the duration of the study.

Using these data, I examined four proximity measures: the frequency with which the calf was < ½ BL from the cow (0.5BL); the frequency with which the calf was <1 BL from the cow (1.0BL); the frequency with which the calf was <1½ BL from the cow (1.5BL); and, the frequency with which the calf was <50m from the cow (<50). Each measure was calculated as the number of surfacings where the calf was less than the relevant distance divided by the total number of surfacings where distances could be confidently estimated. I compared each of these measures across the three observational periods (SEASON) and behavioural states (BEHAVIOUR). In addition, a third independent variable was created (SYNCDIVE) to investigate if proximity behaviour is a function of female and calf dive synchrony. This variable compares surfacing and diving patterns between the female and calf within corresponding dive cycles and has two treatments, synchrony and asynchrony. For SYNCDIVE synchrony to occur (Figure 2, dive cycle 1), the female and calf had to surface within 20s of one another on the last surfacing of a dive cycle (violated in dive cycle 3, Figure 2) and again on the first surfacing of the subsequent cycle (violated in dive cycle 4, Figure 2). In addition, the calf could not surface intermittently during the duration of the female's dive (violated in dive cycle 2, Figure 2). For synchrony to occur, the female and calf had to dive at the same time for the same duration.

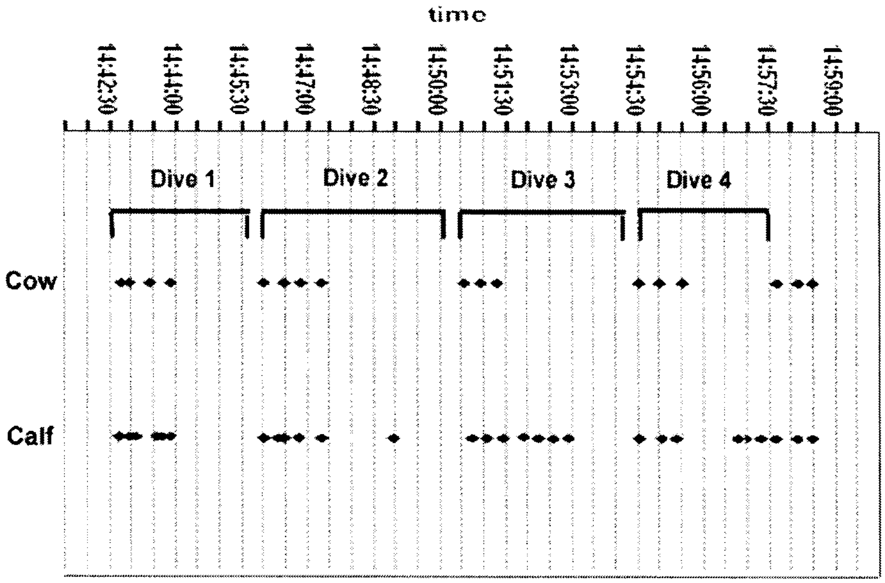

Figure 2. Four typical cow dive cycles are shown (Dive 1 through 4) to illustrate SYNCDIVE synchrony and asynchrony. Diamonds represent individual surfacings for cow (upper series) and calf (lower series). Time is indicated on the horizontal axis; vertical bars are 30s apart.

Dive cycles were coded as either a 1 when the conditions for synchrony were met or a 0 when they were not, and proximity was compared across these two treatments.

Finally, to determine if the presence of an additional animal affected the position of the calf relative to its mother, encounters where a third individual was present were examined. Specifically, I calculated the frequency of surfacings with which the calf and the third animal were separated from one another by the female (as opposed to surfacings where the calf and the third animal were side by side). This variable was compared across the three observation periods.

Following the proximity analysis, I compared the time budgets of cows across the three observation periods: early, mid and late season. Each encounter was partitioned into the four behavioural categories described above. Foraging and surface foraging bouts were subsequently combined into a single category, "foraging". I calculated the proportion of time the cow was observed in each behavioural state during a given encounter as:

time observed in behavioural state X / total time

For this calculation, total time was calculated as the sum of time spent exhibiting all *identified* behaviours within an individual encounter, which typically represented 95-100% of the total encounter duration.

Next, I conducted an analysis of the dive behaviour of both the female and the calf. Initially, I compared the female's dive durations across behaviours (BEHAVIOUR) and observation periods (SEASON). Following that, I compared female and calf dive durations to one another within behaviours and observation periods. In addition to the behavioural and seasonal analysis, I examined the female's dive durations across two synchrony variables (FULLDIVE and DIVE). As with SYNCDIVE, these are based upon specific sets of conditions that identify synchronized behaviour between the female and her calf. Again, each variable reflects surfacing and diving patterns between the female and calf within corresponding dive cycles. For analysis, dive cycles were coded as either a 1 when the conditions for the specific variable were met or a 0 when they were not. Several of the conditions for FULLDIVE synchrony are identical to those for SYNCDIVE; for synchrony to occur (dive cycles 1 and 4, Figure 3), the cow and calf had to surface within 20s of one another on the last surfacing of a dive cycle (violated in dive cycle 2, Figure 3) and again on the first surfacing of the following cycle (violated in dive cycle 3, Figure 3). In addition, the calf could not surface intermittently during the duration of the female's dive. Unlike SYNCDIVE, however, only those cycles where the last surfacing of the dive cycle (terminal dive) for both the female and the calf were within 20s of each other are included in the analysis (therefore dive cycle 2 is omitted from analysis, Figure

3). Therefore, a dive cycle is coded as 1 under FULLDIVE when the calf's dive is completely synchronized with the female, whereas the cycle is coded as 0 when the female and calf *initially dove together,* but the calf surfaced at least 21 seconds prior to the female on the following cycle. In other words, the variable distinguishes between dives where initial synchrony exists but the calf surfaces sooner than the cow and those where it remains with the cow for the entire duration of the dive.

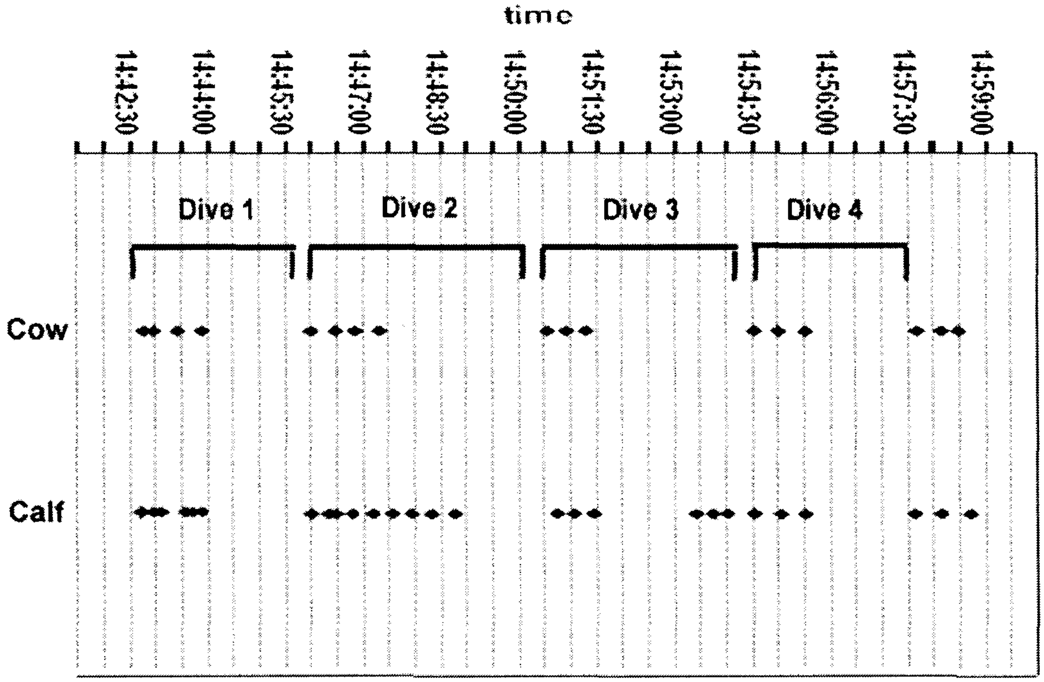

Figure 3. Four typical cow dive cycles are illustrated (DIVE 1 through 4) to indicate FULLDIVE synchrony and asynchrony. Diamonds represent individual surfacings for cow (upper series) and calf (lower series). Time is indicated on the horizontal axis; vertical bars are 30s apart.

For DIVE synchrony to occur (dive cycles 1 and 2, Figure 4), the calf must dive for >90s during a given cow dive cycle (violated in dive cycles 3 and 4, Figure 4). This variable distinguishes between dive cycles where the calf dives, in which case the cycle is coded as 1, and those where it remains at the surface for the duration of the cow's dive, in which case the cycle is coded as 0. For analysis, I compared cow dive durations across the two treatments within each synchrony variable.

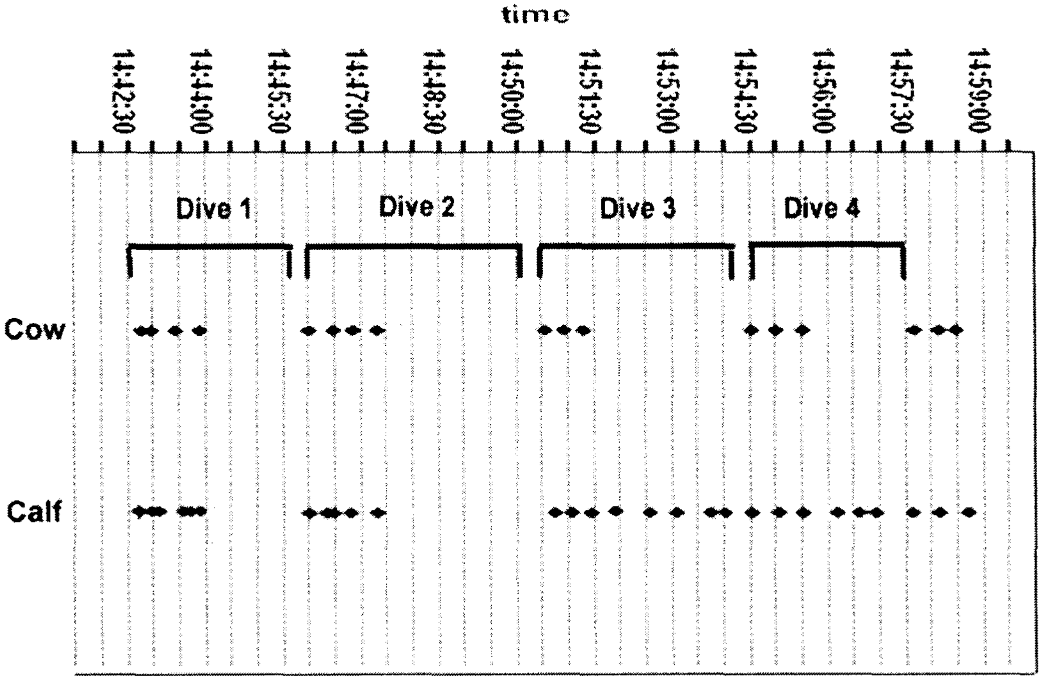

Figure 4. Four typical cow dive cycles are illustrated (DIVE 1 through 4) to demonstrate DIVE synchrony and asynchrony. Diamonds represent individual surfacings for cow (upper series) and calf (lower series). Time is indicated on the horizontal axis; vertical bars are 30s apart.

For the behavioural synchrony analysis, the variables SYNCDIVE and DIVE were treated as dependent variables. To do so, I calculated the frequencies with which the synchronized condition of each variable occurred during each encounter. In other words, for each variable the frequency was calculated as the number of dive cycles where synchrony occurred divided by the total number of dive cycles in that encounter. Only those dive cycles where either synchrony or asynchrony was identified were used in the analysis. To determine whether these frequencies changed with calf development, or were more likely during specific behaviours, values for each dependent variable were compared across both SEASON and BEHAVIOUR.

For all analyses, I determined the mean or frequency of each dependent variable for each individual encounter; each encounter therefore provided only a single measure for each treatment of each relevant independent variable. Once aggregated in this manner, the data were found to be highly skewed and to resist transformation to normality. As a result, I used non-parametric tests (Kruskal Wallis, Mann-Whitney U and Wilcoxon Signed Ranks; SPSS10) to identify differences in dependent variables across all treatments of each individual independent variable (i.e., SEASON, BEHAVIOUR, SYNCDIVE, FULLDIVE and DIVE). Because non-parametric tests do not initially allow for higher order interactions to be identified between variables, these were examined by repeatedly partitioning the dataset to control for each variable. For example, to test for a higher order interaction between BEHAVIOUR and SEASON on dive duration, two series of tests were conducted. In the first, differences in dive duration were examined across behaviours in each of the three SEASON treatments separately. Additionally, in the second series, differences across seasons were examined in each of the three BEHAVIOUR treatments separately.

Results

Proximity Analysis:

Four measures of proximity are used in the following analysis: the frequency with which the calf is within ½ body length (BL) from the cow (0.5BL); the frequency with which the calf is within 1 BL (1.0BL); the frequency with which the calf is within 1 ½ BL (1.5BL); and, the frequency with which the calf is less than 50m from the cow (50M). The effects of observation period (SEASON), behavioural state (BEHAVIOUR) and dive synchrony (SYNCDIVE) on these measures are examined. SYNCDIVE is treated here as an independent variable with two treatments: "synchronous" when the conditions for dive synchrony are met; and, "asynchronous" when they are not. When not included in the text, specific values for dependent variables are reported in the Appendix.

The results from the proximity analysis support hypothesis 1, that cow-calf proximity is greatest during travelling bouts; the frequencies with which the calf is within 0.5 BL, 1.0 BL, 1.5 BL and 50m are all significantly lower during foraging and surface foraging bouts relative to travelling bouts (BEHAVIOUR, Table 1, Figure 5). However, hypothesis 2, that cow-calf proximity decreases as the dyad's association lengthens, is not initially supported; none of the proximity measures differ significantly across the season (SEASON, Table 1, Figure 6).

Table 1. Results of Kruskal-Wallis test for differences in the frequency with which the calf is within 0.5 body lengths (0.5BL), 1.0 body length (1.0BL), 1.5 body lengths (1.5BL) and 50m (50M) from the cow across the season and behaviours. Values in bold type are significant at $p<0.05$.

	Season			**Behaviour**		
	X^2	df	P	X^2	Df	P
0.5BL	1.04	2	0.594	21.93	2	**0.000**
1.0BL	0.70	2	0.716	14.02	2	**0.001**
1.5BL	0.87	2	0.648	13.40	2	**0.001**
50M	0.16	2	0.924	11.65	2	**0.003**

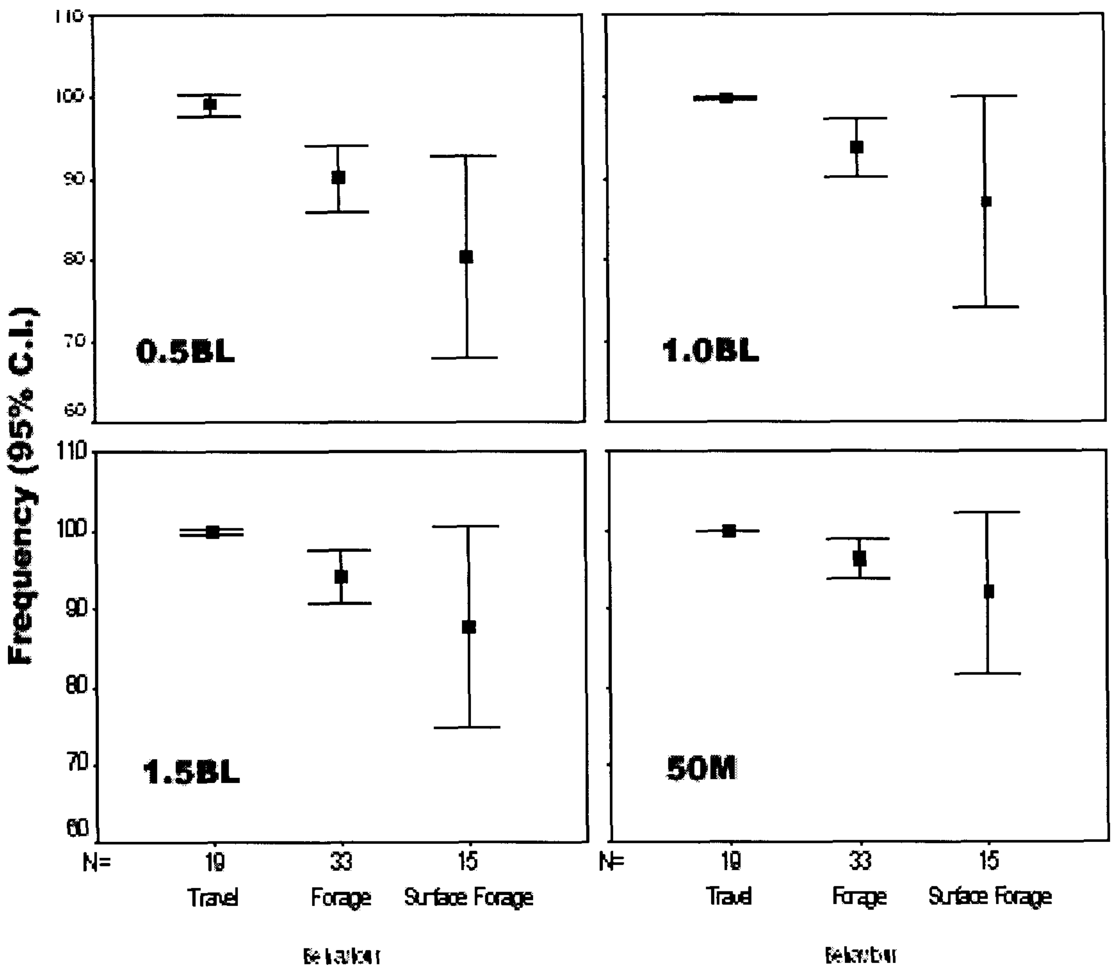

Figure 5. Frequency with which the calf is <0.5 body length (0.5BL), <1.0 body length (1.0BL), <1.5 body lengths (1.5BL) and <50 metres (50M) from the cow during travelling, foraging and surface foraging bouts. Error bars represent 95% confidence intervals.

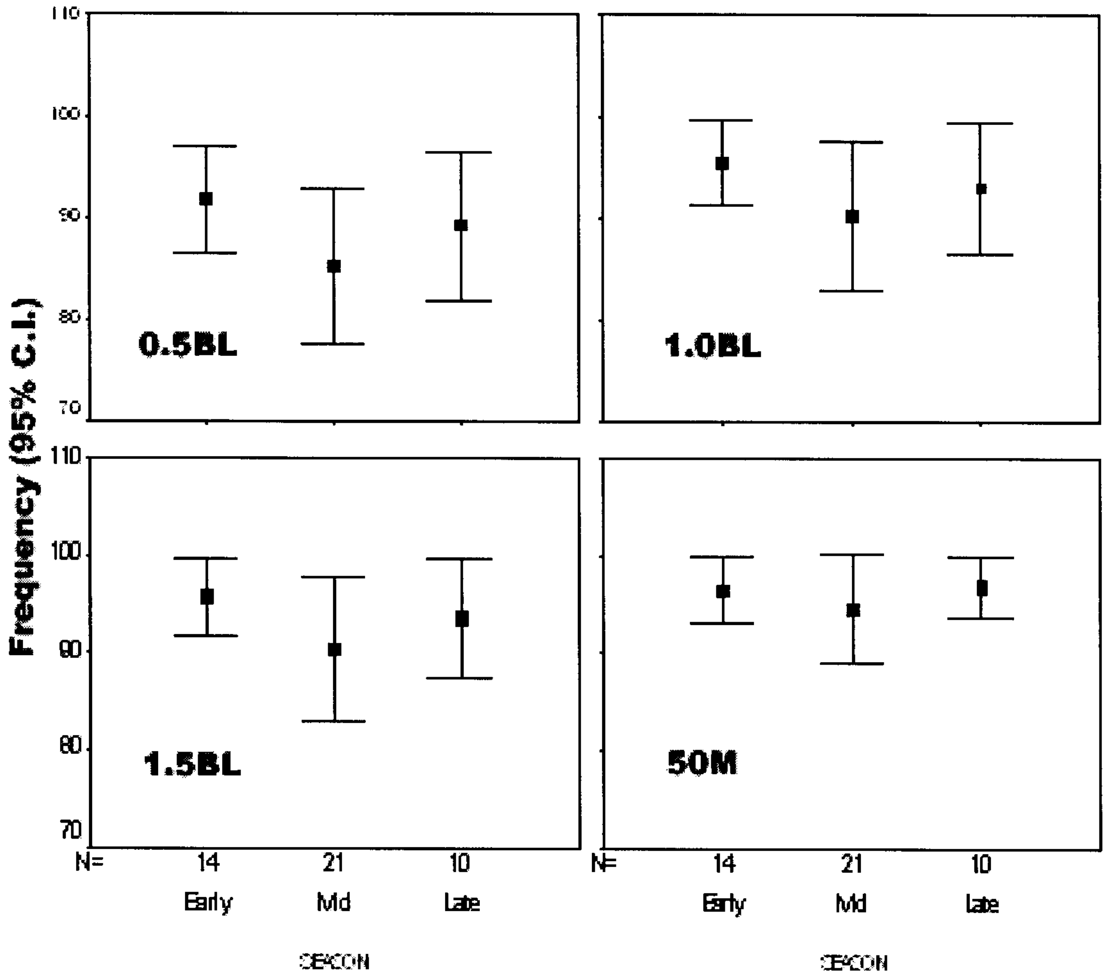

Figure 6. Frequency with which the calf is <0.5 body length (0.5BL), <1.0 body length (1.0BL), <1.5 body lengths (1.5BL) and <50 metres (50M) from the cow during early, mid and late season observations. Error bars represent 95% confidence intervals.

Examination of the interactive effect of SEASON and BEHAVIOUR on proximity, however, reveals that seasonal trends, although not significant, are apparent when individual behaviours are viewed separately (Table 2, Figure 7). During travelling bouts, there is little variation in any of the proximity measures across the season; in nearly 100% of all observations, the calf is within 1BL of the female (Figure 7). Conversely, during foraging bouts there is a tendency for each proximity measure to decrease as the season progresses so that by late season the calf is further than 1.0 BL during approximately 10% of all foraging and surface foraging bouts (Figure 7).

Examination of the interactive effects of behaviour and synchrony on proximity shows that, although in some instances statistically significant, the differences in proximity between behaviours during synchronous dive cycles are small (Table 3, Figure 8); however, there are large significant differences in each

Table 2. Results of Kruskal-Wallis test for differences in the frequency with which the calf is within 0.5 body lengths (0.5BL), 1.0 body length (1.0BL), 1.5 body lengths (1.5BL) and 50m (50M) from the cow across the season during travelling, foraging and surface foraging bouts.

	Travel			**Forage**			**Surface Forage**		
	X^2	Df	p	X^2	df	P	X^2	df	p
0.5BL	3.60	2	0.158	2.57	2	0.277	1.34	2	0.512
1.0BL	3.00	2	0.223	0.85	2	0.655	0.17	2	0.917
1.5BL	3.00	2	0.223	0.71	2	0.702	0.54	2	0.765
50M	0.00	2	1.000	0.98	2	0.612	0.12	2	0.941

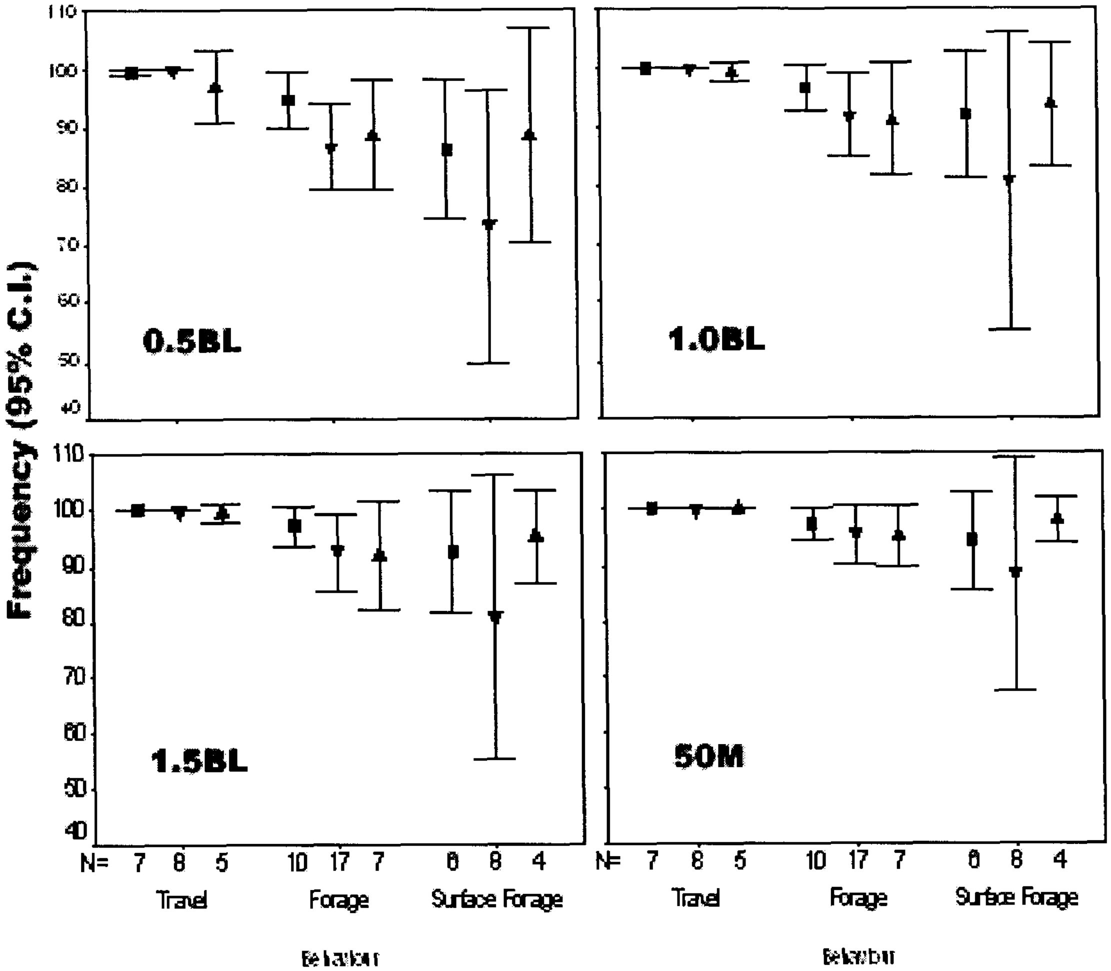

Figure 7. Frequency with which the calf is <0.5 body length (0.5BL), <1.0 body length (1.0BL), <1.5 body lengths (1.5BL) and <50 metres (50M) from the calf within individual behaviours during early (■), mid (▼) and late (▲) season observations. Error bars represent 95% confidence intervals.

Table 3. Results of Kruskal-Wallis test for differences in the frequency with which the calf is within 0.5 body lengths (0.5BL), 1.0 body length (1.0BL), 1.5 body lengths (1.5BL) and 50m (50M) from the cow during either asynchronous or synchronous dive cycles (SYNCDIVE). Values in bold type are significant at $p<0.05$.

	Asynchrony			**Synchrony**		
	X^2	df	P	X^2	df	P
0.5BL	26.30	2	**0.000**	13.82	2	**0.001**
1.0BL	16.81	2	**0.000**	9.51	2	**0.009**
1.5BL	13.11	2	**0.001**	9.49	2	**0.009**
50M	11.16	2	**0.004**	3.16	2	0.206

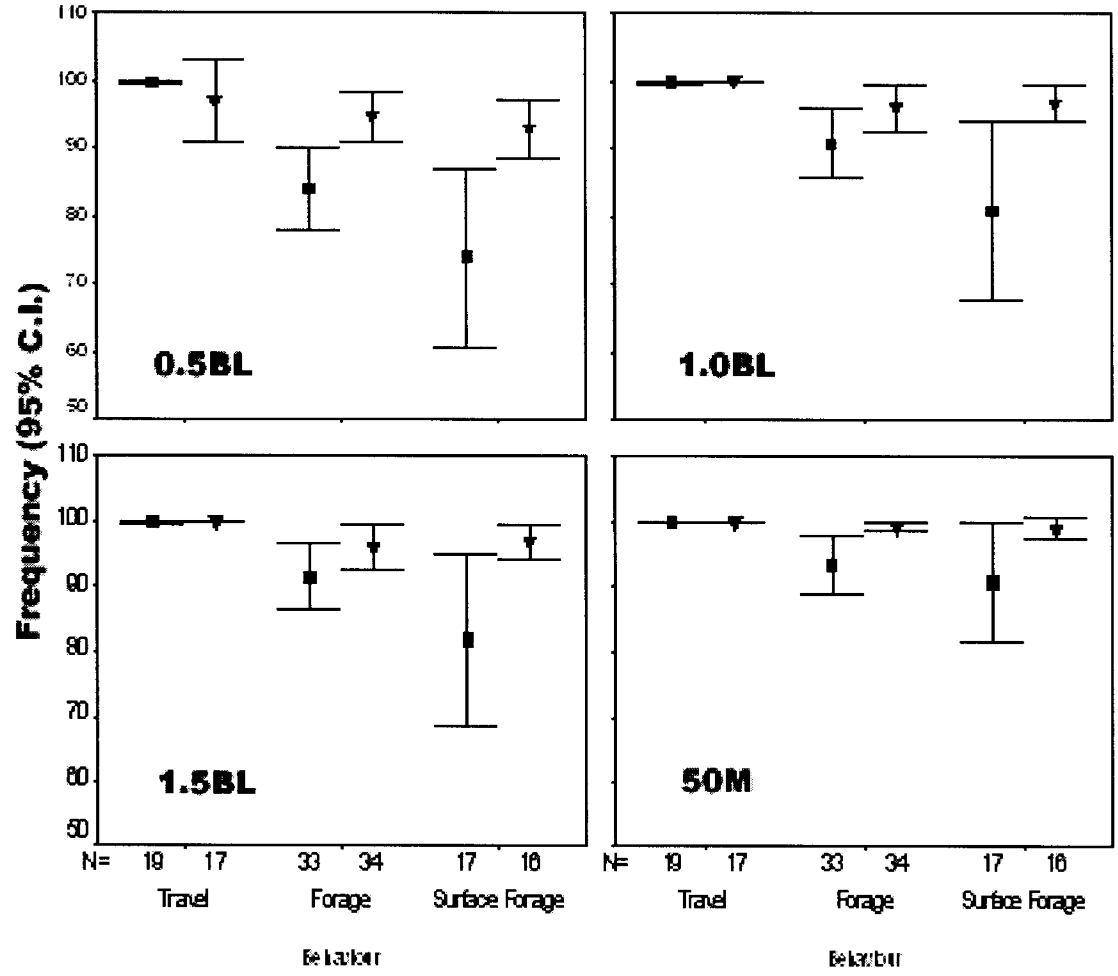

Figure 8. Frequency with which the calf is <0.5 body length (0.5BL), <1.0 body length (1.0BL), <1.5 body lengths (1.5BL) and <50 metres (50M) from the calf during asynchronous (■) and synchronous (▼) SYNCDIVE travel, forage and surface forage bouts. Error bars represent 95% confidence intervals.

proximity measure between behaviours during asynchronous cycles (Table 3, Figure 8). Furthermore, whereas there are no significant differences in any proximity measure between asynchronous and synchronous travel cycles, there are for several proximity measures during foraging and surface foraging cycles (Table 4, Figure 8). Therefore, hypothesis 3, that cow-calf proximity is greatest when the behaviour of the dyad is synchronized, is supported during both types of foraging only.

Although sample sizes preclude meaningful statistical analysis, differences in proximity behaviour that emerge from examination of the interactive effects of SEASON, BEHAVIOUR and synchrony are notable. During travelling bouts, proximity measures vary little between synchronous and asynchronous cycles (Figure 9). With the exceptions of 0.5BL during early season and 0.5BL, 1.0BL and 1.5BL during late season asynchronous cycles, and 0.5BL

Table 4. Results from Mann Whitney U test for differences in the frequency with which the calf is within 0.5 body lengths (0.5BL), 1.0 body length (1.0BL), 1.5 body lengths (1.5BL) and 50m (50M) from the cow between asynchronous and synchronous (SYNCDIVE) travelling, foraging or surface foraging dives. Values in bold type are significant at $p<0.05$.

	Travel		**Forage**		**Surface Forage**	
	Z	**P**	**Z**	**P**	**Z**	**P**
0.5BL	-0.842	0.661	-3.111	**0.002**	-2.704	**0.006**
1.0BL	-0.946	0.802	-1.726	0.084	-2.175	**0.034**
1.5BL	-0.946	0.802	-1.629	0.103	-1.703	0.110
50M	0.000	1.000	-2.723	**0.006**	-1.996	0.094

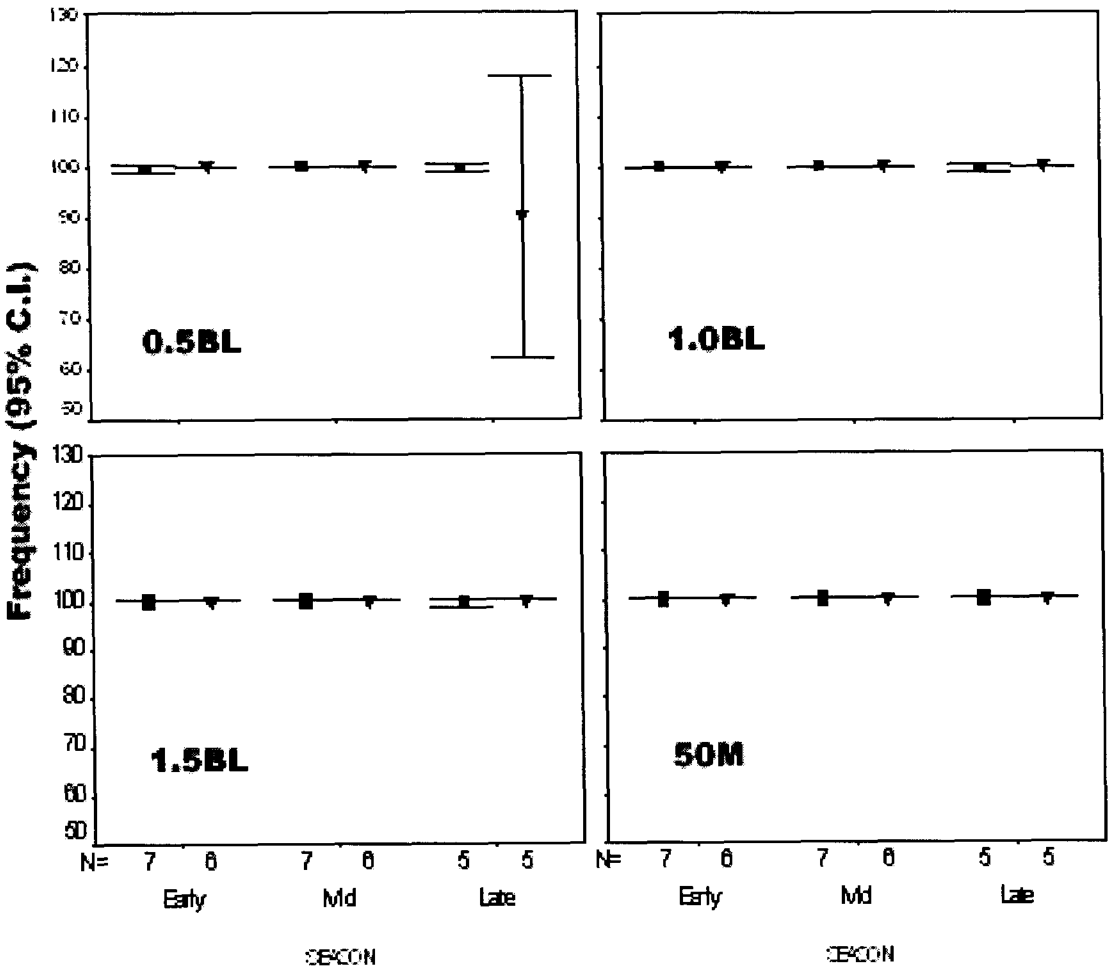

Figure 9. Frequency with which the calf is <0.5 body length (0.5BL), <1.0 body length (1.0BL), <1.5 body lengths (1.5BL) and <50 metres (50M) from the calf during asynchronous (■) and synchronous (▼) SYNCDIVE travel cycles in early, mid and late season. Error bars represent 95% confidence intervals.

during late season synchronous cycles, all values are 100%. Although values tend to be lower, there is a similar tendency for proximity to remain the same across the season during synchronous foraging cycles (Figure 10); however, proximity tends to decrease from early to late season during asynchronous foraging cycles.

Finally, whenever a third animal is present during an observation, there is no difference across the season in the frequency with which the calf is separated from the visitor by the female (X^2=0.620, df=2, p=0.733; Figure 11). In other words, the calf is equally likely to be on the opposite side of the female relative to the third animal as it is to be on the same side (and thus side by side with the visitor).

In summary, the proximity analysis suggests that at all times during travelling bouts the female and calf maintain close proximity. Furthermore, when the female and calf are synchronized during other behavioural states, similar close proximity is maintained. Conversely, the distance between female and calf tends to be greatest during asynchronous non-travel cycles. In addition, there is a tendency for proximity to decrease as the season progresses during these cycles.

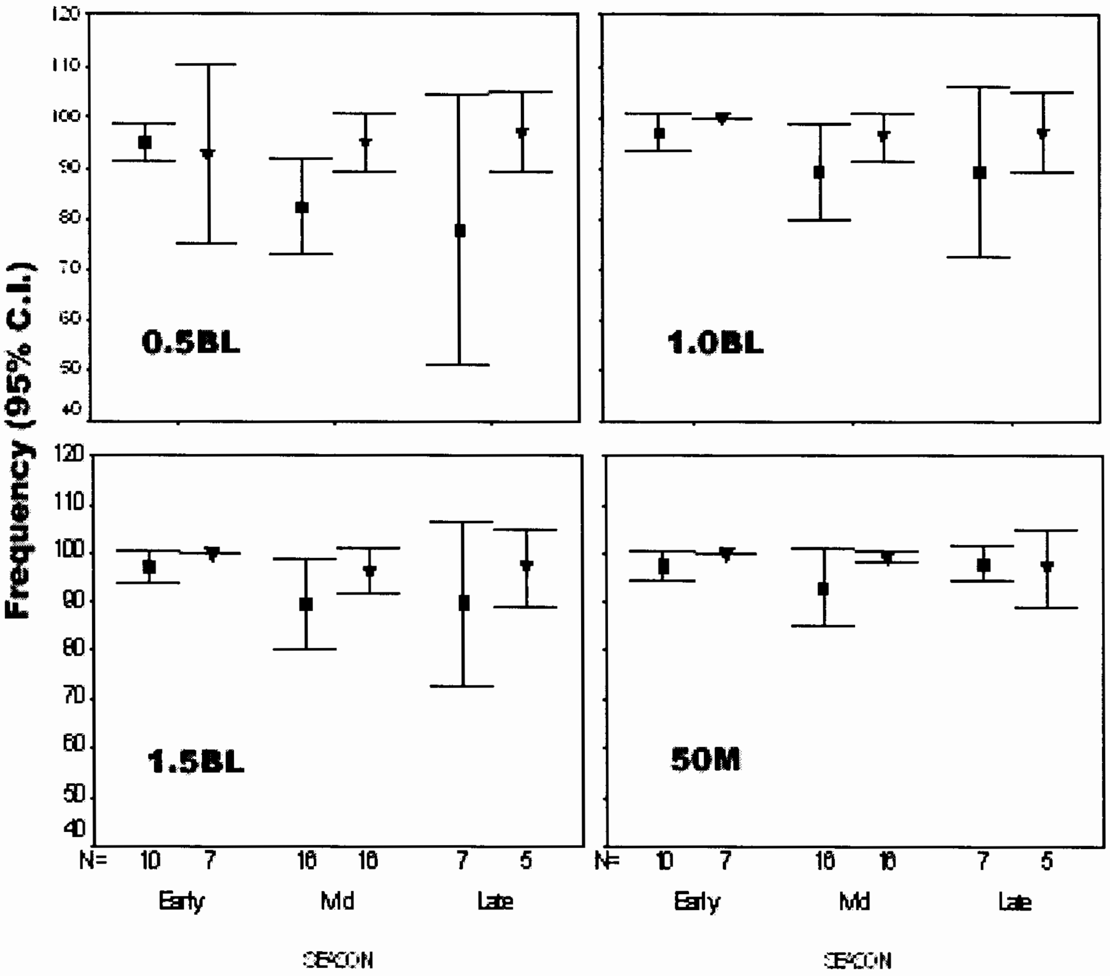

Figure 10. Frequency with which the calf is <0.5 body length (0.5BL), <1.0 body length (1.0BL), <1.5 body lengths (1.5BL) and <50 metres (50M) from the calf during asynchronous (■) and synchronous (▼) SYNCDIVE forage cycles in early, mid and late season. Error bars represent 95% confidence intervals.

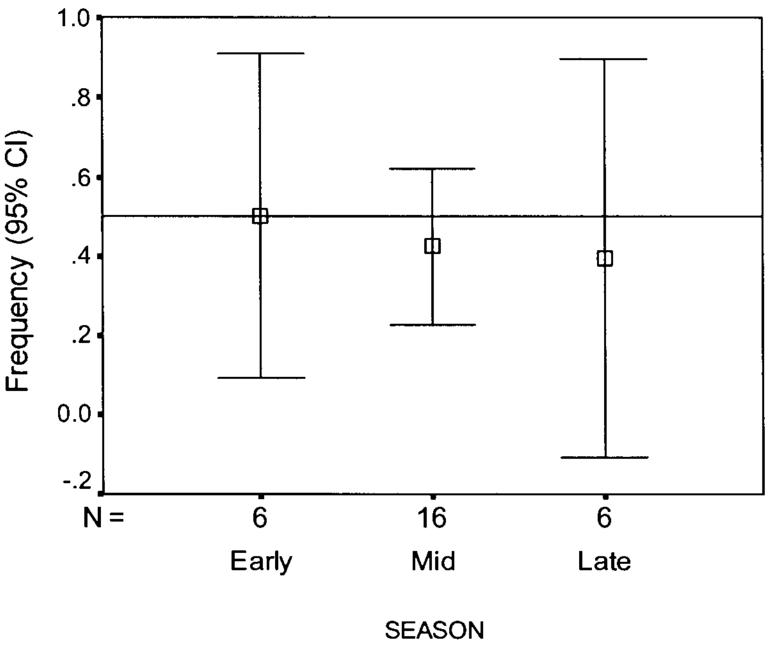

Figure 11. The frequency with which the calf is in the centre of the trio when a third whale is present in early, mid and late season. Error bars represent 95% confidence intervals.

Time Budget Analysis:

Across the season, there are no significant differences in the frequency with which females with calves are observed to be either foraging (foraging and surface foraging combined; $X^2=0.57$, df=2, p=0.752), travelling ($X^2=1.22$, df=2, p=0.543), or resting ($X^2=0.31$, df=2, p=0.858) (Figure 12). Females are observed to forage during approximately 80% of all observations. Conversely, rest behaviour is only observed during approximately 0.2-2% of all observations. Because of the low frequency of its occurrence, rest has been removed from the remaining behavioural analyses.

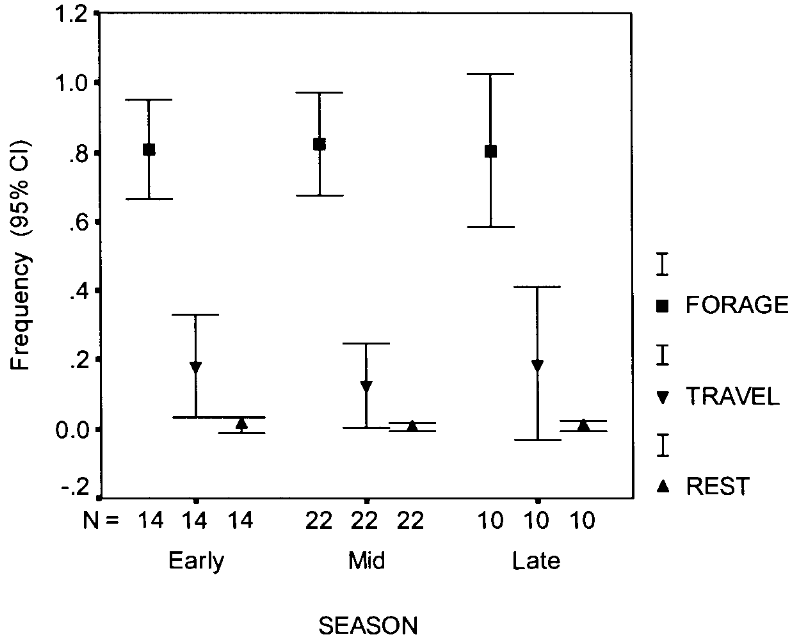

Figure 12. The frequency with which foraging, travelling, and resting are observed during early, mid and late season. Error bars represent 95% confidence intervals.

Dive Behaviour Analysis:

When not included in the text, specific values for dependent variables are reported in the Appendix. Overall, mean cow dive duration (DIVEDUR) is significantly longer during foraging bouts than either travelling or surface foraging bouts ($X^2=33.42$, df=2, $p<0.001$; Figure 13). During foraging bouts, however, mean calf dive duration (CFDIVEDUR) is significantly shorter than DIVEDUR (Wilcoxon Signed Ranks test: Z=-4.208, $p<0.001$). There are no significant differences between CFDIVEDUR and DIVEDUR during either

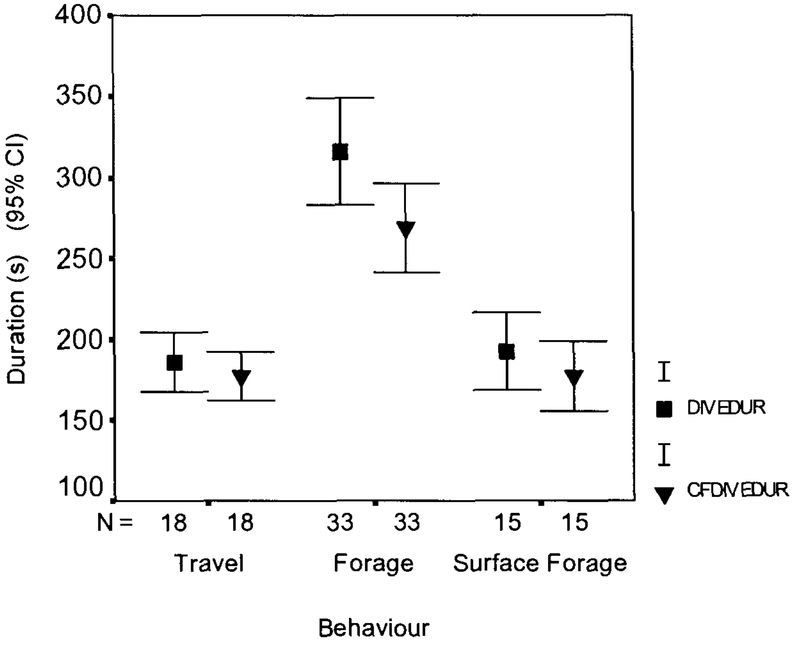

Figure 13. Mean cow (DIVEDUR) and calf (CFDIVEDUR) dive duration during travelling, foraging and surface foraging bouts. Error bars represent 95% confidence intervals.

travelling or surface foraging bouts (Z=-0.762, p=0.446 and Z=-1.931, p=0.053 respectively; Figure 13).

Both DIVEDUR and CFDIVEDUR tend to increase across the season (X^2=2.98, df=2, p=0.226 and X^2=2.60, df=2, p=0.273 respectively) (Figure 14); however, whereas CFDIVEDUR is significantly shorter than DIVEDUR during early (Z=-2.731, p=0.006) and mid (Z=-2.868, p=0.004) season observations, by late season there is no longer a significant difference between the two (Z=-1.784, p=0.074; Figure 14).

Partitioning the data into individual behaviours shows that the differences between DIVEDUR and CFDIVEDUR apparent in the early and mid season are

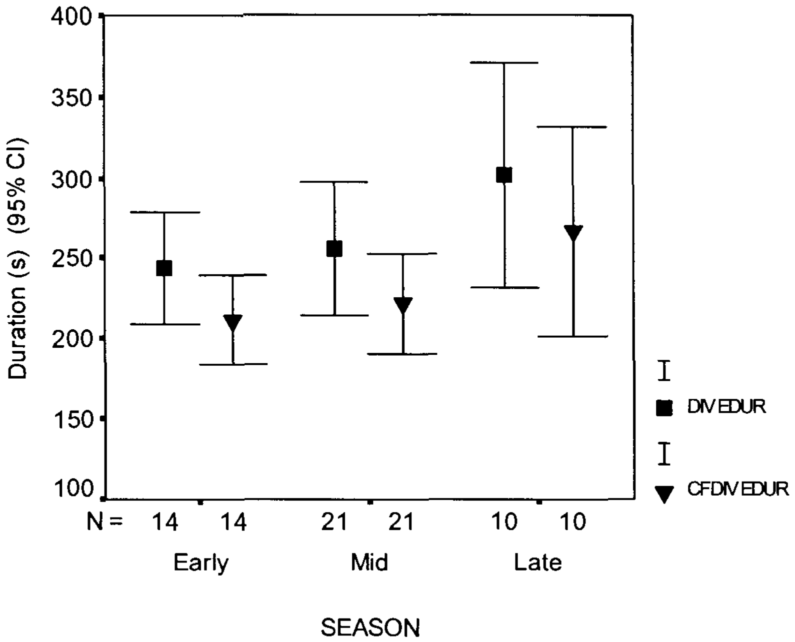

Figure 14. Mean cow (DIVEDUR) and calf (CFDIVEDUR) dive duration during early, mid and late season observations. Error bars represent 95% confidence intervals.

only significant during foraging bouts (Table 5, Figure 15); during travelling and surface foraging bouts, CFDIVEDUR does not differ significantly from DIVEDUR (Table 5). By late season, there are no longer significant differences between DIVEDUR and CFDIVEDUR during any behavioural states (Table 5). Therefore, hypothesis 4, that females dive for longer durations than their calves, is only supported under certain conditions: during early and mid season foraging bouts. There is a tendency for both DIVEDUR and CFDIVEDUR to increase from early to late season during foraging bouts (X^2=3.98, df=2, p=0.137

Table 5. Results of Wilcoxon Signed Ranks test for differences between mean cow dive duration (DIVEDUR) and mean calf dive duration (CFDIVEDUR) during travelling, foraging and surface foraging bouts in early, mid and late season. Values in bold type are significant at $p<0.05$.

	Travel		**Forage**		**Surface Forage**	
Season	Z	p	Z	P	Z	p
Early	-1.352	0.176	-2.803	**0.005**	-1.363	0.173
Mid	0.000	1.000	-2.911	**0.004**	-1.540	0.123
Late	-0.135	0.893	-1.859	0.063	-1.461	0.144

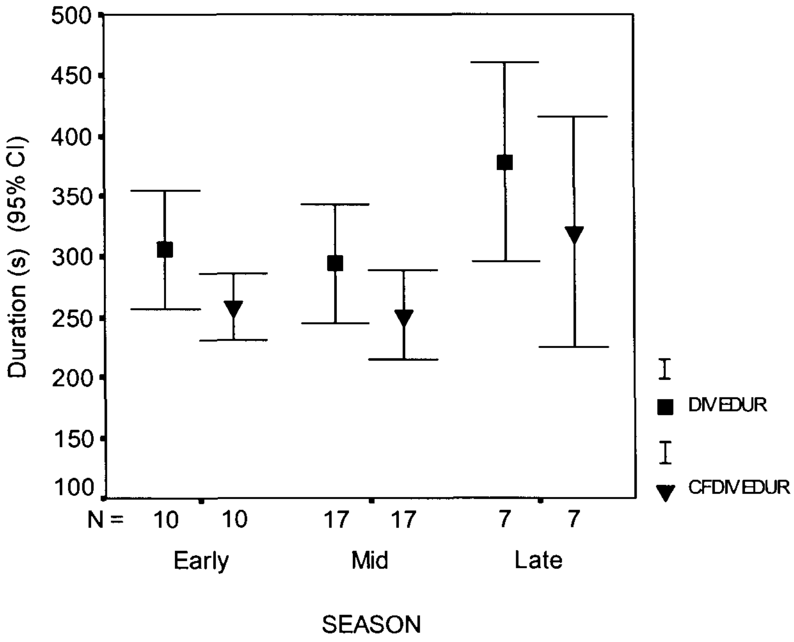

Figure 15. Mean cow (DIVEDUR) and calf (CFDIVEDUR) dive duration during early, mid and late season foraging bouts. Error bars represent 95% confidence intervals.

and $X^2=3.28$, df=2, p=0.194; Figure 15). Therefore, although not significant, there is evidence to support hypothesis 5, that the calf's dive duration increases across the season.

For the remaining dive duration analyses, the synchrony variables DIVE and FULLDIVE are treated as independent variables, each with two treatments: "synchronous" where the conditions for synchrony are met; and, "asynchronous" where they are not. Hypothesis 6, that females dive for shorter durations when the calf does not follow, is supported. Overall, DIVEDUR is significantly longer within cycles where the calf accompanies the female on a dive (DIVE synchrony) relative to those where it remains at the surface (DIVE asynchrony) during all behavioural states (Table 6, Figure 16). The same is true within early, mid and late season observations (Table 7, Figure 17). However, when individual seasons are viewed within each behavioural state, differences in DIVEDUR between

Table 6. Results of Mann Whitney U test for differences in mean cow dive duration (DIVEDUR) between synchronous and asynchronous dive cycles during travelling, foraging and surface foraging bouts. Values in bold type are significant at $p<0.05$.

	Travel		**Forage**		**Surface Forage**	
	Z	p	Z	p	Z	p
FULLDIVE	-2.543	**0.011**	-1.503	0.133	-2.072	**0.038**
DIVE	-3.781	**0.000**	-5.350	**0.000**	-3.071	**0.002**

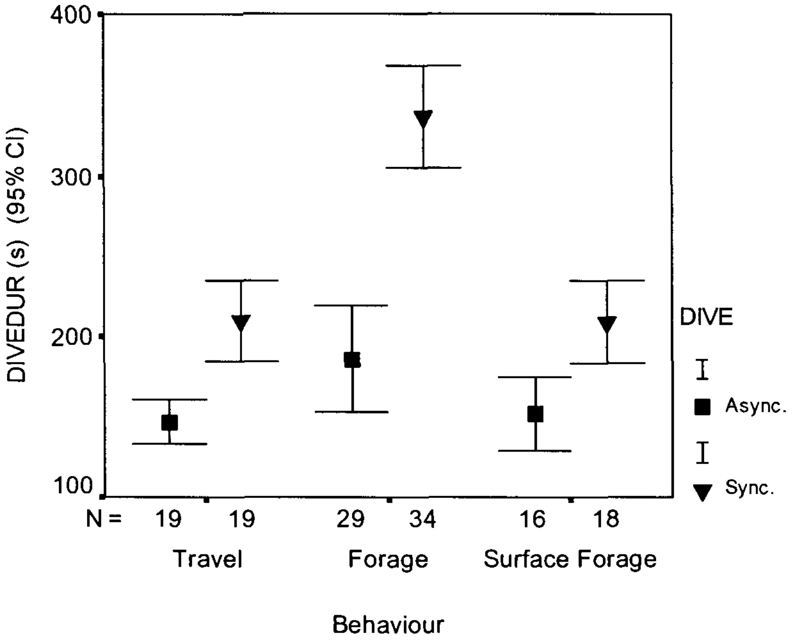

Figure 16. Mean cow dive duration (DIVEDUR) during cycles where the calf accompanies the cow on a dive (DIVE synchrony) and those where it remains at the surface (DIVE asynchrony) during travelling, foraging and surface foraging bouts. Error bars represent 95% confidence intervals.

Table 7. Results of Mann-Whitney U tests for differences in mean cow dive duration (DIVEDUR) between synchronous and asynchronous dive cycles during early, mid and late season observations. Values in bold type are significant at $p<0.05$.

	Early		**Mid**		**Late**	
	Z	**p**	**Z**	**p**	**Z**	**p**
FULLDIVE	-2.451	**0.014**	-1.383	0.167	-0.691	0.490
DIVE	-3.724	**0.000**	-5.401	**0.000**	-2.557	**0.011**

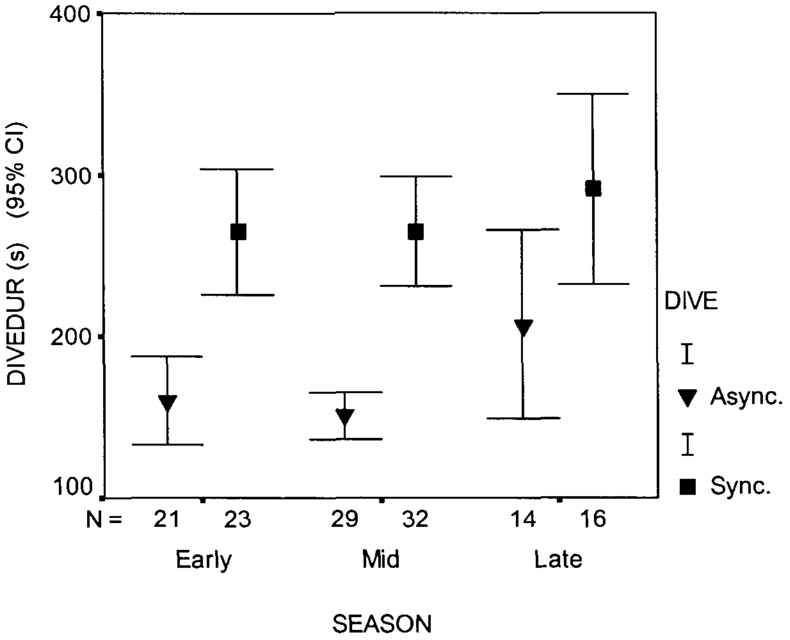

Figure 17. Mean cow dive duration (DIVEDUR) during cycles where the calf accompanies the cow on a dive (DIVE synchrony) and those where it remained at the surface (DIVE asynchrony) in early, mid and late season. Error bars represent 95% confidence intervals.

synchronous and asynchronous DIVE cycles are only significant during early season travelling and foraging bouts, and mid season travelling, foraging and surface foraging bouts (Table 8, Figure 18 and 19). By late season observations, there is no longer a significant difference in DIVEDUR between asynchronous and synchronous DIVE cycles during any behavioural state.

Finally, in the early season DIVEDUR is significantly shorter during cycles where the calf remains submerged for the entire duration of the female's dive (FULLDIVE synchrony) versus those cycles where the calf surfaces sooner (FULLDIVE asynchrony; Table 7, Figure 20); however, by mid and late season this is no longer true. When individual behaviours are examined, DIVEDUR is

Table 8. Results of Mann Whitney U test for differences in mean cow dive duration (DIVEDUR) between synchronous and asynchronous DIVE cycles during early, mid and late season observations of travelling, foraging and surface foraging bouts. Values in bold type are significant at $p<0.05$.

	Early		**Mid**		**Late**	
	Z	**p**	**Z**	**p**	**Z**	**p**
Travel	-1.981	**0.048**	-3.003	**0.003**	-1.149	0.251
Forage	-3.021	**0.003**	-4.247	**0.000**	-1.857	0.063
Surface Forage	-1.278	0.201	-2.205	**0.027**	-2.121	0.057

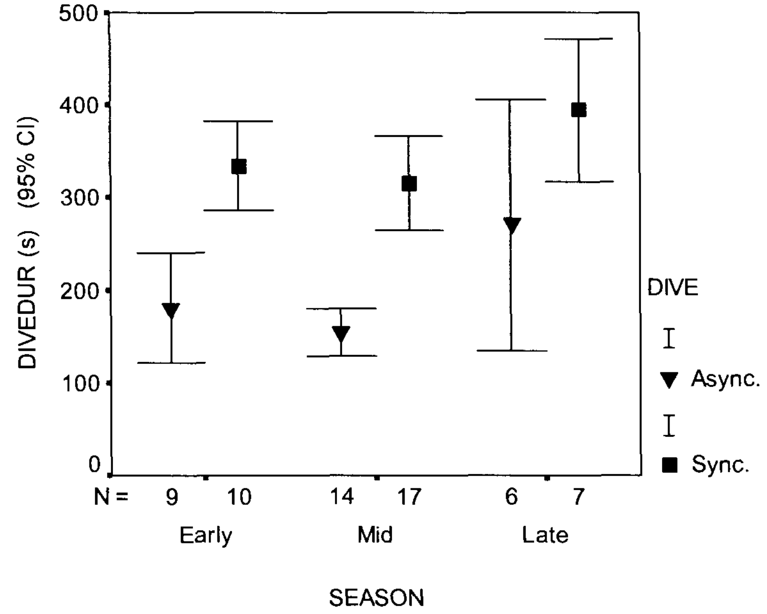

Figure 18. Mean cow dive duration (DIVEDUR) during foraging cycles where the calf accompanies the cow on a dive (DIVE synchrony) and those where it remains at the surface (DIVE asynchrony) in early, mid and late season. Error bars represent 95% confidence intervals.

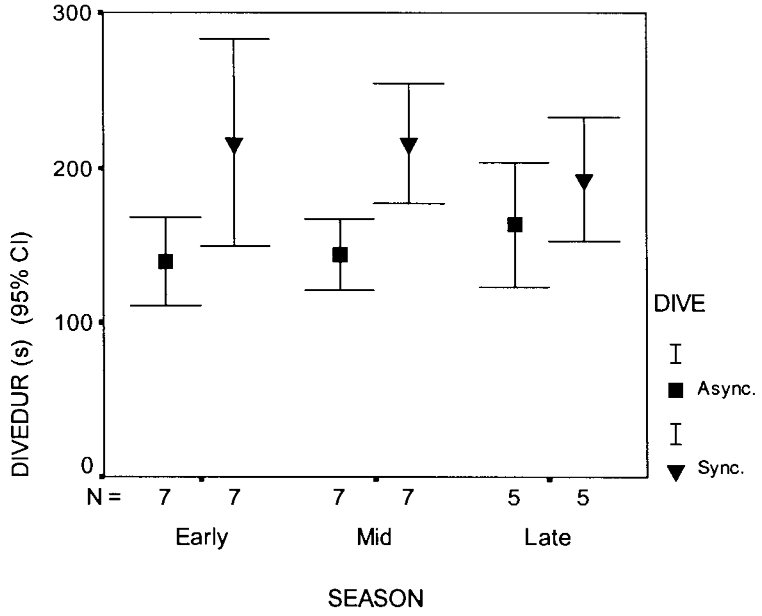

Figure 19. Mean cow dive duration (DIVEDUR) during travelling cycles where the calf accompanies the cow on a dive (DIVE synchrony) and those where it remains at the surface (DIVE asynchrony) in early, mid and late season. Error bars represent 95% confidence intervals.

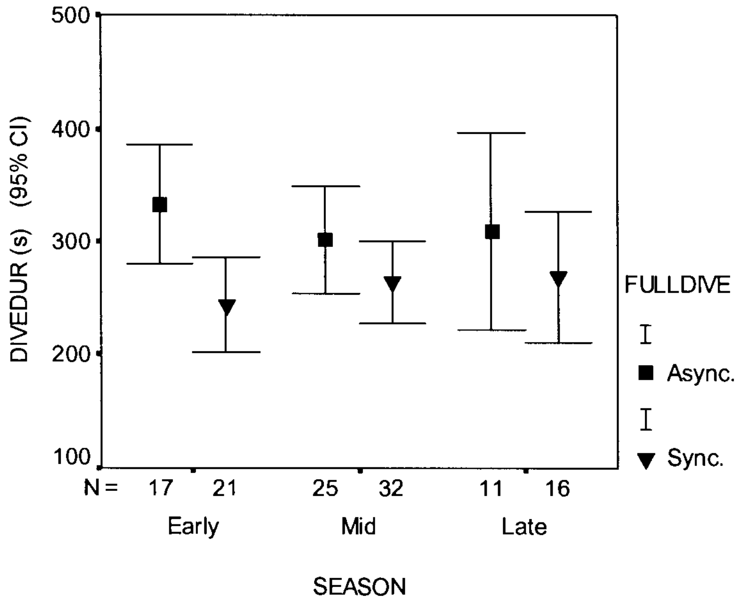

Figure 20. Mean cow dive duration (DIVEDUR) during cycles where the calf remains submerged for the entire duration of the cow's dive (FULLDIVE synchrony) and those where it surfaces sooner (FULLDIVE asynchrony) in early, mid and late season. Error bars represent 95% confidence intervals.

again found to be shorter during synchronous cycles, but only significantly so during traveling and surface foraging bouts (Table 6, Figure 21).

The dive behaviour analysis shows several trends. First, female dive durations (DIVEDUR) are longer during foraging bouts relative to either travel or surface foraging bouts. Moreover, during foraging, but not travel or surface foraging bouts, the calf's dive duration (CFDIVEDUR) is significantly shorter than DIVEDUR, particularly early in the season; however by late season, the two variables no longer differ significantly during any behavioural state. The results further suggest that DIVEDUR is significantly shorter during dive cycles in the early and mid season where the calf does not accompany the female on a dive

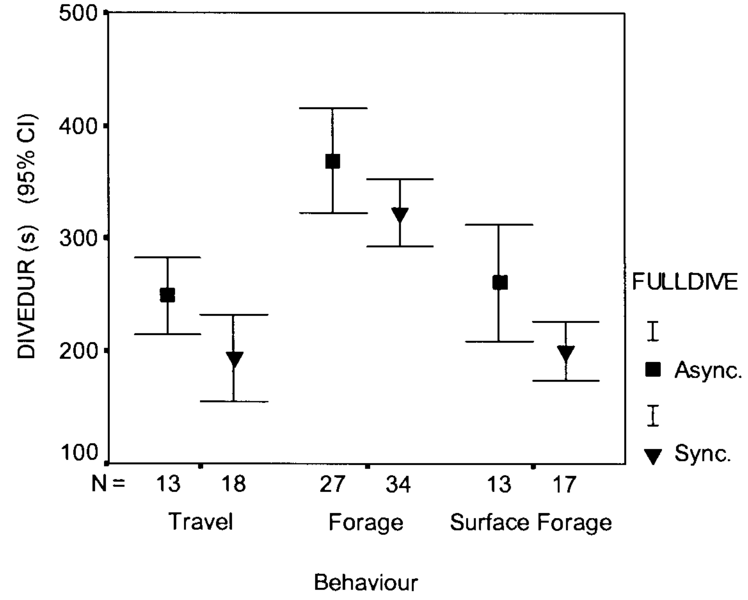

Figure 21. Mean cow dive duration (DIVEDUR) during travelling, foraging and surface foraging cycles where the calf remains submerged for the entire duration of the cow's dive (FULLDIVE synchrony) and those where it surfaces sooner (FULLDIVE asynchrony). Error bars represent 95% confidence intervals.

(either initially or at all). By late season, DIVEDUR increases during these asynchronous cycles such that it no longer differs from cycles where synchrony exists. Finally, in the early season when the calf accompanies the female on a dive, the calf tends to surface early during significantly longer duration cow dives than those where it remains submerged for the duration of the cow's dive; however, by mid and late season, there is no longer a significant difference in female DIVEDUR between cycles where the calf remains submerged and those where it surfaces early.

Synchrony Analysis:

For the remaining analyses, the synchrony variables SYNCDIVE and DIVE are treated as dependent variables. Each represents the frequency with which the synchronized condition was observed. When not included in the text, specific values for dependent variables are reported in Appendix A.

Overall, the frequency with which dive synchrony (SYNCDIVE) occurs is significantly higher during foraging and surface foraging bouts relative to travelling bouts (Table 9, Figure 22). In addition, the results support hypothesis 7, that calves synchronize their dives increasingly often as the season progresses; SYNCDIVE increases significantly from early to late season (Table 9, Figure 23). Further examination of the interactive effect of SEASON and BEHAVIOUR on

Table 9. Results of Kruskal-Wallis tests for differences in the frequency of cow and calf synchrony across the season and behaviours. Values in bold type are significant at p<0.05.

	Season			Behaviour		
	X^2	df	*p*	X^2	df	*P*
SYNCDIVE	6.38	2	**0.041**	11.97	2	**0.003**
DIVE	4.65	2	0.098	19.93	2	**0.000**

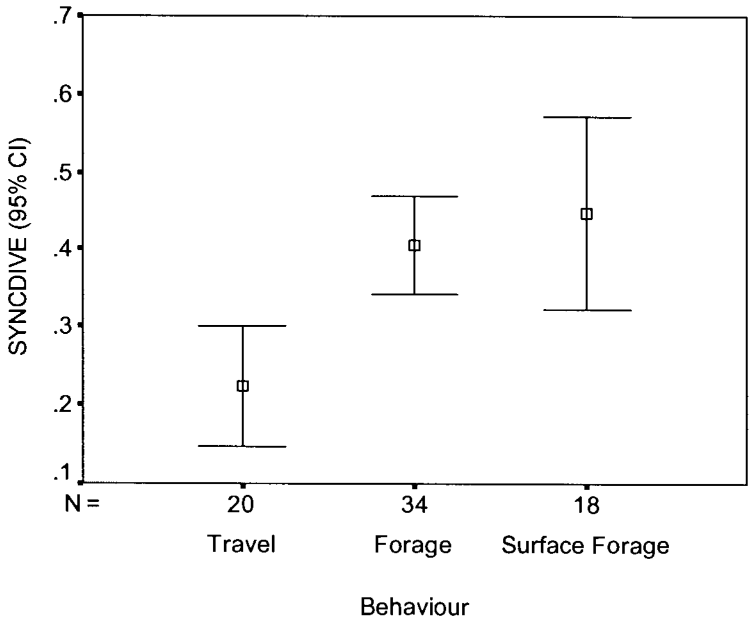

Figure 22. The frequency with which dive synchrony (SYNCDIVE) occurrs during travelling, foraging and surface foraging bouts. Error bars represent 95% confidence intervals.

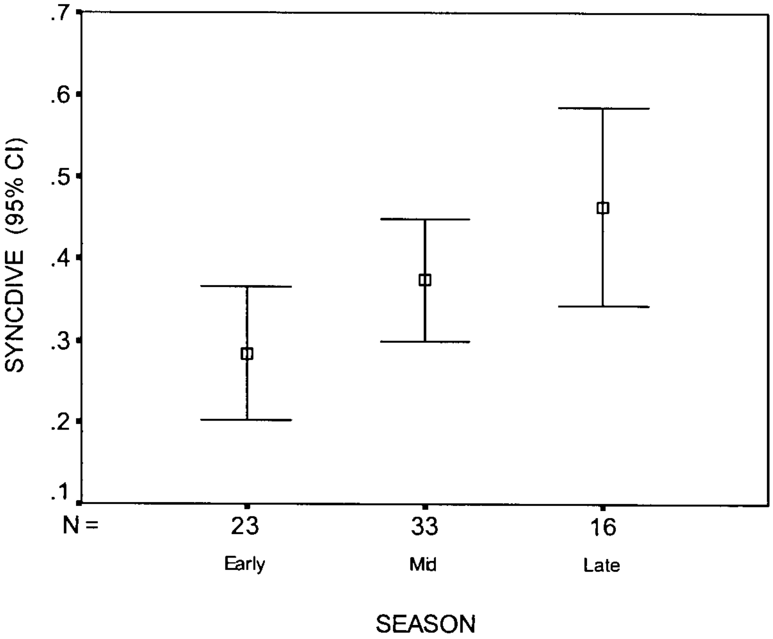

Figure 23. The frequency with which dive synchrony (SYNCDIVE) occurrs during early, mid and late season observations. Error bars represent 95% confidence intervals.

SYNCDIVE reveals that the increase that occurs across the season is evident during both foraging and surface foraging bouts; however, this is only significant during foraging bouts (Table 10, Figure 24).

Analysis of the main effect of BEHAVIOUR on DIVE reveals that the calf dives significantly more frequently during foraging and surface foraging bouts than during traveling bouts (Table 9, Figure 25). In addition, the results support hypothesis 8, that calves dive increasingly often as the season progresses; DIVE is found to increase from early to late season, although this is not significant (Table 9, Figure 26). Examination of the interactive effect of SEASON and BEHAVIOUR suggests that the seasonal effect is more pronounced during foraging and surface

Table 10. Results of Kruskal-Wallis tests for differences in the frequency of cow and calf synchrony behaviour across the season within travel, forage and surface forage bouts. Values in bold type are significant at $p<0.05$.

	Travel			**Forage**			**Surface Forage**		
	X^2	df	*P*	X^2	df	*p*	X^2	Df	*p*
SYNCDIVE	0.38	2	0.825	6.66	2	**0.036**	2.91	2	0.233
DIVE	0.19	2	0.909	2.59	2	0.274	4.03	2	0.133

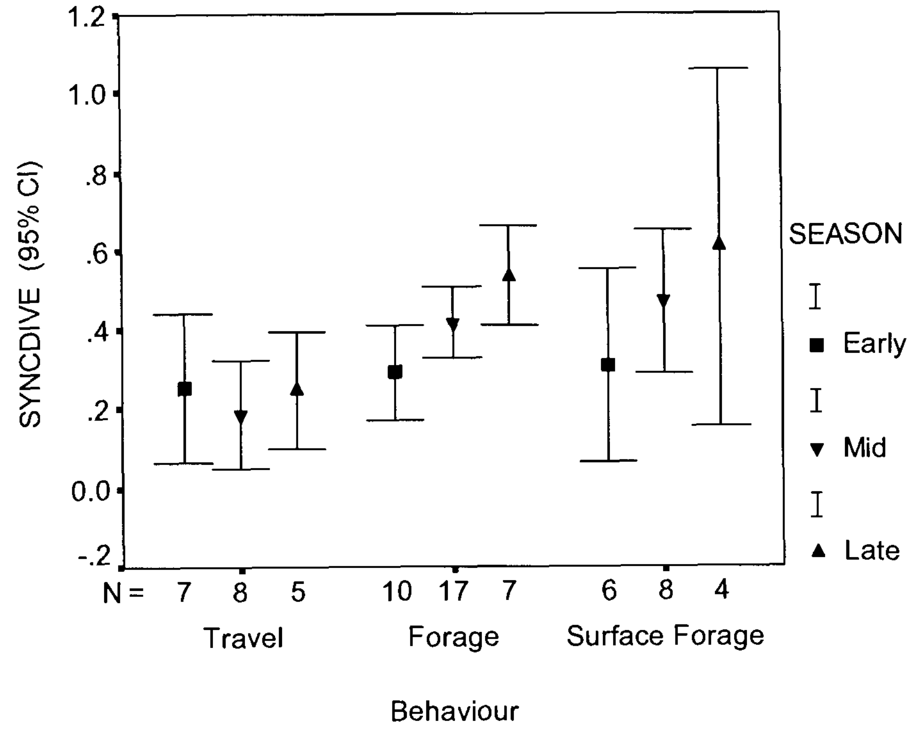

Figure 24. The frequency with which dive synchrony (SYNCDIVE) occurs within behaviours during early, mid and late season observations. Error bars represent 95% confidence intervals.

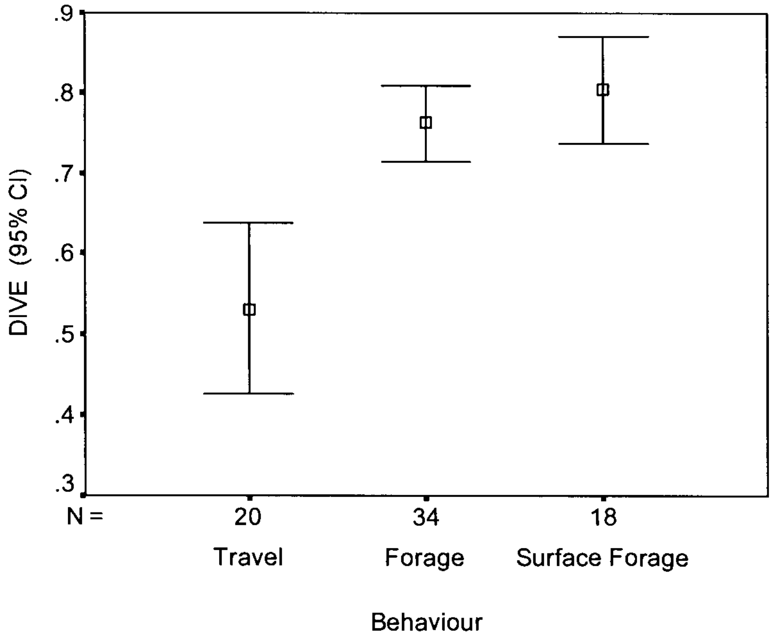

Figure 25. The frequency of cow dive cycles in which the calf dives (DIVE) during travel, forage and surface forage bouts. Error bars represent 95% confidence intervals.

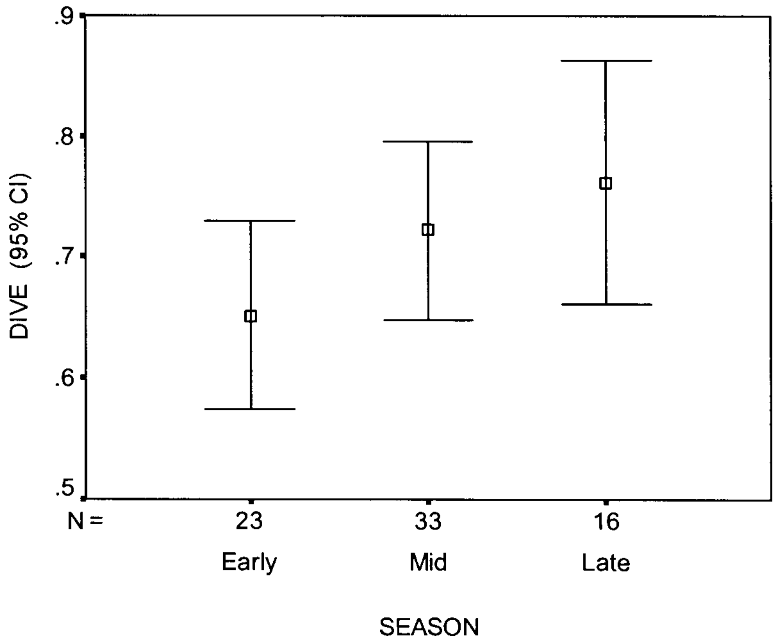

Figure 26. The frequency of cow dive cycles in which the calf dives (DIVE) during early, mid and late season observations. Error bars represent 95% confidence intervals.

foraging bouts relative to travelling bouts (Table 10, Figure 27).

In summary, the preceding analysis indicates that dive synchrony tends to be low during travelling bouts compared to non-travel (foraging) bouts. Furthermore, during non-travel bouts, dive synchrony increases across the season. Finally, the frequency with which the calf dives during a given cow dive cycle also increases across the season.

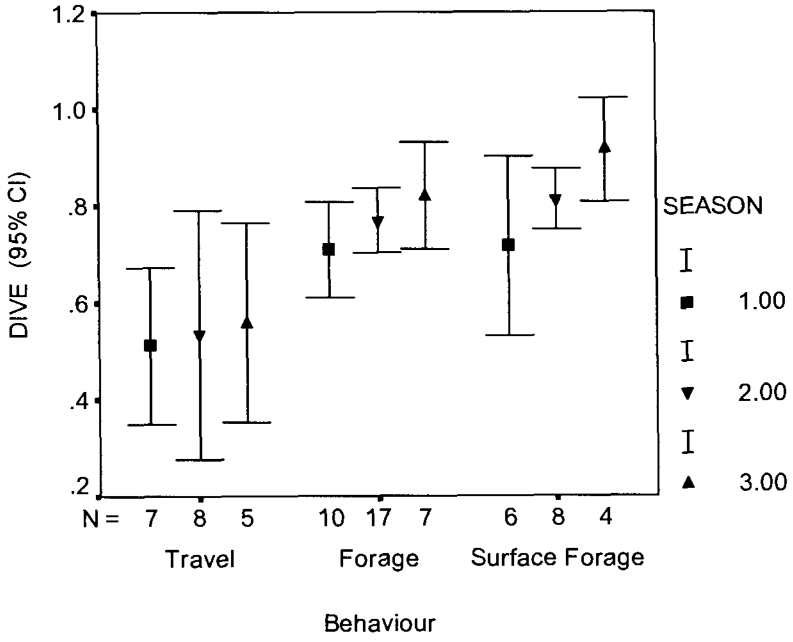

Figure 27. The frequency of cow dive cycles in which the calf dives (DIVE) within behaviours during early (1), mid (2) and late (3) season observations. Error bars represent 95% confidence intervals.

Discussion

Proximity Behaviour

The distance at the surface between female humpback whales and their calves varies with the females' behaviour; distances are greatest during sub-surface and surface foraging bouts relative to travelling bouts. Proximity between mothers and their offspring has been found to differ as a function of the mother's behaviour in several other species as well. For example, Green (1992) indicated that bison calves remain closest to their mother during herd travel. Distances between female reindeer and their offspring have also been found to decrease as their rates of movement increase (Espmark 1971). Presumably an increase in proximity during travel functions to prevent mother-offspring separation at a time when it is most likely to occur (Green 1992). During foraging bouts, however, the female's movements are typically limited to a relatively confined area. As a result, the risk of separation is likely reduced and the need to maintain as close contact can be relaxed.

During foraging bouts it may also be more difficult for the calf to remain close to the female. When foraging, the female's behaviour is outwardly more erratic; the deliberate and comparably predictable surfacing behaviour characteristic of travelling bouts is no longer evident. This is particularly true of surface foraging bouts. During these bouts, the female's behaviour often incorporates a series of coordinated tactics aimed at trapping or corralling prey at or near the water surface (Jurasz & Jurasz 1979, Hain *et al.* 1982, D'Vincent *et al.* 1985, Weinrich *et al.* 1992). Frequently bubbles are observed just prior to the female breaking the surface, which are almost certainly deployed by the whale to aid in prey capture (Hain *et al.* 1982, Weinrich *et al.* 1992, Sharpe & Dill 1997). Moreover, surface foraging bouts can involve several individuals in a coordinated, and likely cooperative, effort using "bubble-nets" and vocalizations to capture herring (Jurasz & Jurasz 1979, D'Vincent *et al.* 1985, Sharpe 2001). For a calf, predicting the female's movements and maintaining close proximity during these events may be more difficult than during travelling bouts.

The initial analysis of temporal variation in humpback whale mother-offspring proximity reveals little change across the duration of the study. This is in contrast to the pattern typically described for follower species. Lent (1974) characterized the spatial relationships between mothers and following offspring as one where early proximity gradually gives way to increased separation. This generalization has been supported by several studies. Among primates, declines in mother-infant proximity over time have been demonstrated in wild vervet monkeys (*Cercopithecus aethiops*, Struhsaker 1971) and baboons (*Papio anubis*, Nash 1978). In ungulates, studies of Welsh ponies (Crowell-Davis 1986), reindeer

(Espmark 1971), moose (*Alces alces*, Altmann 1958) and wild and domestic sheep (Morgan & Arnold 1974, Berger 1979, Gluesing *et al.* 1980) have yielded similar results. Moreover, Ralls *et al.* (1987) observed several captive ungulates described elsewhere as followers, including zebra (*Equus burchelli*), wildebeest (*Connochaetes taurinus*), and bactrian camels (*Camelus bactrianus*), and found that all measures of mother-young association tended to decrease over time. Among mysticetes, Taber & Thomas (1982) suggested that southern right whales also conform to this pattern.

Unlike the aforementioned examples, however, Ralls *et al.* (1987) noted that two species of hippopotamids described as follower species (*Choeropsis liberiensis* and *Hippopotamus amphibious*) demonstrated little change in proximity across their study. They suggested that the duration of their observations was likely insufficient to reveal any decrease in proximity that may have occurred; behavioural changes in large and more slowly maturing species can be expected to occur later than in more quickly maturing species. This is almost certainly a contributing factor with humpback whales; humpback whale cows and their calves typically do not separate until several months after the end of my study (Baker *et al.* 1987, Clapham & Mayo 1987 b, 1990, Baraff & Weinrich 1993). However, partitioning the data into discrete behavioural types, and further, into dive cycles where the calf is either synchronized with the female or not, reveals that temporal variations in proximity behaviour do in fact occur.

As before, while travelling, the female and calf remain in close proximity at all times. In accordance with the argument I presented above, during travelling bouts, close proximity should be maintained to avoid prolonged or distant separation. In contrast, when foraging bout data are examined, the first indication of a temporal trend is revealed; although not statistically significant, there is a clear pattern of decreasing proximity over time. When synchrony is included in the analysis, however, this pattern is only evident during foraging bouts characterized by female and calf dive asynchrony. Similarly, although without reference to a temporal component, Green (1992) indicated that distances are greatest between female bison and their offspring when the behaviour of the dyad is asynchronous. Not surprisingly, if the behaviour of the female and calf are asynchronous, for example if one is resting and the other is foraging, then the chance that either member will move away from the other increases. That the temporal patterns observed in humpback mother-calf pairs are not significant almost certainly reflects the relatively small sample sizes that result from partitioning the data in this manner. Moreover, it is possible that I observed the onset of a behavioural trend that will continue to develop until complete separation occurs. As Ralls *et al.* (1987) suggested, studies with durations that fail to encompass the entire period of association are more likely to fail in recognizing these trends.

The results from the proximity analysis reflect a pattern that in many ways is typical of follower species: differences in proximity occur across behaviours, proximity is greater during synchronous relative to asynchronous behavioural bouts, and proximity decreases through time, although only under certain conditions. That other studies have not commented on the specific conditions under which these temporal patterns occur in follower species is likely due in part to the level of resolution with which these behaviours have been investigated. Although proximity is frequently examined across time, behavioural state, and synchrony, I am unaware of any study that has attempted to identify the interaction of these factors. Furthermore, whether or not the patterns that I observed conform entirely to the 'typical' follower pattern, the overriding signal throughout the analysis is that, as in nearly all followers, proximity is maintained throughout the association of mother and offspring and separation, although it occurs, is infrequent. However, before humpback whale proximity behaviour can be functionally compared to following behaviour in ungulates, it is necessary to review the conditions under which it has arisen in both groups.

As argued earlier, following behaviour has evolved in terrestrial ungulates as a response to predation (Lent 1974, Estes 1976). The large size of an adult mysticete can be expected to afford it considerable protection from predation. Observations of attacks by killer whales (*Orcinus orca*) suggest that these animals are not completely invulnerable, however. Such attacks have been reported on several mysticetes, including humpback (Whitehead & Glass 1985, Florez-Gonzalez *et al.* 1994), gray (Baldridge 1972), minke (Hancock 1965), and blue whales (Tarpy 1979). Observations of actual interactions are relatively rare; however, indirect evidence of detrimental interactions between humpback whales and killer whales exists. The occurrence of scarring patterns characteristic of killer whale attacks on approximately 33% of the 756 identified animals on the east coast of Canada (Katona *et al.* 1980) indicates that attacks occur more frequently than the paucity of reports would suggest. Moreover, that mainly small animals show new scars indicates that juveniles are likely most susceptible to attack (Dolphin 1987c). This is further supported by reports of humpback whale mortality on the Hawaiian breeding grounds; although only anecdotally attributed to predation, it is predominantly juveniles that are lost from the population (Mazzuca *et al.* 1998). Similarly, killer whale attacks have been suggested to contribute significantly to the deaths of young gray whales (Swartz & Jones 1983).

Combined, these observations suggest that humpback whales, and juveniles in particular, experience some threat of predation. Moreover, recent human exploitation of both predator and prey (see Clapham *et al.* 1999) has left us with an incomplete record of the former abundance of either species. Thus, our ability to comment on historical relationships between predator and prey is limited at best; if either were previously more abundant the opportunity for interactions to occur would have been greater than at present. Consequently, predation may have represented an even greater selective force historically than it does now. In this regard, Crowell-Davis (1986) suggested that predator avoidance behaviour continues to exist in the Welsh pony (*Equus caballus*) after several generations of predator absence because it is primarily inherited rather than learned. The same may be true in humpback whales as well.

Whether or not it is possible to speculate on the magnitude of either past or present threat, it is reasonable to assume that predation has been a selective force in the behaviour of humpback whale maternal pairs. Therefore, given the similarities in maternal behaviour, I argue that humpback whale proximity behaviour is commensurate in function with that of the terrestrial ungulate followers. What remains then, is a clearer interpretation of the patterns of proximity behaviour.

The results suggest that, with the exception of asynchronous foraging bouts, at all times the female and calf remain close to one another. This should not be surprising. If the benefits of following behaviour come from close proximity, then any deviation from this can be expected to result in an increase in predation risk. Moreover, during foraging bouts there are probably other advantages to the calf in remaining close to the female. The opportunity to exploit the same prey patches and to observe the female's behaviour may be important and will be discussed later. Perhaps what should be surprising, therefore, is that there is a decrease in proximity at any time during the female and calf's association.

The ontogeny of independence, as indicated by decreasing proximity, results from an interaction of the requirements of both the female and calf. Independence can afford the offspring an opportunity to develop other behaviours such as social or play behaviour (Fitzgibbon 1990). The change in female and calf proximity, however, might be more accurately viewed from the female's perspective. Several studies have suggested that the energy demands imposed upon female mammals increase during lactation (Kaczmarski 1966, Millar 1975, 1977). If this is so, the female can offset this increase in energetic demands by either foraging more often, more efficiently, or both. If having a following offspring in some way reduces the female's opportunity to forage or her ability to forage efficiently, then as the season progresses and the costs of lactation increase, she can be expected to separate from the calf increasingly often during foraging bouts. To examine this hypothesis, however, it is necessary to first examine the foraging behaviour of the female and the consequences, if any, of maintaining proximity.

Time Budget And Dive Behaviour

Foraging is arguably the most important behaviour for female humpback whales in southeast Alaska. It is widely believed that humpbacks rarely feed on their low latitude breeding grounds (Chittleborough 1965, Dawbin 1966, Lockyer 1981). Moreover, lactation, which commences on the breeding grounds, is suggested to be the most costly aspect of reproduction for these animals (Lockyer 1984). Therefore, upon arriving on their foraging grounds, the female's need to replenish her energy stores is likely great. In this regard, on average, females were considered to be foraging during approximately 80% of each encounter, whereas travel behaviour represented approximately 15% and rest behaviour less than 2% of each encounter. Moreover, 80% is likely an underestimate of the actual time that females engage in foraging behaviour. Travelling bouts often included long duration dives that likely included searching forays. Little is known about why humpbacks leave foraging sites or how they locate prey;

however, it is reasonable to assume that intermittent sampling of the water column by diving to depths frequented by prey would be advantageous, and possibly necessary, for these animals in locating suitable foraging sites.

The average dive durations of foraging females are significantly longer than observed during travelling bouts. A similar trend has been noted in gray whales (Wursig *et al.* 1986). Foraging in cetaceans is intimately tied to diving; even surface foraging, where prey are located near the surface, likely requires that the animal dives below the prey aggregations. When foraging, an individual's dive behaviour, although ultimately constrained by the animal's physiology, is therefore driven largely by the behaviour of its prey. Conversely, during travelling bouts, the individual is generally free to ventilate unconstrained by external factors (i.e., prey behaviour). Since the influencing factors differ as a function of the animal's behavioural state, differences in dive behaviour across these states can be expected to occur as well.

The duration of a humpback whale's dive is positively correlated to the depth of that dive (Dolphin 1987b). In the study area, euphausiid crustaceans are believed to be the primary prey of humpback whales (Bryant *et al.* 1981, Krieger & Wing 1984, Dolphin 1987a). Dolphin (1987b) found that although humpbacks typically dove no deeper than 60m while foraging on these organisms, they were capable of diving to depths greater than 120m. During travelling bouts, dives to these depths are unnecessary. Although the work being performed at depth likely differs between foraging and travelling, foraging dives to 120m are more than five times as costly in terms of oxygen utilization and energy expenditure as dives to 20m (Dolphin 1987b). Therefore, it would follow that animals not required to dive as deeply should avoid doing so. In this regard, Heide-Jorgensen *et al.* (2001) have noted that in narwhals (*Monodon monoceros*) and beluga whales (*Delphinapterus leucas*) travelling typically takes place at the surface. The short dive durations associated with surface foraging bouts are in agreement with this as well. During such bouts, the whales employ several techniques of corralling and or capturing prey at or near the surface (Ingebrigsten 1929 *in* Jurasz & Jurasz 1979, Jurasz and Jurasz 1979, Hain *et al.* 1982). Presumably, for this technique to be effective the prey must be located relatively close to the surface and therefore to exploit them individuals are not required to dive as deep as they would when accessing deeper prey aggregations.

During foraging bouts calves dive for significantly shorter durations than their mothers. This difference in diving performance almost certainly results from differences between adults and juveniles in their physiological capacity to dive. As indicated earlier, the duration for which a diving animal can remain submerged is related to its oxygen storage capacity, the rate at which it utilizes stored oxygen, and its anaerobic capacity (Schreer & Kovacs 1997), all of which are positively correlated with size (Kleiber 1961, Hochachka & Somero 1984, Schreer & Kovacs 1997). The aerobic limits and diving performance of at least two species of phocids, Weddell seals (*Leptonychotes weddellii*), and northern elephant seals (*Mirounga angustirostris*), are less in juveniles than in adults (Kooyman *et al.* 1983, Le Boeuf *et al.* 1996). Among cetaceans, Papastavrou *et al.* (1989) noted that sperm whale calves do not often make the prolonged dives characteristic of adults. In addition, juvenile bowhead whales (*Balaena mysticetus*) typically dive for shorter durations than older conspecifics (Wursig *et al.* 1984). That the difference in humpback whale mother and calf dive durations was only evident during sub-surface foraging bouts almost certainly reflects the difference in dive durations characteristic of the different behavioural states; while foraging at depth, the female's dive durations are significantly longer than during either surface foraging or travelling bouts. The shorter dive durations characteristic of surface foraging and travelling bouts are likely within the physiological dive limits of the calf.

As humpback calves mature across the season the durations of their dives increase such that by late season they no longer differ significantly from the dive durations of foraging females. Although I am unaware of a similar temporal comparison of dive behaviour between female mysticetes and their calves, such a trend should be expected. As the size of the juvenile increases, so should its dive capacity. Moreover, an increase in calf dive capacity towards juvenile independence is likely necessary if the calf is to forage effectively on its own. At least one species of phocid has been reported to demonstrate a similar trend; juvenile elephant seals increase their diving performance over the course of their first three foraging trips such that by the fourth trip they no longer differ from the adults (Le Boeuf *et al.* 1996).

While foraging, female humpbacks dive for shorter durations during the early and mid season relative to the late season. Wursig *et al.* (1984) reported that at least in some years, bowhead whale mothers and calves dove for significantly shorter lengths of time than did other whales. Presumably, shorter dives allow the calf to accompany the female for a greater proportion of a given dive. This seems to be the case; overall, the calf remains submerged for the entire duration of the female's dive (i.e., dives for the same duration) on significantly shorter cow dives relative to dive cycles where it surfaces sooner than the female (i.e., dives for shorter durations). In other species, similar behavioural adjustments appear to be made by the female. Heide-Jorgensen *et al.* (2001) found that beluga whale mothers with calves spend more time at the surface than other female conspecifics. Moreover, both lactating belugas and narwhals have lower dive rates (number of dives per hour) than non-lactating females. It would appear that the females modify their behaviour to limit the time they spend submerged. The increase in the dive duration that occurs later in the field season, although not significant, appears to mirror an increase in the calf's ability to dive. A similar trend has been observed in female harbour seals (*Phoca vitulina*), which Bowen *et al.* (1999) attributed to an increase in the diving abilities of their pups.

The data further indicate that in the early and mid season when the calf remains at the surface for the entire duration of the female's dive (DIVE asynchrony), the female responds by shortening the duration of that dive. Presumably, separation is greatest during a dive when the calf does not follow, and therefore in an effort to minimize this, the female surfaces sooner than she would if the calf were to accompany her. This response, however, wanes as the season progresses such that by late season the duration of the female's dive no longer differs between cycles where the calf remained at the surface and those where it followed.

In summary, the dive data suggest that initially humpback calves are unable to dive for the duration characteristic of their mother during foraging bouts. As a result, females alter their dive behaviour in response to their calf. By shortening their dives, they likely increase the opportunity for the calf to remain with them for the duration of that dive. If, however, the calf does not accompany the female on a dive, she further reduces the duration of that dive. In both situations, her behaviour appears to result from an effort to minimize the duration of separation from her calf. In doing so, however, the female's foraging efficiency is likely compromised. Presumably, the 5-6min dive durations characteristic of foraging dives where the calf accompanies the cow are more efficient than the shorter duration dives observed when the calf remains at the surface. These longer dive durations correlate well with Dolphin's (1987b) postulated 4-6min aerobic limit of humpback whales, and are nearly double that of dives when the calf does not follow. That the duration of dives where the calf followed did not change significantly across the season, whereas the duration of dives where the calf remained at the surface increased to approximately 5min by late season further suggests that dives in the 5-6min range are more efficient.

The observation that the female's response to the calf remaining at the surface wanes across the season can perhaps best be explained as follows. Several studies have demonstrated that the demands of mammalian offspring increase throughout lactation (Hadjipieris & Holmes 1966, Kaczmarski 1966, Millar 1975) so that late lactation is the most energetically critical period of the breeding cycle (Millar 1977). To offset this, the female can increase either the frequency with which she forages, the efficiency of her foraging bouts, or both. Increased foraging efforts by lactating females have been demonstrated for several species (Lee & Cockburn 1985, Clutton-Brock 1991, Thompson 1992;

Rydell 1993). The time budget analysis suggests, however, that foraging effort (i.e., time spent foraging) is consistent in female humpbacks across the season. Admittedly, this analysis is limited to observations made during daylight only and therefore the possibility that foraging behaviour increases at night cannot be discounted. However, given that foraging represents at least 80% of the diurnal time budget of these animals, it is unlikely that it increases substantially outside of the daily observation period. Therefore, to offset the increasing demands of lactation, the female is likely required to increase her foraging efficiency. It appears that she accomplishes this through increasing the duration of her dives during which the calf remains at the surface such that by late season they are similar in duration to the presumed optimal duration of dives when the calf follows.

Essentially, females appear to optimize their foraging behaviour through decreasing their responsiveness to their calves' behaviour and ultimately diving for longer durations. Altmann (1958) similarly noted that as the association between moose cows and their calves lengthens, the female becomes less responsive to her calf and no longer retrieves it when it does not follow. Crowell-Davis (1986) also suggested that whereas in the first several weeks Welsh ponies would respond to their foals' recumbency by approaching them, as time progressed the female became more likely to continue grazing when the foal lay down. Furthermore, several studies have suggested that later in their association, mother-offspring separation occurs predominantly as a result of the female leaving her offspring (Altmann 1958, Hinde & Atkinson 1970, Berman 1980, Taber & Thomas 1982, Crowell-Davis 1986). Returning to the earlier proximity analysis, this provides an explanation for the increased separation observed during asynchronous foraging bouts. Although increasing juvenile independence may contribute to decreased proximity between the female and the calf, separation likely also correlates with the increasing energy demands imposed upon the female and her consequent unresponsiveness to her calf .

This recognition that the foraging efficiency of female humpback whales is reduced as a result of tending to their calf may be able to provide an explanation for the solitary nature of lactating females noted by Whitehead (1983) and Clapham & Mayo (1987b). Clapham & Mayo have indicated that females with calves were found in association with other individuals in less than one quarter of all sightings whereas the same individuals in years without calves associated with other whales nearly three times as frequently. Presumably, by associating with conspecifics on the foraging grounds, individuals benefit by increasing their individual foraging efficiency (Hain *et al.* 1982, Whitehead 1983, Baker & Herman 1984, Weinrich 1991). If so, females with calves should be expected to associate more frequently with other individuals because of the high energetic demands associated with lactation. Although it is possible that the pair become increasingly asocial in an effort to avoid harrassment from conspecifics, as has been suggested for humpbacks on the breeding grounds (Tyack & Whitehead 1983, Smultea 1994), this is unlikely to be the sole reason. Several researchers have noted a general lack of aggression between humpbacks on the foraging grounds (e.g., Clapham 1996). Moreover, when associations occur, there appears to be no effort by the female to keep the calf separated from the third individual; the calf is equally likely to be found in the middle of the trio as is the female. Clapham & Mayo (1987b) found that during these associations, the third individual was a female over half of the time (61% of 91 encounters), which suggests that the associations are not tied to mating. Given the results from this study, an alternate explanation for the solitary nature of the pair reflects the female's reduced foraging ability. If individuals benefit from cooperating with conspecifics, they would do better to cooperate with an individual that does not need to attend to a calf and therefore alter its dive behaviour. Viewed in this way, the asocial nature of lactating females is less a result of the female's avoidance of other conspecifics than it is of other individuals avoiding the pair.

Synchrony Behaviour

Overall, the frequency with which the calf dives during a given (cow) dive cycle and the frequency with which the calf exhibits dive synchrony (diving at the same time as the female, and for the same duration) are higher during foraging and surface foraging bouts relative to travelling bouts. Moreover, whereas there is no increase in either measure across the season during travelling bouts, there is during both types of foraging bouts. As mentioned earlier, presumably the calf does not need to synchronize its dive behaviour with the female during travelling bouts to remain close to her; since the female is likely close to the surface, the calf is free to ventilate at its own rate without separating from her. Therefore, differences in dive behaviour that lead to asynchrony during travel are likely the result of differences in physiology between the two. Conversely, if the calf does not dive with the cow during foraging bouts, it almost certainly separates from her. That synchrony increases across the season during either type of foraging bout initially suggests that the calf's increasing physiological capacity to dive permits it to accompany the female more often. This, however, does not appear to be the sole determining factor. At all times, the female's dive durations during surface foraging bouts appear well within the limits of the calf's diving abilities. Therefore, if diving ability were the sole predictor of dive synchrony, it should be considerably higher during surface foraging bouts, and furthermore, it should be less likely to increase across the season. However, both the frequency and temporal patterns of synchrony are nearly identical for both sub-surface and surface foraging bouts, which suggests that other factors influence the synchrony behaviour of the pair.

Arguably, an increase in female and calf synchrony across the season during foraging bouts correlates with an increase in foraging effort by the calf. In the western Atlantic, first observations of feeding in humpback whale calves typically occur in late July and early August (Clapham & Mayo 1987b). Although I observed apparent foraging behaviour in a calf on only one occasion (repeated surface lateral lunges in association with schooling fish), this does not mean that it did not occur. It is nearly impossible to confirm whether the calf feeds while underwater. Even during surface foraging bouts where the whale's behaviour is often betrayed solely by the presence of bubble rings, the prey is frequently engulfed below the surface. In addition, Clapham & Mayo's report correlates well with the timing of the increase in dive synchrony. As discussed earlier, it has been demonstrated that the juveniles of several species gradually increase the proportion of solid food in their diet while still nursing (e.g., Poole & Pilton 1964, Lackey 1967, Sparks 1968, Fenton 1969, Kruuk 1972). In this way, the energetic demands of lactation imposed upon the female can be reduced.

By synchronizing its behaviour with the female, the calf likely also benefits from learning foraging tactics through observing the female. A wide variety of species have been suggested to learn through following and observing their mother, including birds (Neuringer & Neuringer 1974), rodents (Galef & Clark 1971), felids (Chesler 1969), ursids (Stirling & Latour 1978) and ungulates (Altmann 1963, Bergerud & Noland 1970, Edwards 1975). It is difficult to identify the role that the association between female humpbacks and their calves plays in juvenile learning. There is, however, both genetic and photo-identification evidence to suggest that maternal influence results in a high degree of site fidelity in juveniles (Baker *et al.* 1993, 1994, Clapham & Mayo 1987b, Weinrich 1998). In addition, Clapham & Mayo (1987b) have observed a juvenile humpback whale blowing bubbles in a manner which suggested that it was imitating the behaviour of its mother. Further, Weinrich *et al.* (1992) have reported the spread of an apparent novel foraging behaviour through a population of Atlantic humpbacks that appears to be transmitted at least in part maternally. It is therefore reasonable to assume that observational learning occurs in humpback whales as well. If so, the increase in synchrony later in the season likely also functions to allow the juvenile to observe and acquire foraging tactics as they become increasingly necessary towards juvenile independence.

Conclusion

The results from this study demonstrate that humpback whale mothers and their offspring behave similarly to terrestrial ungulate followers. Presumably, the association between the two provides both protection for the offspring and an opportunity for the calf to observe and participate in foraging. There appears, however, to be at least one notable consequence associated with this strategy; the female's foraging efficiency is likely compromised by having to attend to her calf. Not surprisingly then, juvenile independence, as indicated by decreasing proximity during asynchronous foraging bouts, correlates with an increase in the energetic requirements of the female. Although increasing independence may afford the calf an opportunity to develop adult-like behaviour, proximity likely decreases in part as a result of the female's increasing willingness to separate from the calf and forage without interruption. At the same time, an overall increase in female and calf synchrony occurs that likely correlates with an increase in foraging effort by the calf. In this way, the calf can both lessen the energetic demands it imposes upon the female, and learn the foraging tactics it will require once it is independent from its mother.

In comparing humpbacks to ungulate followers, this study further demonstrates that similar parental care patterns can be observed among diverse species found in varied habitats. In addition, it underscores the notion that ecological and life history attributes can play a key role in determining the parental care tactics that an organism employs. In this regard, following behaviour has almost certainly arisen in humpbacks as a result of several factors. First, humpbacks are migratory, and as in many migratory species (e.g., bison, Green 1992; reindeer, Espmark 1971), following behaviour provides a mechanism whereby the maternal dyad can maintain close proximity during periods of travel. Second, as with many follower species, humpbacks can rely upon their large size as a means of defence against offspring predation. Third, although obvious differences exist between the habitats in which humpbacks and ungulate followers reside, arguably both habitats lack the cover necessary to allow for offspring concealment. Thus, by considering these and other similar factors, predictions can be made regarding the parental care tactics that other heretofore unstudied species should employ.

This study also draws attention to at least one aspect of the biology of many marine mammals that makes them unique subjects for study: the necessary separation between foraging and ventilation. As organisms that typically need to dive to exploit prey, humpbacks appear to encounter problems that terrestrial organism do not; for example, their offspring may be prevented from accompanying them on foraging bouts. The results shed light on how this spatial separation of necessary behaviours can affect other important behaviours, and on some of the mechanisms employed by the animals that serve to reduce the negative consequences that may result.

Finally, this study provides a starting point for future work focussing on the suite of behaviours and behavioural modifications associated with parental care in humpback whales. For example, further studies could involve a comparison of the time budgeting and dive behaviour of lactating females to that of other, non-lactating individuals. In doing so, a clearer picture of the behavioural modifications associated with maternal care and their resulting costs could be presented. Ultimately, humpbacks provide a novel opportunity, given both the relative scarcity of information on their maternal behaviour, in combination with the unique constraints imposed upon them as air-breathing mammals in an aquatic environment, to further our understanding of the myriad tactics that organisms employ to raise their offspring.

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Appendix

Table A1. Mean percent of surfacings within individual encounters where the calf is less than 0.5 body lengths (0.5BL), 1.0 body length (1.0BL), 1.5 body lengths (1.5BL) and 50m (50M) from the cow during travel, forage and surface forage bouts. Standard deviation (S.D.) and number of encounters (N) are included.

Behaviour

	Travel			**Forage**			**Surface Forage**		
	Mean	**S.D.**	**N**	**Mean**	**S.D.**	**N**	**Mean**	**S.D.**	**N**
0.5BL	99.1	2.68	19	90.1	11.15	33	80.4	22.52	15
1.0BL	99.8	0.64	19	93.8	10.25	33	87.2	23.40	15
1.5BL	99.9	0.64	19	94.1	10.13	33	87.5	23.46	15
50M	100	---	19	96.3	7.41	33	92.0	18.72	15

Table A2. Mean percent of surfacings within individual encounters where the calf is less than 0.5 body lengths (0.5BL), 1.0 body length (1.0BL), 1.5 body lengths (1.5BL) and 50m (50M) from the cow during early, mid and late season. Standard deviation (S.D.) and number of encounters (N) are included.

Season

	Early			**Mid**			**Late**		
	Mean	**S.D.**	**N**	**Mean**	**S.D.**	**N**	**Mean**	**S.D.**	**N**
0.5BL	91.8	9.01	14	85.3	16.77	21	89.2	10.16	10
1.0BL	95.5	7.17	14	90.2	16.15	21	93.0	8.89	10
1.5BL	95.8	7.00	14	90.4	15.99	21	93.5	8.66	10
50M	96.5	5.80	14	94.6	12.33	21	96.8	4.48	10

Table A3. Mean percent of surfacings within individual encounters where the calf is less than 0.5 body lengths (0.5BL), 1.0 body length (1.0BL), 1.5 body lengths (1.5BL) and 50m (50M) from the cow during early, mid and late season travel, forage and surface forage bouts. Standard deviation (S.D.) and number of encounters (N) are included.

		Season								
		Early			Mid			Late		
		Mean	**S.D.**	**N**	**Mean**	**S.D.**	**N**	**Mean**	**S.D.**	**N**
0.5BL	**Travel**	99.7	0.52	7	100.0	---	8	97.1	5.00	5
	Forage	94.8	6.42	10	86.8	14.37	17	89.0	10.04	7
	S.Forage	86.4	11.28	6	73.2	27.83	8	88.7	11.58	4
1.0BL	**Travel**	100.0	---	7	100.0	---	8	99.4	1.26	5
	Forage	96.8	5.39	10	92.0	13.60	17	91.3	10.51	7
	S.Forage	92.2	10.27	6	80.7	30.53	8	93.7	6.68	4
1.5BL	**Travel**	100.0	---	7	100.0	---	8	99.4	1.26	5
	Forage	97.1	4.90	10	85.5	13.45	17	91.9	10.53	7
	S.Forage	92.5	10.47	6	80.8	30.59	8	95.1	5.22	4
50M	**Travel**	100.0	---	7	100.0	---	8	100.0	---	5
	Forage	97.3	4.30	10	95.5	10.36	17	95.2	6.08	7
	S.Forage	94.3	8.42	6	88.4	25.12	8	97.9	2.55	4

Table A4. Mean percent of surfacings within individual encounters where the calf is less than 0.5 body lengths (0.5BL), 1.0 body length (1.0BL), 1.5 body lengths (1.5BL) and 50m (50M) from the cow during SYNCDIVE synchronous and asynchronous travel, forage and surface forage bouts. Standard deviation (S.D.) and number of encounters (N) are included.

		Synchrony			Asynchrony		
		Mean	**S.D.**	**N**	**Mean**	**S.D.**	**N**
0.5BL	**Travel**	96.9	12.50	16	99.8	0.59	18
	Forage	95.2	10.55	32	84.5	16.84	33
	S.Forage	94.2	7.50	13	71.7	27.23	14
1.0BL	**Travel**	100.0	---	16	99.9	0.36	18
	Forage	96.1	9.92	32	91.4	13.82	33
	S.Forage	97.2	4.80	13	79.8	28.16	14
1.5BL	**Travel**	100.0	---	16	99.9	0.36	18
	Forage	96.2	9.92	32	91.9	13.62	33
	S.Forage	97.4	4.71	13	80.6	28.01	14
50M	**Travel**	100.0	---	16	100.0	---	18
	Forage	99.3	2.15	32	93.8	12.14	33
	S.Forage	98.9	3.01	13	90.0	19.54	14

Table A5. Mean percent of surfacings within individual encounters where the calf is less than 0.5 body lengths (0.5BL), 1.0 body length (1.0BL), 1.5 body lengths (1.5BL) and 50m (50M) from the cow during early, mid and late season SYNCDIVE synchronous and asynchronous bouts. Standard deviation (S.D.) and number of encounters (N) are included.

		Season								
		Early			**Mid**			**Late**		
		Mean	**S.D.**	**N**	**Mean**	**S.D.**	**N**	**Mean**	**S.D.**	**N**
Synchrony	**0.5BL**	100.0	---	7	100.0	---	7	90.0	22.36	5
	1.0BL	100.0	---	7	100.0	---	7	100.0	---	5
	1.5BL	100.0	---	7	100.0	---	7	100.0	---	5
	50M	100.0	---	7	100.0	---	7	100.0	---	5
Asynchrony	**0.5BL**	99.6	0.66	7	100.0	---	7	97.2	5.47	5
	1.0BL	100.0	---	7	100.0	---	7	99.7	0.64	5
	1.5BL	100.0	---	7	100.0	---	7	100.0	---	5
	50M	100.0	---	7	100.0	---	7	100.0	---	5

Table A6. Mean percent of surfacings within individual encounters where the calf is less than 0.5 body lengths (0.5BL), 1.0 body length (1.0BL), 1.5 body lengths (1.5BL) and 50m (50M) from the cow during early, mid and late season SYNCDIVE synchronous and asynchronous forage bouts. Standard deviation (S.D.) and number of encounters (N) are included.

		Season								
		Early			**Mid**			**Late**		
		Mean	**S.D.**	**N**	**Mean**	**S.D.**	**N**	**Mean**	**S.D.**	**N**
Synchrony	**0.5BL**	92.9	18.90	10	95.1	10.92	16	97.1	6.39	7
	1.0BL	100.0	---	10	96.3	8.89	16	97.1	6.39	7
	1.5BL	100.0	---	10	99.5	2.14	16	97.1	6.39	7
	50M	100.0	---	10	99.5	2.14	16	97.1	6.39	7
Asynchrony	**0.5BL**	95.2	5.29	10	82.5	17.60	16	77.7	28.86	7
	1.0BL	97.0	5.24	10	89.3	17.75	16	89.3	18.30	7
	1.5BL	97.5	4.03	10	92.9	14.90	16	97.3	3.75	7
	50M	97.5	4.03	10	92.9	14.90	16	97.3	3.75	7

Table A7. Mean percent of surfacings within individual encounters where the calf is less than 0.5 body lengths (0.5BL), 1.0 body length (1.0BL), 1.5 body lengths (1.5BL) and 50m (50M) from the cow during early, mid and late season SYNCDIVE synchronous and asynchronous surface forage bouts. Standard deviation (S.D.) and number of encounters (N) are included.

		Season								
		Early			**Mid**			**Late**		
		Mean	**S.D.**	**N**	**Mean**	**S.D.**	**N**	**Mean**	**S.D.**	**N**
Synchrony	**0.5BL**	98.7	1.45	6	96.8	5.17	8	94.9	5.46	4
	1.0BL	99.4	1.26	6	98.7	3.54	8	99.2	0.96	4
	1.5BL	99.4	1.26	6	100.0	---	8	99.2	0.96	4
	50M	99.8	0.34	6	100.0	---	8	100.0	---	4
Asynchrony	**0.5BL**	86.1	15.00	6	64.1	29.65	8	82.1	13.09	4
	1.0BL	89.2	14.36	6	74.9	33.29	8	90.1	7.43	4
	1.5BL	89.2	14.36	6	74.9	33.29	8	90.1	7.43	4
	50M	91.6	12.66	6	87.8	24.67	8	96.5	3.69	4

Table A8. Mean frequency with which the calf is observed to be in between the female and a third animal in early, mid and late season. Standard deviation (S.D.) and number of encounters (N) are included.

	Mean	S.D.	N
Early	0.50	0.390	6
Mid	0.43	0.372	16
Late	0.40	0.478	6

Table A9. Mean frequency with which cow is observed to be foraging (foraging and surface foraging combined), travelling or resting during early, mid and late season encounters. Standard deviation (S.D.) and number of encounters (N) are included.

	Season								
	Early			**Mid**			**Late**		
	Mean	**S.D.**	**N**	**Mean**	**S.D.**	**N**	**Mean**	**S.D.**	**N**
Forage	0.81	0.248	14	0.82	0.328	22	0.80	0.310	10
Travel	0.18	0.253	14	0.13	0.275	22	0.19	0.310	10
Rest	0.01	0.042	14	0.01	0.027	22	0.01	0.023	10

Table A10. Mean cow (DIVEDUR) and calf (CFDIVEDUR) dive durations (s) during travel, forage and surface forage bouts. Standard deviation (S.D.) and number of encounters (N) are included.

	Behaviour								
	Travel			**Forage**			**Surface Forage**		
	Mean	**S.D.**	**N**	**Mean**	**S.D.**	**N**	**Mean**	**S.D.**	**N**
DIVEDUR	185.2	35.84	19	315.8	91.39	33	192.5	43.18	15
CFDIVEDUR	177.5	30.54	18	268.9	76.26	33	177.2	39.23	15

Table A11. Mean cow (DIVEDUR) and calf (CFDIVEDUR) dive durations (s) during early, mid and late season. Standard deviation (S.D.) and number of encounters (N) are included.

	Season								
	Early			**Mid**			**Late**		
	Mean	**S.D.**	**N**	**Mean**	**S.D.**	**N**	**Mean**	**S.D.**	**N**
DIVEDUR	243.7	60.01	14	255.7	91.47	21	301.5	97.10	10
CFDIVEDUR	211.8	47.83	14	221.9	67.66	21	266.9	90.70	10

Table A12. Mean cow (DIVEDUR) and calf (CFDIVEDUR) dive durations (s) during early, mid and late season travel, forage and surface forage bouts. Standard deviation (S.D.) and number of encounters (N) are included.

		Season								
		Early			**Mid**			**Late**		
		Mean	**S.D.**	**N**	**Mean**	**S.D.**	**N**	**Mean**	**S.D.**	**N**
Travel	**DIVEDUR**	183.5	55.87	7	185.1	22.63	8	177.9	30.03	5
	CFDIVEDUR	163.6	35.62	7	182.5	38.86	7	179.0	21.30	5
Forage	**DIVEDUR**	306.0	68.27	10	294.5	94.79	17	378.4	89.48	7
	CFDIVEDUR	258.2	38.93	10	251.8	73.05	17	320.1	103.39	7
S.Forage	**DIVEDUR**	200.4	72.60	6	192.6	46.52	8	230.9	19.01	4
	CFDIVEDUR	173.3	51.53	6	172.5	29.83	8	216.5	16.31	4

Table A13. Mean cow dive duration (s) (DIVEDUR) during DIVE and FULLDIVE synchronous and asynchronous travel, forage and surface forage bouts. Standard deviation (S.D.) and number of encounters (N) are included.

		Synchrony			Asynchrony		
		Mean	**S.D.**	**N**	**Mean**	**S.D.**	**N**
DIVE	**Travel**	209.9	51.53	19	147.4	29.27	19
	Forage	336.8	90.34	34	186.5	86.74	29
	S.Forage	209.3	51.71	18	152.5	43.79	17
FULLDIVE	**Travel**	194.3	77.66	18	249.5	56.90	13
	Forage	323.1	86.87	34	369.2	117.39	27
	S.Forage	200.1	51.06	17	261.3	23.74	13

Table A14. Mean cow dive duration (s) (DIVEDUR) during DIVE and FULLDIVE synchronous and asynchronous early, mid and late season. Standard deviation (S.D.) and number of encounters (N) are included.

		Synchrony			Asynchrony		
		Mean	**S.D.**	**N**	**Mean**	**S.D.**	**N**
DIVE	**Early**	264.5	90.08	23	160.3	59.91	21
	Mid	264.6	94.87	32	151.1	38.90	29
	Late	291.0	110.42	16	207.4	100.48	14
FULLDIVE	**Early**	243.9	20.08	21	333.3	103.30	17
	Mid	264.5	99.94	32	301.60	113.18	25
	Late	268.6	109.94	16	309.4	129.99	11

Table A15. Mean cow dive duration (s) (DIVEDUR) during DIVE and FULLDIVE synchronous and asynchronous travel bouts in early, mid and late season. Standard deviation (S.D.) and number of encounters (N) are included.

		Synchrony			Asynchrony		
		Mean	**S.D.**	**N**	**Mean**	**S.D.**	**N**
DIVE	**Early**	216.2	71.96	7	139.3	30.60	7
	Mid	215.9	41.90	7	144.1	25.17	7
	Late	192.5	32.17	5	163.5	32.29	5
FULLDIVE	**Early**	165.8	48.10	6	257.3	74.07	5
	Mid	234.3	101.62	7	255.0	43.98	4
	Late	172.3	51.23	5	234.3	57.02	4

Table A16. Mean cow dive duration (s) (DIVEDUR) during DIVE and FULLDIVE synchronous and asynchronous forage bouts in early, mid and late season. Standard deviation (S.D.) and number of encounters (N) are included.

		Synchrony			Asynchrony		
		Mean	**S.D.**	**N**	**Mean**	**S.D.**	**N**
DIVE	**Early**	333.4	66.71	10	180.7	76.68	9
	Mid	315.2	98.90	17	154.5	43.59	14
	Late	394.0	83.48	7	270.1	128.32	6
FULLDIVE	**Early**	316.2	62.94	10	378.6	98.92	9
	Mid	310.5	95.72	17	346.5	121.38	14
	Late	363.6	93.17	7	427.88	149.10	4

Table A17. Mean cow dive duration (s) (DIVEDUR) during DIVE and FULLDIVE synchronous and asynchronous surface forage bouts in early, mid and late season. Standard deviation (S.D.) and number of encounters (N) are included.

		Synchrony			Asynchrony		
		Mean	**S.D.**	**N**	**Mean**	**S.D.**	**N**
DIVE	**Early**	205.9	67.80	6	152.9	54.81	5
	Mid	199.6	50.90	8	151.2	43.69	8
	Late	233.8	19.28	4	155.3	40.93	3
FULLDIVE	**Early**	192.8	70.92	5	324.5	107.03	3
	Mid	193.3	50.98	8	238.4	86.90	7
	Late	222.7	15.43	4	251.6	43.44	3

Table A18. Mean frequency of SYNCDIVE and DIVE synchronous cycles during travel, forage and surface forage bouts. Standard deviations (S.D.) and sample sizes (N) are included.

	Behaviour								
	Travel			Forage			Surface Forage		
	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N
SYNCDIVE	0.26	0.146	17	0.41	0.181	34	0.47	0.231	17
DIVE	0.57	0.196	17	0.76	0.133	34	0.82	0.114	17

Table A19. Mean frequency of SYNCDIVE and DIVE synchronous cycles during early, mid and late season. Standard deviations (S.D.) and sample sizes (N) are included.

	Season								
	Early			Mid			Late		
	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N
SYNCDIVE	0.31	0.174	21	0.40	0.191	31	0.46	0.225	16
DIVE	0.67	0.170	21	0.75	0.164	31	0.76	0.189	16

Table A20. Mean frequency of SYNCDIVE and DIVE synchronous cycles during early, mid and late season travel, forage and surface forage bouts. Standard deviations (S.D.) and sample sizes (N) are included.

		Season								
		Early			Mid			Late		
		Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N
SYNCDIVE	**Travel**	0.29	0.189	6	0.25	0.139	6	0.25	0.119	5
	Forage	0.29	0.166	10	0.42	0.173	17	0.53	0.135	7
	S.Forage	0.37	0.197	5	0.47	0.220	8	0.61	0.283	4
DIVE	**Travel**	0.54	0.173	6	0.61	0.259	6	0.56	0.166	5
	Forage	0.71	0.137	10	0.77	0.133	17	0.82	0.119	7
	S.Forage	0.76	0.158	5	0.81	0.075	8	0.92	0.068	4