

**BEHAVIORAL DEVELOPMENT OF
DUSKY DOLPHINS**

A Thesis

by

SIERRA MICHELLE DEUTSCH

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2008

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

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ABSTRACT

Behavioral Development of Dusky Dolphins. (August 2008)

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Chair of Advisory Committee: Dr. Bernd Würsig

This thesis examines the characteristics of dusky dolphin (*Lagenorhynchus obscurus*) nursery groups and ontogeny of dusky dolphin calves. Data were collected via boat-based group focal follows of nurseries from October 2006-May 2007. A total of 87 nursery groups were encountered. Data were analyzed according to age category (infant or yearling) and season (early or late). Nursery group membership was lowest in the early season and when yearlings were present. The average number of yearlings in a nursery group was less than that of infants. The predominant activity of calves was rest. Early infants rested the most, while travel seemed most important for late infants, and early yearlings were most likely to forage. With the exception of early infants, all calves were more likely than adults to interact with boats. When taking month into account, yearlings were more social in general than infants. Infants showed a positive trend in sociality, while yearling sociality remained relatively stable. Nursery groups are markedly segregated by calf age, and 80% of nursery groups contained calves of only one age group. Dusky dolphin calves show a similar trend in preference for position in relation to the mother as that in bottlenose dolphins (*Tursiops* sp.), with echelon swim decreasing with age. However, all calves appear to prefer echelon swim when nursery groups are traveling. Calves were more likely to swim independently in the late part of

the season and while foraging or socializing, and were more likely to be in close proximity to their mothers while resting or traveling. Calves learned noisy leaps, followed by clean, coordinated, and acrobatic leaps, in that order. There was no clear relationship between behavioral state and types of leaps performed by calves. Early infants leapt less often than older calves, but leap frequency did not differ among the older calves. The overall pattern in the ontogeny of dusky dolphin leaps indicates that the physical development of leaps is learned individually, while the context in which the leaps are performed is learned from conspecifics. These results indicate that nursery groups represent an important environment for healthy physical and social development of calves.

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CHAPTER I

INTRODUCTION

Dusky dolphins (“duskies”) are an acrobatic and social delphinid that occur in temperate coastal waters off South America, Southern Africa, and New Zealand (Brownell & Cipriano, 1999). After approximately 11.4 months in gestation, New Zealand duskies are born during the austral summer, from November to mid-January. Both sexes reach sexual maturity at 7-8 years of age and can live to about 36 years (Cipriano, 1992). One of the smaller delphinid species, duskies occur in groups numbering from a few to the thousands (Würsig et al., 1997). Off Kaikoura, south island New Zealand (42.30° S and 173.32° E), there is usually one large group of several hundred animals throughout the day for most of the year (Cipriano, 1992; Yin, 1999). This prevalence and general easy approachability of duskies in large groups (although they are often elusive in small groups; see below) by humans have led to a successful dolphin watching and "swim with dolphin" tourism program since the late nineteen-eighties.

Dusky dolphins off Kaikoura live in a fission-fusion society. Individuals split off from the large central group to form smaller clusters. Markowitz (2004) identified three of these groups as mating adults, non-mating adults, and nursery groups. Mating groups consist of 4-8 males typically chasing a female, presumed to be in estrus. Non-mating adult groups consist of a mean of 9 adults and 1 juvenile with little or no sexual activity. Nursery groups are defined by Markowitz (2004) as fewer than 50 individuals with

This thesis follows the format and style of the *International Journal of Comparative Psychology*.

calves. Other researchers have used different definitions for nursery groups, including "groups containing calves" (Karczmarski, 1999), or groups "having at least 2 calves per 6 non calves" (Weir, 2007). I define a nursery group as any group of fewer than 50 individuals containing at least 25% calves. Because nursery groups spend much of their time in shallow waters (Weir, 2007), they tend to split around obstacles such as rocks and seaweed, but appear to maintain contact with each other as they move back together upon passing the obstacle. Therefore, I further define a group as individuals within 100 meters of each other, although group members were typically within 10m of another individual ("10-meter chain rule" (Smolker, Richards, Connor, & Pepper, 1992)) when not moving through obstacles.

The transience, behavioral ecology and sometimes elusive nature of duskies in small groups make it nearly impossible to perform a longitudinal study on calf development, so transverse studies with an occasional longitudinal element have been utilized to date.

AGE CLASSIFICATION

Through this work in the field, as well as descriptions from other authors (Cockcroft & Ross, 1990; Mann & Smuts, 1999) we can identify four main age groups of dusky dolphins, hereafter referred to as infants, yearlings, juveniles, and adults. Infants and yearlings are still dependent on maternal care and are further categorized as calves.

Calves: Infants

Infants are less than one year old. While there is not much information on length at birth for New Zealand duskie, Cipriano (1985) obtained lengths of 97-102 cm from three small animals believed to be newborns. Peruvian duskie, a slightly larger morphotype, are around 91 cm long and weigh roughly 9.6 kg (Van Waerebeek & Read, 1994) at birth, so Cipriano's data may have been biased by slightly older, not newborn, infants. Newborns are recognizable by fetal folds and floppy dorsal fins (Cipriano, 1992; Cockcroft & Ross, 1990; Mann & Smuts, 1999) (Figure 1). Within one to two weeks of birth, the dorsal fin becomes rigid (McBride & Kritzler, 1951), fetal folds smooth out and the infant is left with fetal lines for one to three months (Cockcroft & Ross, 1990; Mann & Smuts, 1999) (Figure 1). Infants range from about one-fifth to one-third the size of an adult and have a yellow hue that fades as they grow (pers. obs.). They exhibit "cork-like" breathing (Weir, 2007) (Figure 1), as they tend to overshoot the surface for each breath instead of exhibiting the smooth rolling pattern of older youngsters and adults. This age group is also characterized by their almost constant close proximity to adults.



Figure 1. Cork breathing, fetal folds (left), and fetal lines (right).

Calves: Yearlings

Yearlings are 1-2 years old, and are physically similar to adults, but with subtle differences, such as somewhat smaller size at roughly three-fourths to four-fifths the length of an adult (Cipriano, 1992). As well, the dorsal fin of a yearling is typically slightly more triangular than the falcate (concave trailing edge) fin of a mature adult, and is more uniformly dark, while an adult fin generally shows a mottled graduation of darker to lighter skin from the leading to trailing edges (Figure 2). Yearling dorsal fins also tend to be unmarked by the splotches and trailing edge marks that are more characteristic of older animals. Yearlings spend most of their time in close proximity to adults, but swim independently more often than infants and rarely exhibit cork breathing.



Figure 2. The dorsal fin of an adult (top) and a yearling.

Juveniles

Juveniles range from 2 to 7-8 years old, and become progressively more difficult to distinguish from adults as they age. Although probably weaned and not greatly dependent on their mothers, they are not yet sexually mature (Cipriano, 1992).

Adults

Adults are sexually mature and are 7-8+ years old (Cipriano, 1992); no evidence has been found for reproductive senescence.

Table 1
Dolphin age groups

Age Class	Age Range	Length	Other Defining Characteristics
Calf: Infant	< 1 year	1/5 – 1/3 adult	Cork-like breathing, constant close proximity to a specific adult
Calf: Yearling	1 – 2 years	3/4 - 4/5 adult	No cork-like breathing, less constant close proximity to adult
Juvenile	2 – 8 years	155-160 cm	Independent of a specific adult; not sexually mature
Adult	7-8+ years	165-186+ cm	Sexually mature

MOTOR DEVELOPMENT

Dolphins are precocious at birth, just like terrestrial ungulates from which they evolved (Dearolf, McLellan, Dillaman, Frierson, & Pabst, 2000). Because they are born in water, they must be able to swim immediately after parturition to reach the surface. However, dolphins are by no means expert swimmers at birth and must master motor skills to survive (Noren, Biedenbach, & Edwards, 2006). The cork-like breathing of infants is probably costly in terms of energy since it involves almost fully breaking the air-water boundary and is most pronounced in neonates, gradually decreasing with age.

Newborn bottlenose dolphins (*Tursiops truncatus*) have a higher tailbeat frequency than older animals (Noren, Biedenbach, & Edwards, 2006), and so do duskies. This suggests that younger animals need to use more energy per size than an adult per its size to achieve the same speed and maneuverability. Dusky calves also frequently

continue beating their tail flukes upon executing a leap, even after they have cleared the surface of the water; this fades with age and is only rarely seen in adults.

RESEARCH OBJECTIVES

While there have been several studies of development in wild delphinids, particularly bottlenose dolphins (*Tursiops* sp.), (Mann & Smuts, 1998; Mann & Smuts, 1999), few have described development and behavior in nursery groups in detail (Markowitz, 2004; Weir, 2007; Wells, Scott, & Irvine, 1987; Yin, 1999). Weir (2007) described distribution, behaviors, and composition of dusky dolphin nursery groups, as well as possible causes for the formation of nursery groups. In this thesis, I focus on how nursery groups and the prolonged mother-calf bond are of benefit to the calf.

The goal of this research is to describe behavioral development of dusky dolphin calves in nursery groups. My general research questions are 1) How does behavior differ by calf age? 2) What factors predict composition of nursery groups? 3) What role does calf position, relative to the mother, play in calf development and how does it differ by age group and behavioral state? and 4) How does learning of leaps occur?

SIGNIFICANCE

This project is an attempt to systematically describe the importance of nursery groups in calf development. Although we have some information on life history traits of dusky dolphins (Cipriano, 1992; Würsig et al., 1997), we have yet to shed light on the

developmental processes of calves. It is important to understand the origins of shared behaviors, in part to ensure that human activities are not interfering with the process.

Dolphins share a recent ancestor with ungulates (Milinkovitch, 1992) and exhibit many similar life history strategies (Mann & Smuts, 1999; Noren & Edwards, 2007; Würsig, 1989). However, among ungulate relatives, they have the distinction of being carnivorous and this requires adaptive strategies to ensure successful hunting. They are also large brained and live in a three-dimensional environment, so we see many converging strategies with those of primates (Bearzi & Stanford, 2007; Gowans, Würsig, & Karczmarski, 2008). Thus, they are unique among mammals and a better understanding of their behavioral development may help fit them into the broader context of shared life history strategies and improve our understanding of selective pressures on these strategies.

The timing of this project is especially appropriate as it coincides with a moratorium on the granting of new permits for dolphin tourist operations in Kaikoura, due to expire in 2010. Currently, nursery groups are not targeted by these tourist operations and my experience with the two existing tour operators leads me to believe this will not become an issue with them. However, if more permits are granted, crowding issues may lead new tour operators to seek out such groups to satisfy their clientele in an effort to compete with the presently well-established and successful dolphin tourism operations. Further, recreational vessel traffic in Kaikoura is likely to increase as tourism increases and these vessels may not follow or be aware of regulations protecting nursery groups (Duprey, 2007). Information provided by this

study could serve to enable officials to make a more informed decision regarding commercial permits and permit stipulations, as well as highlight the importance of education and enforcement of regulations, especially with regard to recreational vessels.

CHAPTER II

NURSERY GROUP CHARACTERISTICS: SIZE, CALF BEHAVIOR AND AGE COMPOSITION

INTRODUCTION

Dusky dolphin groups range in size from fewer than one dozen to thousands, with the largest groups forming in fall and winter (Cipriano, 1992; Markowitz, 2004). Group living has many benefits, including reduced risk of predation and non-socially transmitted parasites, cooperative defense, minimization of risks from challenges in the habitat, cooperative foraging, and shared care of young (Connor, 2000). However, the benefits of group living must outweigh the costs that include parasite transmission, resource competition, and increased detection by predators and aggressive conspecifics. Presumably, group size is limited by these costs. Weir (2007) found that the average size of dusky dolphin nursery groups in Kaikoura, New Zealand, was 21, while Markowitz (2004) reported a similar value of 18 as the average nursery size.

Delphinids are born with a high blubber to muscle ratio and limited motor skills, and must expend more energy to achieve the same speed and maneuverability as older calves (Cockcroft & Ross, 1990; Dearolf, McLellan, Dillaman, Frierson, & Pabst, 2000; Noren, Biedenbach, & Edwards, 2006). Therefore, it seems more efficient for animals to synchronize their energy levels by segregating into groups with calves of roughly the same age. Weir (2007) noted that dusky nursery groups appear to be composed of mothers with calves of similar age. However, mixed groups are also found, and infants and yearlings interact within these groups.

The sociality of calves is often studied in populations where a mother and her calf have few interactions with conspecifics, i.e. are relatively solitary (Connor, Wells, Mann, & Read, 2000; Mann & Smuts, 1999). Although Weir (2007) and Markowitz (2004) examined predominant behavioral states of nursery groups, they did not separately analyze calves of different ages. The examination of behavioral state preference by calf age may bring insight to the apparent age segregation of nursery groups.

Dolphin tourism operations are becoming increasingly popular around the world, including New Zealand (Bejder & Samuels, 2003; Constantine, 1999), and Constantine (2001) found that juvenile dusky dolphins are more likely than adults to interact with swimmers during swim-with-dolphin tourism interactions. Similarly, Markowitz (2004) reported that bow riding by individuals of nursery groups increased as calves matured. No studies have investigated differences in sociality towards boats by calf age in nursery groups, and this seems an important question in an area such as Kaikoura, which is subject to recreational boat traffic and high dolphin tourism pressures.

This study was carried out to examine (1) variations in nursery group size by calf age, (2) differences in behavior of calf age groups with a focus on boat interactions and sociality, and (3) nursery group age composition.

METHODS

Study Area

Kaikoura is on the east coast of the south island of New Zealand, at 42.30° S and 173.32° E. The Kaikoura Canyon, south of the Kaikoura Peninsula, ends about 500m from shore and within 200m of rocky outcrops with depths ranging up to 1200m (Lewis & Barnes, 1999). This study encompassed an area approximately 100km² between the Kaikoura Peninsula and Haumuri Bluffs roughly 22 km to the southwest (Figure 3).

Survey Methods

I performed one-hour focal follows on nursery groups from a 5.5m rigid-hull inflatable vessel, “Punua Aihe,” with an 80hp 4-stroke Yamaha engine. Weir (2007) established that nursery groups prefer habitat close to shore during the day, and therefore I located nursery groups through systematic surveys along the coastline. I performed these surveys by paralleling the shore at approximately 0.5 km along roughly 22 km of shoreline from the Kaikoura Peninsula to Haumuri Bluffs (Figure 3). Survey speed ranged from 10 to 13 knots (18.5 to 24.1 km/hr), and one 22 km “sweep” took about 2 hours to complete. During surveys, there were at least 3 people present on the boat: one driver and two observers. Using the bow of the boat as our 12 O’clock reference, the driver scanned from 9 to 3 for signs of dolphins; one observer assisted the driver in looking for hazards and also scanned from 9 to 3, while the other observer scanned from 3 to 9 (toward the stern). If no dolphins were discovered after completion of the first 22 km sweep, I positioned the boat parallel to shore in the opposite direction and about 2

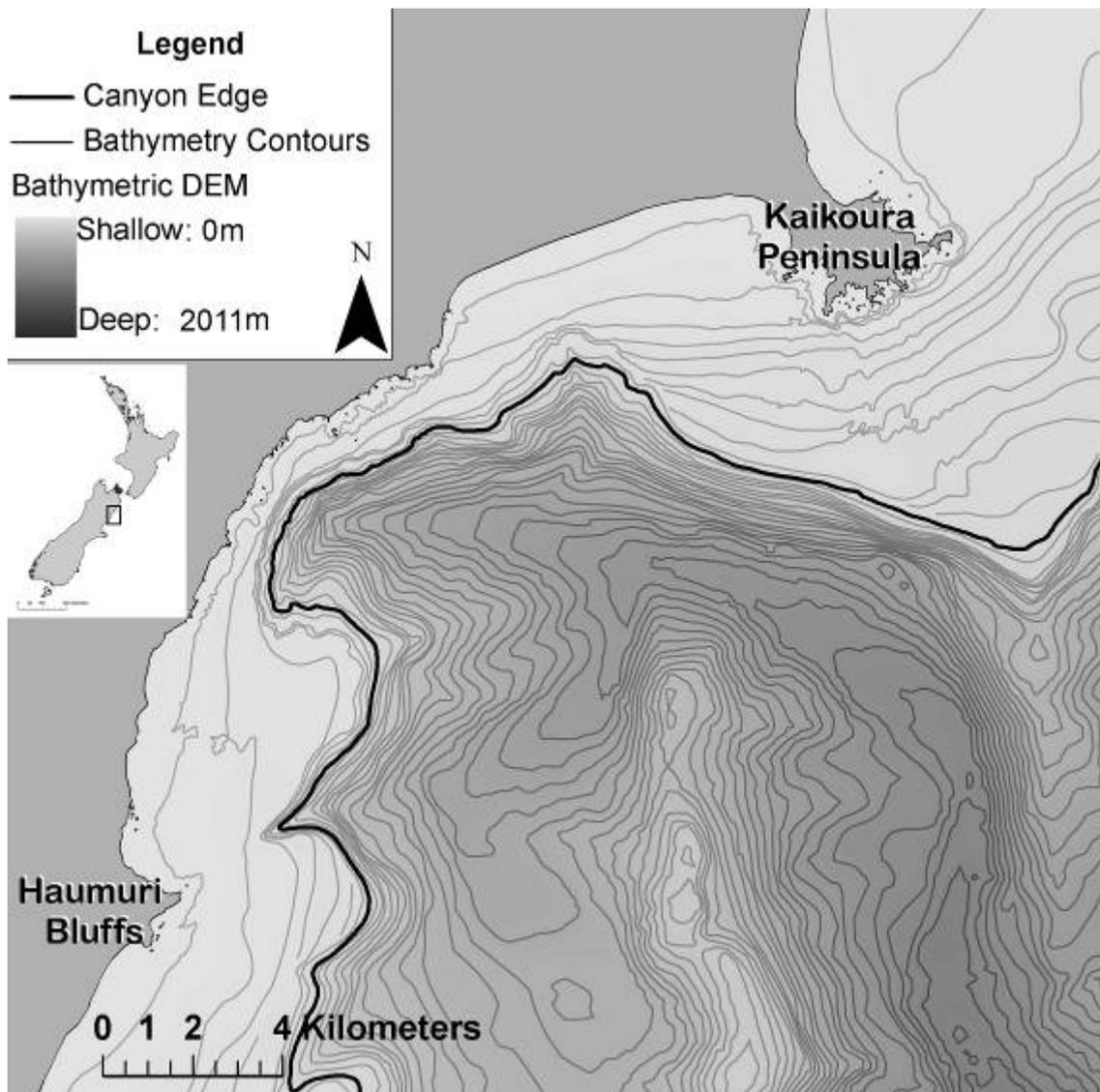


Figure 3. Study area. South Bay, Kaikoura, New Zealand. Bathymetric data provided by New Zealand's Institute of Water and Atmospheric Science. Full details can be found in Lewis & Barnes, 1999.

km from shore before continuing the survey back. If no nursery groups were spotted, this process was repeated twice, covering a total of 88 linear km, before retiring for the day. An effort was made to balance survey start positions between South Bay and Haumuri Bluffs.

Focal follows were only performed if the group was determined to be a nursery group, as defined in Chapter I. If at any point during the survey, it became difficult to keep track of group members due to joining of larger groups or inclement sea/weather conditions, I terminated the follow.

Behavioral Sampling

Encounter and focal follow data were gathered using Logger 2000, a data collection software program produced by the International Fund for Animal Welfare (IFAW), on a Dell Inspiron 1150 laptop computer. For consistency, I determined every parameter that was recorded throughout the season. Once we found a nursery group, I recorded group size, activity, and location before beginning a follow. During follows, I recorded samples in 2-min intervals, with a stopwatch signal sounding every two minutes (a “beep”). Time, date, and GPS data were logged at the beginning of each interval using Logger 2000. All other focal follow data were recorded on paper and entered into an MSAccess (Microsoft Corporation) database at the end of the day.

I used instantaneous sampling to determine number of adults, infants, and yearlings in the group, group spread, and distance from shore. If the group was underwater at the 2-min. beep, these data were assessed at next surfacing. Depth was recorded every 5th interval, or every 10 minutes.

Behavioral state definitions were adapted from Mann and Smuts (1999). These states include forage, rest, socialize, and travel, as defined in Table 2. Although dusky dolphins in Kaikoura forage offshore at night, opportunistic foraging sometimes occurs

in nursery groups (Weir, 2007). I performed scan sampling to determine predominant activity for each individual. Thus, any behavioral state that was predominantly seen in at least one individual was scored for that interval. Behavioral state for each age group was scored separately.

Table 2
Behavioral states

Behavioral State	Description
Forage	Rapid movement with frequent direction changes, often accompanied by leaps, fish present, birds diving near center of dolphin activity
Rest	Slow movement, speed < 3.5 km/hr, frequent direction change, regular respirations
Socialize	Physical contact and/or inspection of conspecifics and objects such as the boat or seaweed, lasting longer than 30 seconds
Travel	Rapid steady movement in one direction, speed > 3.5 km/hr

Data were compiled into one MSAccess database. Since thirty minutes appeared to be an adequate amount of time to determine nursery group parameters and yielded a large sample size, all follows were truncated to the first 15 intervals of two minutes each, and any follows shorter than 15 intervals were eliminated from analyses. Nursery groups are highly synchronous (Weir, 2007), so it is relatively easy to keep track of individual behaviors in groups of animals up to 50. Since calving in duskies is roughly seasonal (Cipriano, 1992; Van Waerebeek & Read, 1994; Würsig & Würsig, 1980), follows were then divided by season into “early” (through December 27, 2006) and

“late” (after December 27, 2006) categories. This yielded four groups: “Early Infants” (EI), “Late Infants” (LI), “Early Yearlings” (EY), and “Late Yearlings” (LY).

Group Size

All 87 nursery groups encountered were used in the analyses for group size, with means calculated for each follow. Since, these data were found to be normally distributed with equal variances, using Kolmogorov-Smirnov and Levene tests, respectively, group size was analyzed using an independent samples t-test to determine differences between the two age categories (infants and yearlings) and ANOVA to determine differences among the four age groups, with the least significant difference (LSD) test for post hoc analyses (Dytham, 2003). Data for mean number of calves in each nursery group were nonparametric and were compared by age category with a Mann-Whitney U test, and by age group with Kruskal-Wallis tests with the Bonferonni correction on individual Mann-Whitney U tests for post hoc analyses (Rice, 1989). Groups were only included in analysis if the age category or group in question was present.

Calf Behavior

Only follows containing 15 intervals were used in the analyses on behavioral states. Behavioral state ratios were determined using the sum of intervals for which that behavior was observed in each age group. These sums were compared across the four age groups with the G-test statistic in a 4x4 contingency table.

Examination of differences in sociality among age groups had three components. First, I used the G-test statistic in contingency tables to assess differences in frequency of interactions with boats. Second, I used an independent samples t-test to determine differences between the two age categories and ANOVA to inspect differences in amount of time each age group spent socializing in general (after establishing normal distribution and heterogeneity with Kolmogorov-Smirnov and Levene tests). Third, to get a closer look at where differences between age groups might be occurring, I compared the two age categories (infant and yearling) while controlling for month using ANCOVA (Dytham, 2003).

Age Composition

Since only the first interval of each encounter was used to estimate age composition, all 87 follows were used in the analysis of age composition. Groups were categorized as segregated or mixed, based on the presence of either infants or yearlings (segregated) or both (mixed) when the group was initially encountered. The G-test statistic was used to assess the prevalence of segregated groups by month and part of season, and chi-square goodness of fit test was used to test the prevalence of segregated groups over the entire season.

RESULTS

Survey Effort

We spent 318.2 (127 through Dec 27, 2006 and 191.2 after) hours on 70 days (23 through Dec 27, 2006 and 47 after) surveying the waters between Kaikoura Peninsula and Haumuri Bluffs. A total of 87 nursery group focal follows were performed, of which 66 contained infants and 48 contained yearlings. Of these 87 follows, 74 were used in the analyses, unless otherwise stated, of which 54 contained infants and 38 contained yearlings. This included 27 follows of groups with infants through Dec 27, 2006 (EI); 27 follows of groups with infants after Dec 27, 2006 (LI); 25 follows of groups with yearlings through Dec 27, 2006 (EY); and 13 follows of groups with yearlings after Dec 27, 2006 (LY).

Group Size

Mean group size for nursery groups (Table 3) containing infants was significantly larger than for nursery groups containing yearlings ($t = 2.012$, $P = 0.047$) (Figure 4a). The difference in group size for each of the four age groups was significant ($\chi^2 = 379.582$, $P = 0.001$) (Figure 4b). Mean group size was smaller for early infants than for late infants ($P = 0.003$), larger for late infants than early yearlings ($P < 0.0001$), and smaller for early yearlings than late yearlings ($P = 0.047$) (Table 4).

Table 3
Nursery group size by age category

Age Category	N	mean	standard error
Infants	65	16.9	1.15
Yearlings	48	13.7	1.35

Table 4
Nursery group size by age group

Age Group	N	mean	standard error
Early Infants	34	14.2	1.63
Late Infants	31	20.0	1.45
Early Yearlings	30	11.6	1.44
Late Yearlings	18	17.4	2.50

Number of calves by age category is shown in Table 5. Mean number of infants present in nursery groups was significantly higher than mean number of yearlings ($Z = -5.586$, $P < 0.001$) (Figure 4c). The difference in mean number of individuals in each of the four age groups was significant ($\chi^2 = 45.788$, $P < 0.001$) (Figure 4d). The number of early infants present in nursery groups was less than the number of late infants ($Z = -3.596$, $P < 0.0001$), but greater than the number of early ($Z = -2.113$, $P = 0.035$) and late ($Z = -2.437$, $P = 0.015$) yearlings. The number of late infants present in nursery groups

was also greater than early ($Z = -5.932$, $P < 0.001$) and late ($Z = -5.536$, $P < 0.001$) yearlings (Table 6). To improve the power of the Bonferonni corrections on individual Mann-Whitney U tests, a comparison was not made between number of early and late yearlings since they appeared very similar in mean, standard deviation, and mean rank.

Table 5
Number of calves in nurseries by age category

Age Category	N	mean	standard error
Infants	65	16.9	1.15
Yearlings	48	13.7	1.35

Table 6
Number of calves in nurseries by age group

Age Group	N	mean	standard error
Early Infants	34	14.2	1.63
Late Infants	31	20.0	1.45
Early Yearlings	30	11.6	1.44
Late Yearlings	18	17.4	2.50

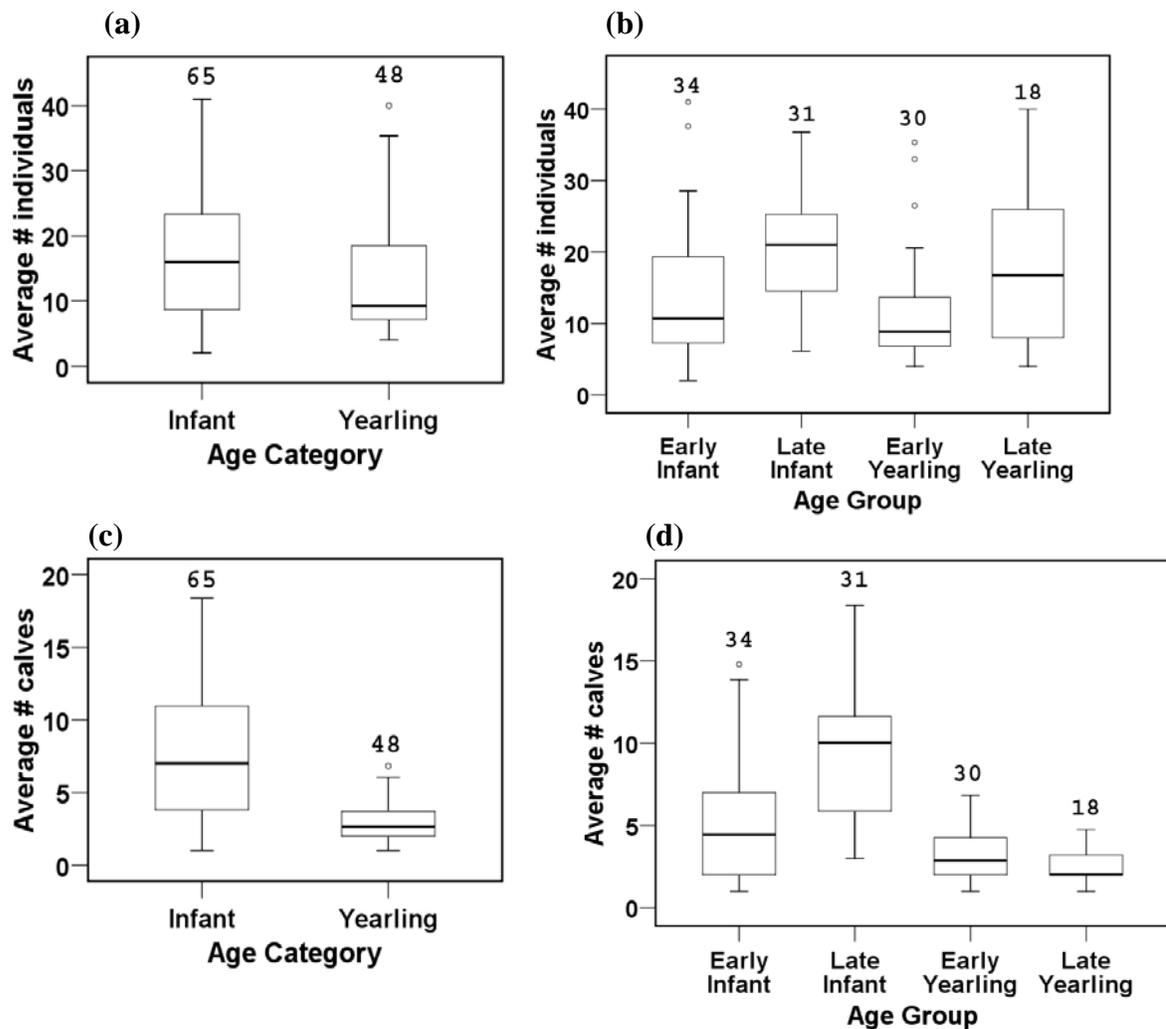


Figure 4. Number of individuals in a nursery group by (a) age category and (b) age group; and number of calves present in a nursery group by (c) age category and (d) age group. Numbers above data bars represent sample size. Central lines represent medians, and boxes contain 50% of cases. Whiskers include all other cases, excluding outliers, represented by the symbol \circ .

Behavioral States

Behavioral states were analyzed by each of the four age groups discussed above.

All age groups spent the majority of their time resting (Figure 5).

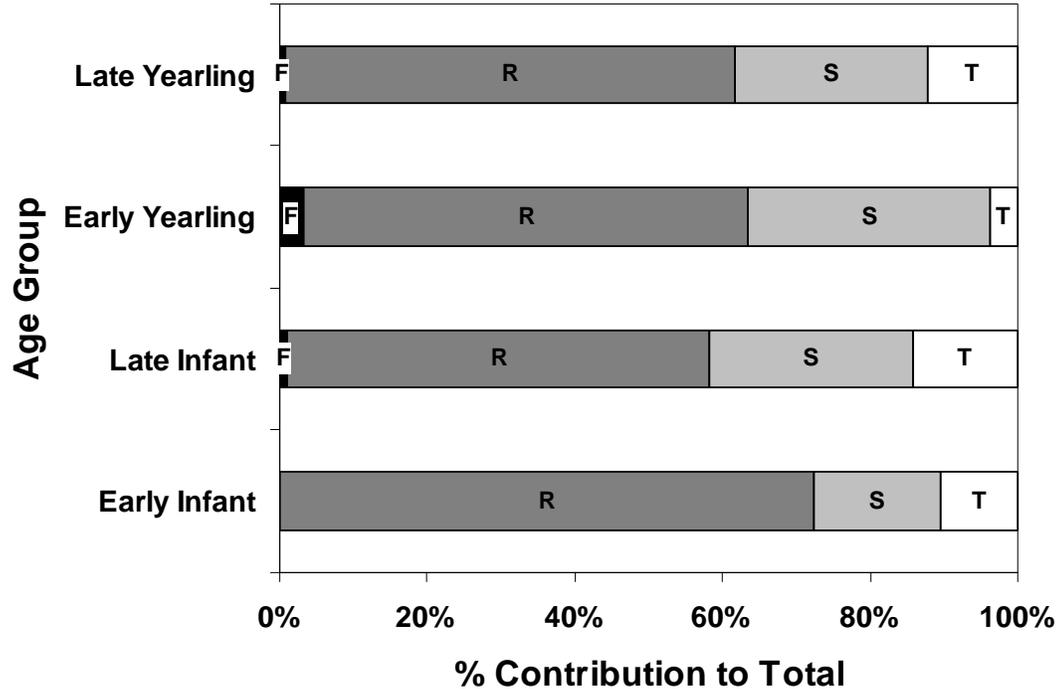


Figure 5. Behavioral state by calf age. F=Forage, R=Rest, S=Socialize, T=Travel.

Early infants (EI) were less likely to forage ($z = -2.47$, $P = 0.007$) and socialize ($z = -4.41$, $P < 0.001$), and more likely to rest ($z = 4.37$, $P < 0.001$) than any other age group. Late infants (LI) were less likely to rest ($z = -2.54$, $P = 0.006$) and more likely to travel ($z = 3.24$, $P < 0.001$) than any other age group. Early yearlings (EY) were more likely to forage ($z = 3.94$, $P < 0.001$) and socialize ($z = 3.48$, $P < 0.001$), and less likely to travel ($z = -4.70$, $P < 0.001$) than any other age group. The number of intervals spent in each behavioral state by late yearlings (LY) did not differ from chance.

Calf Sociality

When adults were excluded from analyses, early infants were less likely ($z = -5.14$, $P < 0.001$) and early yearlings were more likely ($z = 4.69$, $P < 0.001$) to interact with the boat than other calves.

Results differed when adults were included in the analyses. Early infants were still less likely to interact with boats than other calves ($z = -3.28$, $P < 0.001$), but not less likely than adults ($z = -6.92$, $P < 0.001$). All other calves were more likely to interact with boats than early infants and adults ($z = 3.77$, $P < 0.001$ (LI); $z = 9.40$, $P < 0.001$ (EY); $z = 3.01$, $P = 0.001$ (LY)). Figure 6 shows the percent of intervals each age group interacted with a boat.

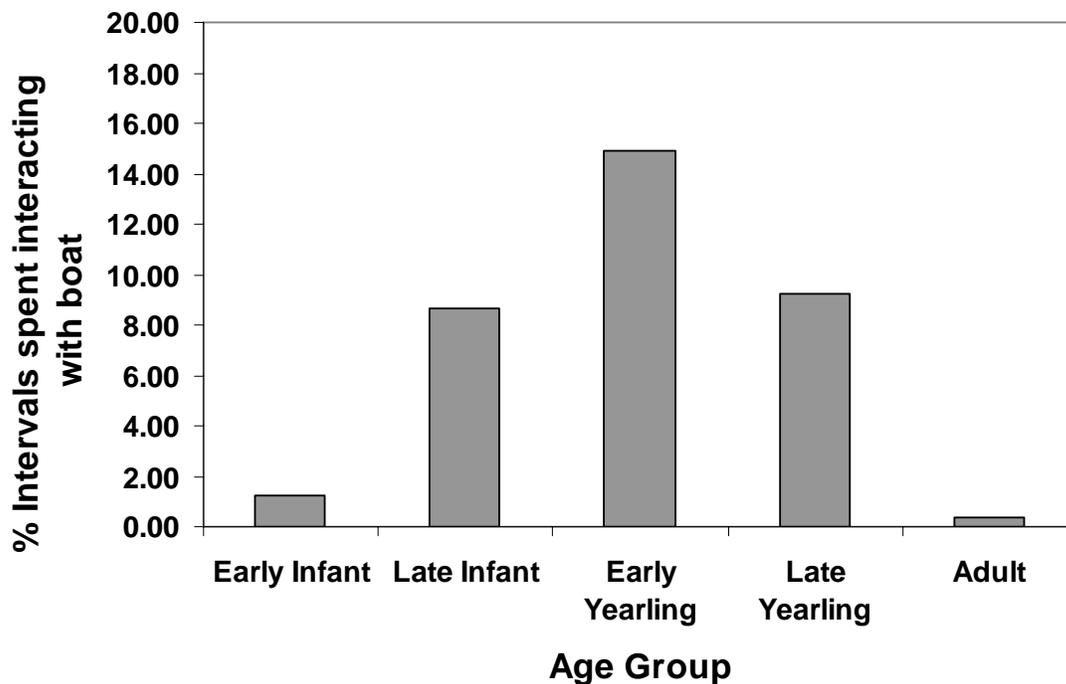


Figure 6. Interactions with boats by age group.

There was no difference in amount of time spent socializing among the four age groups or the two age categories. However, when controlling for month, there was a significant difference in sociality between infants and yearlings ($F = 5.117$, $P = 0.026$) (Figure 7).

Age Composition

Of 87 follows, 70 (80%) were segregated and 17 (20%) were mixed (Figure 8a). A goodness of fit test showed that groups were much more likely to be segregated than mixed ($\chi^2 = 32.30$, $P < 0.001$). There was no difference in segregation between early and late parts of the season (Figure 8b). Analysis by month showed that there was no difference in nursery group segregation among months, except for February, when mixed nursery groups were more common than segregated ones ($z = -2.28$, $P = 0.01$ for segregated and $z = 2.28$, $P = 0.01$ for mixed nursery groups) (Figure 8c).

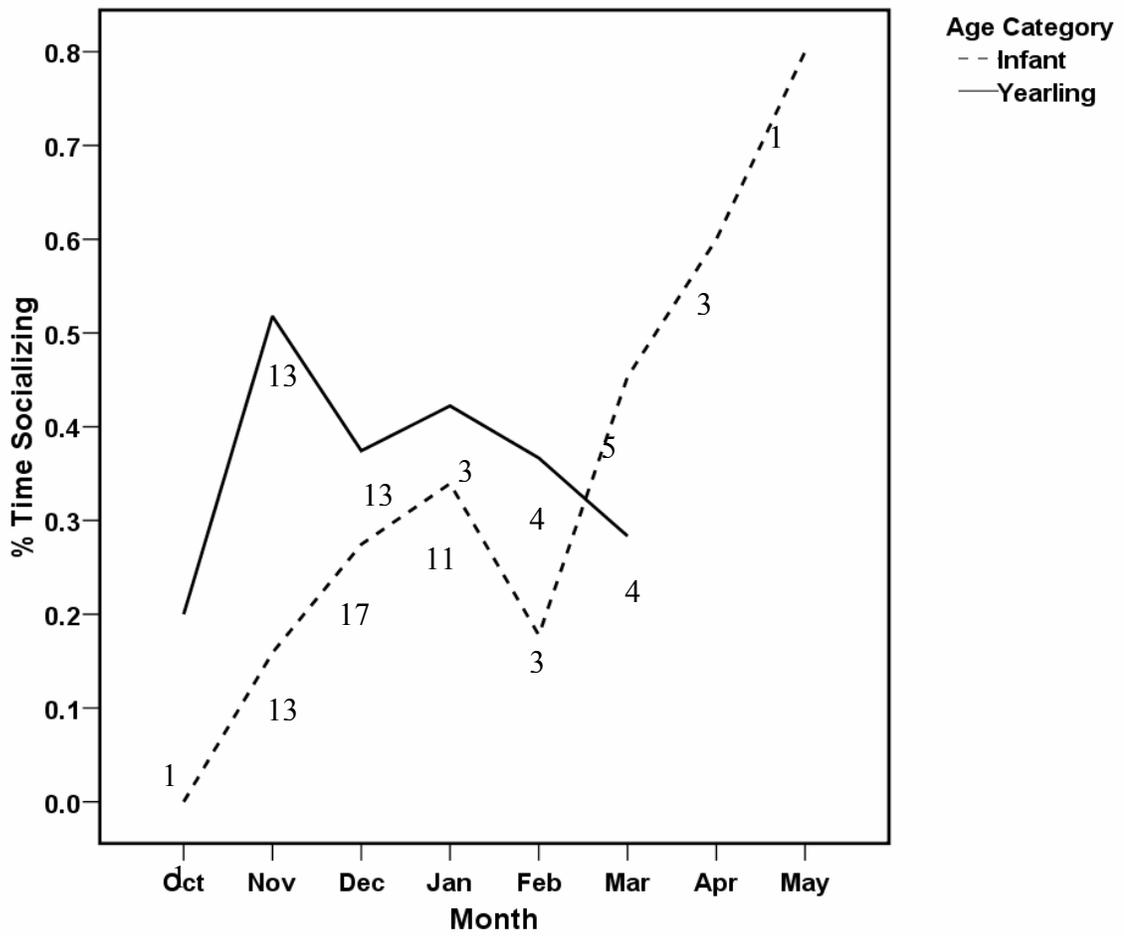


Figure 7. Sociality by calf age. Numbers represent sample size.

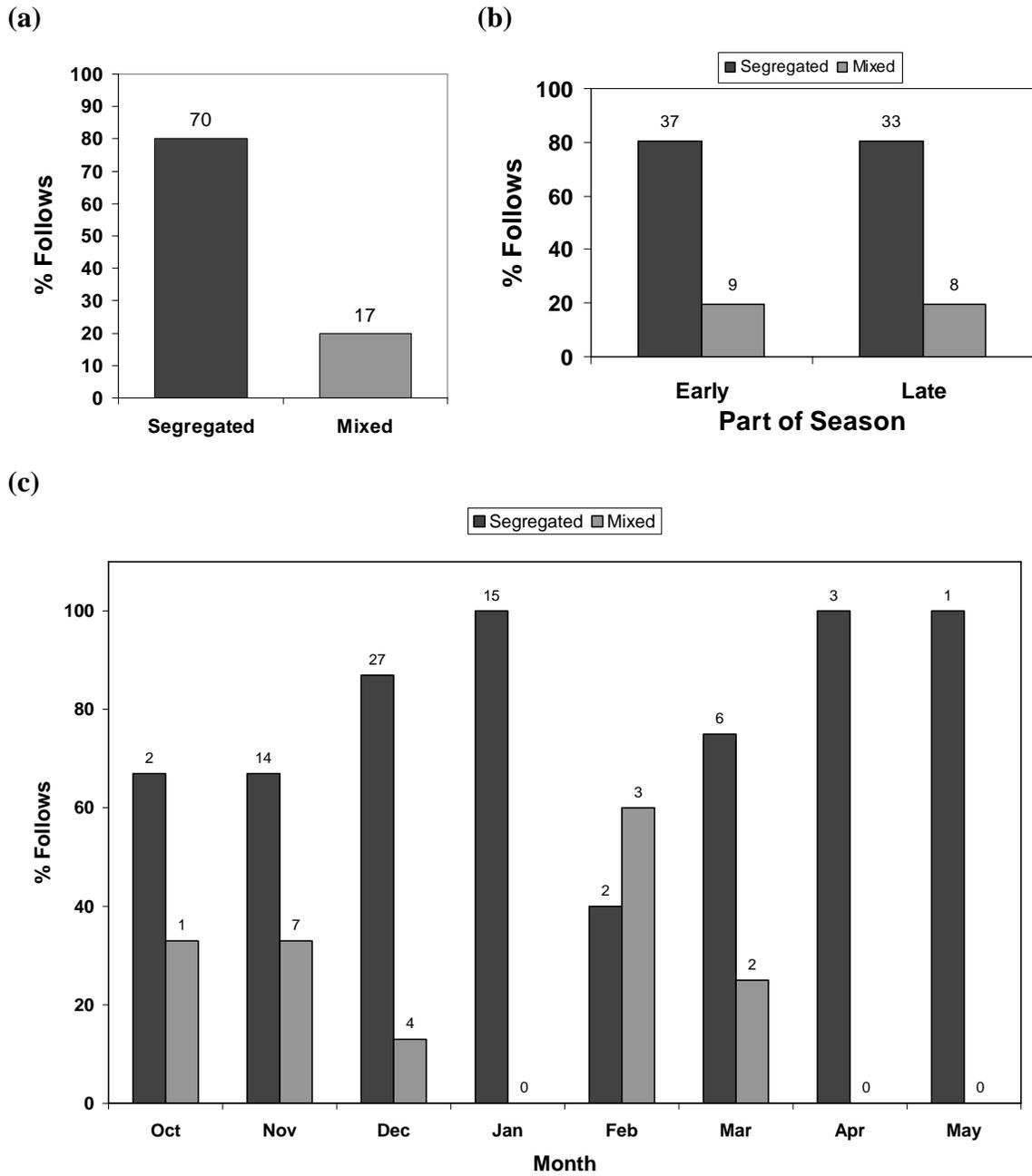


Figure 8. Nursery group age composition by (a) entire season (b) part of season, and (c) month (with sample sizes above bars).

DISCUSSION

Group Size

Nursery group size was larger when infants were present than when yearlings were present. Further, the number of yearlings in nursery groups was smaller than number of infants. Considering the high mortality rates in wild delphinid calves (Herzing, 1997; Mann, Connor, Barre, & Heithaus, 2000) and likely dispersal, this seems appropriate.

Nursery group sizes from smallest to largest were those that contained early yearlings, early infants, late yearlings, and late infants. The number of calves in each age group from lowest to highest was late and early yearlings, early infants, and late infants.

The overall trend seems to be smaller groups with fewer calves earlier in the season and larger groups with more calves later in the season. During the earlier part of the calving season, mating behavior in dusky dolphins is at its peak (Markowitz, 2004) and aggressive males may be attracted to new mothers undergoing hormonal changes (Weir, 2007). It is likely that smaller group sizes are less detectable by potential harassers, due to the encounter effect. Stanford (1995) found that red colobus monkeys (*Colobus badius tephrosceles*) living in the heart of the hunting area of chimpanzee (*Pan troglodytes*) predators formed groups that were 46% smaller than those living on the boundaries of the hunting area. Similarly, Ioannou and Krause (2008) found that *Daphnia sp.* in groups of two were approached and attacked by three-spined sticklebacks (*Gasterosteus aculeatus L.*) much less often than groups of one-hundred.

It is also probable that the dilution effect plays a role in nursery group size. Each individual that joins the group reduces the chance of a particular individual being attacked by a potential predator or aggressive conspecifics. This may be one reason why solitary mother-calf pairs are rarely seen, although social learning in a group and other reasons are likely to be important in group formation as well.

Behavioral States

All calf age groups spent the majority of their time resting, and previous studies support these results (Markowitz, 2004; Weir, 2007), suggesting that nursery groups may serve an important function in insuring that calves get enough rest. This should be an important consideration in development of new boater regulations in the area as recreational and commercial traffic increases.

Rest appears to be particularly important for early infants. Although others have noticed a distinct absence of rest in captive delphinid calves (Lyamin, Pryaslova, Kosenko, & Siegel, 2007; Lyamin, Shpak, & Siegel, 2003), sleep occupies the majority of time in most newborn mammals (Ellingson, 1972; Jouvet-Mounier, Astic, & Lacote, 1970; Louis, Cannard, Bastuji, & Challamel, 1997). Further, nursery groups with very young calves may remain quiet to reduce detection by aggressive males or potential predators.

Travel appears to be more important for late infants than for other age groups. Similarly, Atlantic spotted dolphin calves spend more time traveling during their first year than in later years (Miles & Herzog, 2003), and bottlenose dolphin calves spend

more time traveling in their second month than in their first (Mann & Smuts, 1999). Thomas and Taber (1982) reported that right whale (*Eubalaena australis*) calves spend the majority of their time traveling during their first year, and postulated that this may aid in muscle development. Given that delphinids are born with a high blubber to muscle mass (Cockcroft & Ross, 1990; Dearolf, McLellan, Dillaman, Frierson, & Pabst, 2000; Noren, Biedenbach, & Edwards, 2006) and limited aerobic capability (Dearolf, McLellan, Dillaman, Frierson, & Pabst, 2000), it may follow that duskies would need conditioning to develop motor capacity.

Bottlenose dolphin calves begin mouthing fish when they are as young as one month old, although infants do not catch fish until the age of 4-6 months (Mann & Smuts, 1999). Generally, little daytime foraging occurs in the Kaikoura area, where duskies rely principally on night-time feeding on the Deep Scattering Layer (DSL), an aggregation of organisms that ascend from deep in the canyon at dusk and descend again at dawn (Cipriano, 1992; Markowitz, 2004; Würsig et al., 1997). However, daytime foraging appears to be most important for early yearlings. Although this may be partly due to underestimation of foraging events given my strict definition of foraging, it may reflect ontogeny of learning to forage. Duskies likely learn to forage in shallower waters to hone their capturing skills before attempting it at depths where they are known to dive up to 130 meters (Benoit-Bird, Würsig, & McFadden, 2004). Noren et al. (2002) discovered that bottlenose dolphins aged 0-2 years have a much lower oxygen storing capacity than those aged 3-12 years. They estimate aerobic dive limits to be 1.9 – 3.6 and 4.8 – 5.4 minutes, for younger and older ages respectively, so perhaps dusky early

yearlings are physiologically confined to daytime foraging, which occurs in shallower waters.

Cipriano (1992) performed a gut-content analysis on twenty-six dusky dolphin specimens and found only milk in the stomachs of four calves ranging in size from 97-120 cm, although a similar sized animal (118 cm) had several types of fishes in its gut. He estimated the age of animals in this size range as less than one year, while specimens ranging from 130-150 cm were estimated to be 1-2 years old and had all fed on fish. It is possible that dusky dolphins may begin learning to chase and mouth prey as infants, but it appears that serious foraging does not occur until they are in their second year. Similarly, Atlantic spotted dolphins begin foraging successfully in their second year (Miles & Herzog, 2003). The fact that the early yearlings were seen foraging more than late yearlings may reflect a transition to nighttime foraging, but further research into diurnal movement patterns of nursery groups is needed.

Sociality

Early infants rarely interacted with boats, and this may indicate the importance of rest and/or a need to maintain proximity with their mothers, who rarely interacted with boats. All other calves showed much more interest in boats than adults. These findings, along with others that have suggested calves are particularly interested in swimmers and boats (Constantine, 1999; Markowitz, 2004), may have implications for healthy calf development. As recreational boating and boat-based dolphin tourism increases with demand, nursery groups may be more likely to be disturbed. Countless studies have

indicated detrimental effects of dolphin tourism activities if not regulated properly (Bejder & Samuels, 2003; Bejder et al., 2006; Constantine, 1999, , 2001; Lusseau, 2004; Orams, 1997; Stockin, Lusseau, Binedell, Wiseman, & Orams, 2008; Van Parijs & Corkeron, 2001). Humans tend to be particularly drawn to “cute baby animals” and this, combined with the fact that calves are more likely to be receptive to boater interactions, could further put nursery groups at risk for increased contact with boaters. Although more data are needed, consideration of preemptive regulations for boaters encountering nursery groups is recommended.

Social interactions with conspecifics are important in the behavioral development of delphinids, and dolphins may learn behaviors from these interactions (Fripp et al., 2005). Dusky dolphin infants appear to participate in more social activities as they mature, while yearlings seem to maintain a relatively stable level of sociality. This is similar to trends seen in other social cetaceans. Mann and Smuts (1999) found that bottlenose dolphin infants socialized more in month two than month one. During their first year, right whale calves play much more during the later months than during the earlier ones (Thomas & Taber, 1982). In belugas, level of social activity increases with age until it approaches that of adults (Krasnova, Bel'kovich, & Chernetsky, 2006). These trends indicate that social development is an important part of normal cetacean development in social species.

Age Composition

Group segregation by age is fairly common in social mammals and has been recorded in several cetacean taxa, including humpback dolphins (Karczmarski, 1999), beluga (Loseto, Richard, Stern, Orr, & Ferguson, 2006), bowhead whales (Cosens & Blouw, 2003; Würsig, Dorsey, Richardson, & Wells, 1989), bottlenose dolphins (Connor, Wells, Mann, & Read, 2000) and dusky dolphins (Markowitz, 2004; Würsig & Würsig, 1980). Dusky dolphins in nursery groups show a marked preference for associating with mothers with calves around the same age. Similarly, bonnet macaque (*Macaca radiata*) infants show a preference for socializing with age mates, although this decreases over time (Handen & Rodman, 1980).

There are several possible causes for group segregation by age, and I discuss two here. First, mothers may want to synchronize activity levels of their calves to achieve optimal use of energy for both mothers and calves. Different behavioral states retain variable levels of importance for different age groups. Travel may be important for infant muscle development and yearlings are more social than infants when month is factored in. If calves of all ages were always in the same group, infants might become overwhelmed by comparatively socially active yearlings. However, an increase in sociality such that it surpasses those of yearlings, occurs between the months of February and March (Figure 7). February is also the only month in which mixed nursery groups comprise the majority (60%; Figure 8c). It is possible that this increase in infant sociality occurred as a result of increased interactions with yearlings. Conversely, a natural boost in infant sociality may have resulted in more mixed groups due to similar

levels of sociality between age categories. The latter is the more likely explanation, given that infant sociality continued to increase after nursery groups returned to their previous pattern of segregation.

Group segregation may also reflect differing energetic needs of the mothers. Calves appear to forage fairly regularly in their second year (Cipriano, 1992) and this suggests that mothers may have reduced energy costs associated with lactation (Cockcroft & Ross, 1990). Mothers who have higher energy needs (i.e. mothers with younger calves) may want to associate more often with mothers with similar energetic demands to aid in cooperative foraging.

CONCLUSION

Nursery groups were smaller in size in the early half of the season than in the late half, and this may reflect a desire to avoid aggressive males. Additionally, nursery groups were smaller when yearlings were present and fewer yearlings were found in nursery groups, possibly due to high calf mortality or dispersal.

The predominant activity of calves in nursery groups was rest and this was most pronounced for early infants. This may be due to high requirements of sleep in mammalian infants or may again reflect a desire to avoid detection by insistent males. Travel appears most important for late infants, and a preference for travel is seen in several other cetacean young. Dusky infants may need to travel often to condition muscles of small mass and with poor aerobic capacity. While infants may practice foraging, it appears that serious foraging does not occur until the dusky dolphin's second

year of life. Further, early yearlings may be more likely to forage in shallower waters during the day than late yearlings that may have improved diving capacity, allowing them to forage on the DSL at night.

All calves, with the exception of early infants, are more likely than adults to interact with boats, and this could have significant implications for normal ontogeny and subsequent survival if they are distracted from other important activities. Additionally, the levels of sociality in infants versus yearlings indicate that the first year of life may be most important in social development as levels of sociality steadily increase.

Nursery groups are strikingly segregated by calf age, with infants and yearlings interacting only 20% of the time. This segregation is likely a result of many contributing factors including energetic needs of lactating mothers and energetic efficiency for calves participating in different behaviors.

In conclusion, a closer inspection of nursery groups reveals a complex interaction of several factors that dictate nursery group size and composition. It also appears that nursery groups form to meet the diverse needs of different age groups in dusky dolphin society.

CHAPTER III

SWIM POSITIONS

INTRODUCTION

Mammalian mothers need to keep their infants safe while performing other important tasks, and have evolved strategies for doing so. Mothers may either hide their infants while remaining nearby or adopt an infant carrying strategy (Fisher, Blomberg, & Owens, 2002; Fitzgibbon, 1990; Ross, 2001). In cases where mothers are unable to carry their infants but need to travel some distance, the infants assume a following strategy, as documented in most but not all ungulates (Lent, 1974), insectivores (Tsuji & Ishikawa, 1984), xenarthrans (armadillos and anteaters), rodents, aardvarks, sirenians, and cetaceans (Gubbins, McCowan, Lynn, Hooper, & Reiss, 1999; Tavalga & Essapian, 1957) (see Ross 2001 for a review). Another strategy is to leave the infant with a designated caretaker (Riedman, 1982). This behavior, known as alloparental care, is seen in many mammals including, but not limited to, sperm whales (*Physeter macrocephalus*, Whitehead, 1996), primates (Fairbanks, 1990; Nicolson, 1987), elephants (*Loxodonta africana*, Rapaport & Haight, 1987), bighorn sheep (*Ovis canadensis canadensis*, Hass, 1990), prairie dogs (*Cynomys ludovicianus*, Hoogland, Tamarin, & Levy, 1989), and bottlenose dolphins (*Tursiops sp.*, Shane 1990).

Since the ocean is an open three-dimensional environment, there are few places to hide and the streamlined bodies of most cetaceans discourage the carrying of an infant. Although alloparental behavior may play a small role in the care of young dusky dolphins (Markowitz, 2004), it seems impractical to leave the calf with another

individual every time the mother must perform tasks, such as foraging, on her own. So in addition to alloparenting, dolphin mothers and calves, like other cetaceans (Gubbins, McCowan, Lynn, Hooper, & Reiss, 1999; Mann & Smuts, 1999; Taber & Thomas, 1982; Thomas & Taber, 1982; Würsig, Koski, & Richardson, 1999), have developed a hybrid of the carrying and following strategies in which they maintain close proximity to each other. Calves maintain proximity by swimming in one of two positions (Cockcroft & Ross, 1990; Gubbins, McCowan, Lynn, Hooper, & Reiss, 1999; Mann & Smuts, 1999; Tavolga & Essapian, 1957): in echelon slightly above the mother and just to one side by her dorsal fin, and in infant position slightly behind and to one side of the ventral surface of the mother, near her mammary slits (Figure 9). Younger calves may benefit from echelon by easier access to the surface for respiration, increased protection from predators from below, and minimized energy expenditure. Würsig et al. (1999) observed bowhead whale calves “riding” on the backs of their mothers and suggest that this behavior may allow calves to achieve greater distances under ice flows than if the calf were traveling alone.



Figure 9. Echelon swim (left) and infant position swim (right). In both photos, the calf is at the bottom.

Bottlenose dolphin infants are more likely to be found in echelon swim immediately after parturition, and this tendency decreases with age, while infant position increases (Cockcroft & Ross, 1990; Gubbins, McCowan, Lynn, Hooper, & Reiss, 1999; Mann & Smuts, 1999). Two hypotheses have been proposed to explain this shift in positions as the calf ages. Norris and Prescott (1961) postulated that echelon position allows the calf to ride the pressure wave produced by its mother, but as the calf grows, it may become too large to maintain its position on that wave. Alternatively, the calf may become more energy efficient as it grows and may not need to be as close to the surface for respirations, so it may be more beneficial to be in a position where it has easy access to nursing (Gubbins, McCowan, Lynn, Hooper, & Reiss, 1999).

This study was carried out to examine differences in swim positions of dusky dolphin calves by different age groups and different behavioral states.

Dusky dolphins are smaller than bottlenose dolphins; while comparisons of different swim positions have been made in the latter (Cockcroft & Ross, 1990; Gubbins, McCowan, Lynn, Hooper, & Reiss, 1999; Mann & Smuts, 1999), no studies have made such comparisons in duskies. Dusky mothers and calves differ from the bottlenose dolphins in these studies since dusky mother-calf pairs form nursery groups, while the bottlenose were relatively solitary (Mann & Smuts, 1999) or confined in small unisex social groups in captivity (Cockcroft & Ross, 1990; Gubbins, McCowan, Lynn, Hooper, & Reiss, 1999). However, although there are currently no data on first year growth curves for duskies, they share similar life history traits and mother/calf mass ratios with

bottlenose dolphins (Whitehead & Mann, 2000). Therefore, I predict a similar trend in position transition in duskies as that seen in bottlenose.

While recent studies have compared the efficiency of echelon swimming to that of the calf swimming independently (Noren, 2008; Noren, Biedenbach, Redfern, & Edwards, 2008), no studies have examined the differences in utilization of echelon, infant, and independent swimming with differing behavioral states. Noren (2008) showed that mothers with infants in echelon swim expended significantly more energy through increased swimming effort than when swimming alone. Although he did not include an analysis of infant position swim, it likely has a similar effect on the mother's energy costs. However, calves swimming on their own are more vulnerable to predation and/or harassment by conspecifics. Therefore, I predict that infants are more likely to swim independently in activities where the added cost to the mother outweighs the increased risks to a calf left to fend for itself.

METHODS

Study Area and Survey Methods were as described in Chapter II.

Behavioral Sampling

Behavioral data were collected and compiled as described in Chapter II.

Because it is difficult to determine positions at all times during an interval, positions were scored using one-zero sampling (Smith, 1985). Positions for infants and yearlings were scored separately. Table 7 outlines the four possible non-mutually exclusive categories of positioning.

Table 7
Calf swim positions

Calf Position	Description
By Adult (BA)	Calf within one meter of an adult, but position was not determined
Echelon Swim (ES)	Calf swimming slightly above adult near the dorsal fin
Infant Position Swim (IPS)	Calf swimming below and slightly behind adult's pectoral fin, breaking position only briefly for respirations
Swimming Independently (SI)	Calf swimming at least three meters from nearest adult and usually in different orientation for more than 10 seconds

Preference for positions was quantified by taking the sum of intervals for which that position was seen in an age group. These sums were compared across the four age groups using the G-test statistic in a 4x4 contingency table. While there is potential for re-sampling the same mother and calf disproportionately during one follow, I believe the analysis to be fair among follows, because all positions had an equal probability of being seen during each interval. Further, all follows had 15 intervals represented and the data essentially represent ratios of amount of certain activities per age group.

Similarly, to determine whether preference for position changed with behavioral state, it appeared most appropriate to compare ratios of time spent in each position during each behavioral state. Sums of intervals in which a behavioral state and position were simultaneously seen were calculated. These sums were also compared using the G-test statistic in a 4x4 contingency table.

RESULTS

For *Survey Effort*, see Chapter II.

Swim Position Preference

The number of intervals calves spent in each position was not as expected by chance ($G^2 = 215.74$, $P < 0.001$). However, binomial scores showed that the number of intervals in which calves were close to adults but position was not determined (BA) did not differ from chance for any age group. Therefore, BA was not included in Figure 10, which summarizes the proportion of intervals of each age group in which each position was observed.

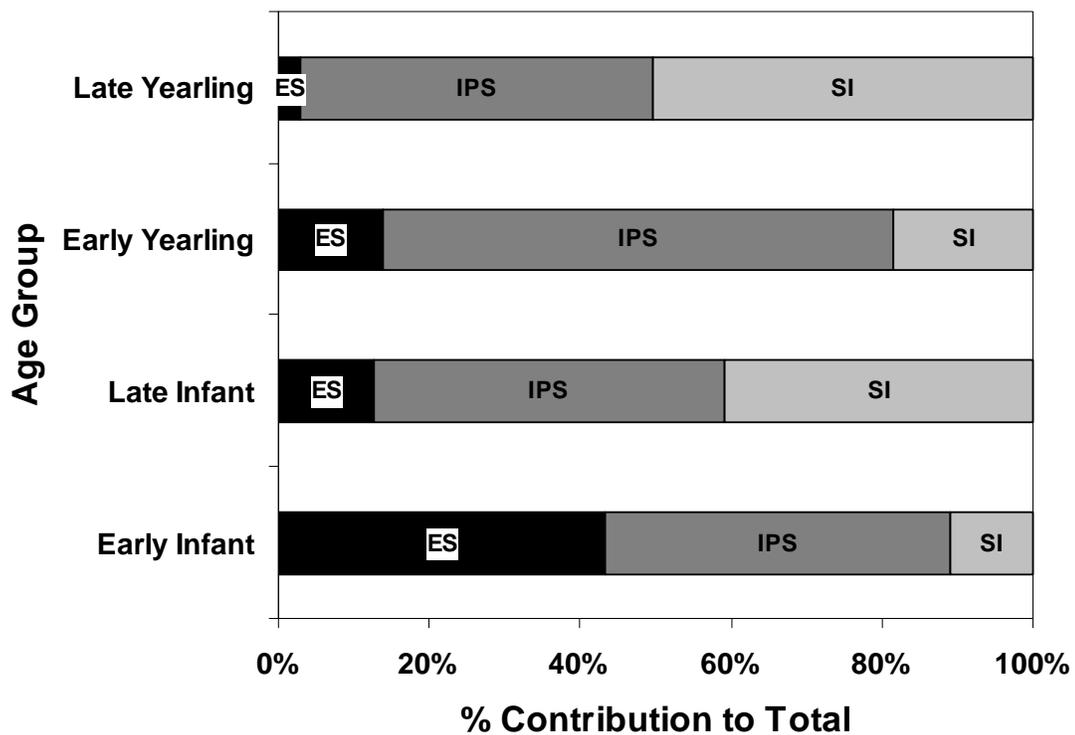


Figure 10. Calf position by age group. ES = Echelon Swim, IPS = Infant Position Swim, SI = Swimming Independently.

Early infants swam in echelon significantly more often than expected by chance ($z = 9.47, P < 0.001$), while all other age groups swam in echelon significantly less often than expected by chance ($z = -3.18, P < 0.001$ (LI); $z = -2.58, P = 0.005$ (EY); $z = -5.18, P < 0.001$ (LY)) (Figure 11a).

Number of intervals in which calves swam in infant position was not significantly different than expected by chance in all but one age group. Early yearlings swam in infant position significantly more than expected by chance ($z = 3.08, P = 0.001$) (Figure 11b).

Finally, the number of intervals in which calves swam independently differed significantly from that expected by chance for all age groups. Early infants and early yearlings swam independently less than expected ($z = -6.29, P < 0.001$ and $z = -3.50, P < 0.001$, respectively), while late infants and late yearlings swam independently more than expected ($z = 5.49, P < 0.001$ and $z = 4.28, P < 0.001$, respectively) (Figure 11c).

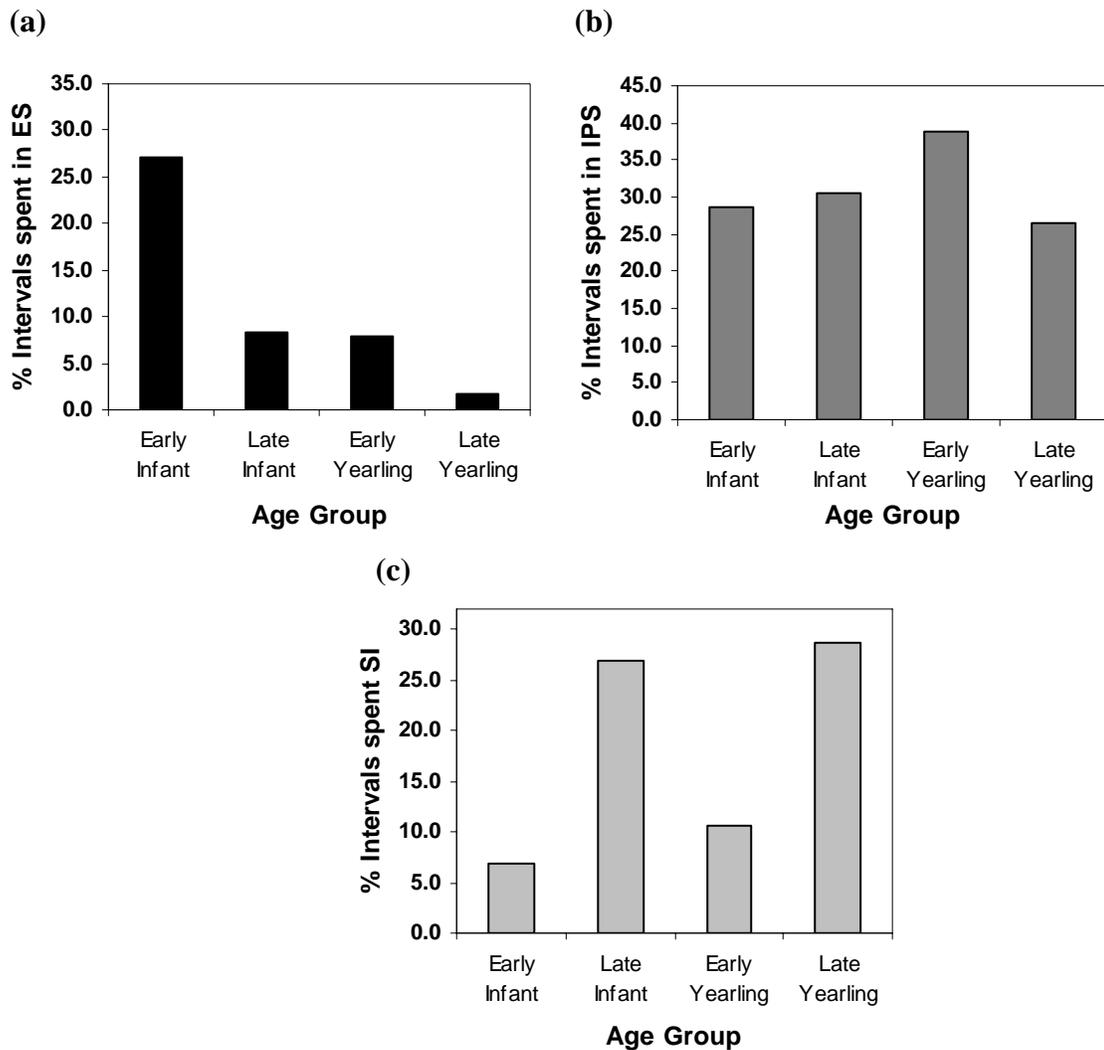


Figure 11. a) Echelon swim, b) infant position swim, and c) independent swimming by calf age group.

Swim Position by Behavioral State

The number of intervals calves spent in each position during each behavioral state differed significantly from that expected by chance ($G^2 = 145.59$, $P < 0.001$).

Figure 12 summarizes proportion of intervals for each behavioral state in which each position occurred.

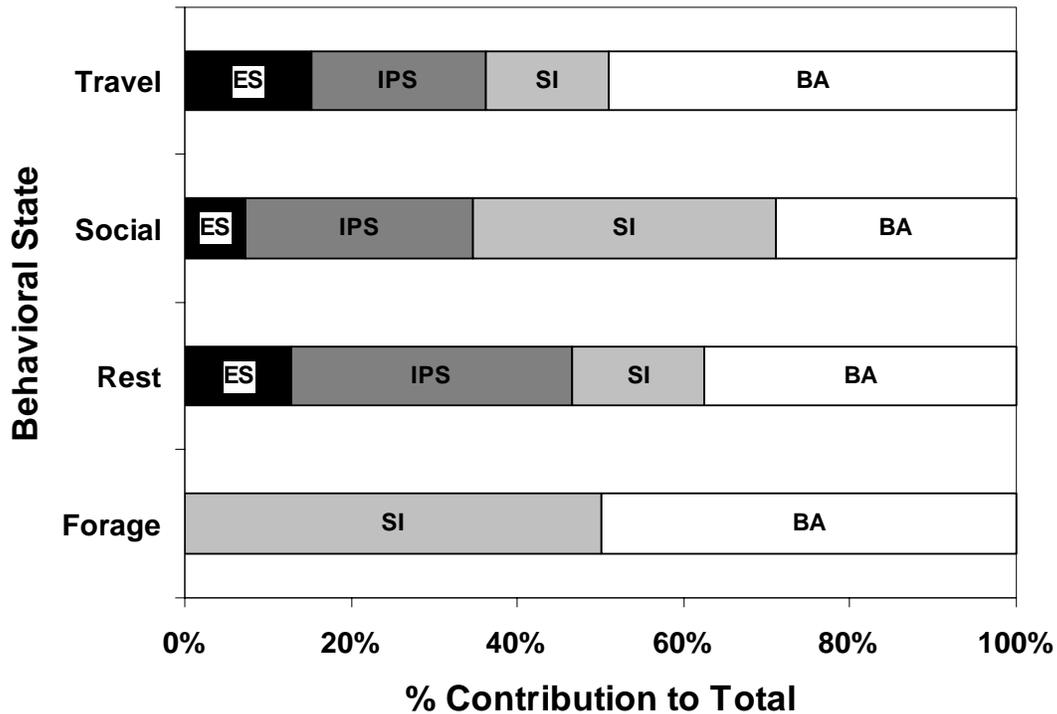


Figure 12. Calf position by behavioral state. ES = Echelon Swim, IPS = Infant Position Swim, SI = Swimming Independently, BA = By Adult

While foraging, number of intervals in which calves swam in echelon did not differ significantly from chance. Also, number of intervals in which calves swam near adults but with position unknown, did not differ. However, calves were significantly more likely to swim independently ($z = 2.71$, $P = 0.003$), but less likely to be in infant position ($z = 2.65$, $P = 0.003$) than expected by chance while foraging (Figure 13a).

While resting, number of intervals in which calves swam in echelon did not differ from chance. Number of intervals in which calves swam near adults but with position unknown, also did not differ from chance. However, calves were significantly

more likely to be in infant position ($z = 2.57$, $P = 0.005$), but less likely to swim independently ($z = -5.30$, $P < 0.001$) than expected while resting (Figure 13b).

While socializing, number of intervals in which calves swam in infant position did not differ from chance. However, calves swam independently more often ($z = 8.78$, $P < 0.001$), and in echelon less often than expected ($z = -3.23$, $P < 0.001$). Further, it was more likely for me to be able to determine the positions of calves near adults ($z = -3.80$, $P < 0.001$) while calves were socializing than during any other behavioral state (Figure 13c).

While dolphins were traveling, number of intervals in which calves swam in echelon did not differ significantly from chance. On the other hand, calves swam significantly less in infant position and independently than by chance ($z = -2.92$, $P = 0.002$ and $z = -2.50$, $P = 0.006$, respectively). However, I was less likely to be able to determine the positions of calves near adults ($z = 3.80$, $P < 0.001$) while calves were traveling than during any other behavioral state (Figure 13d).

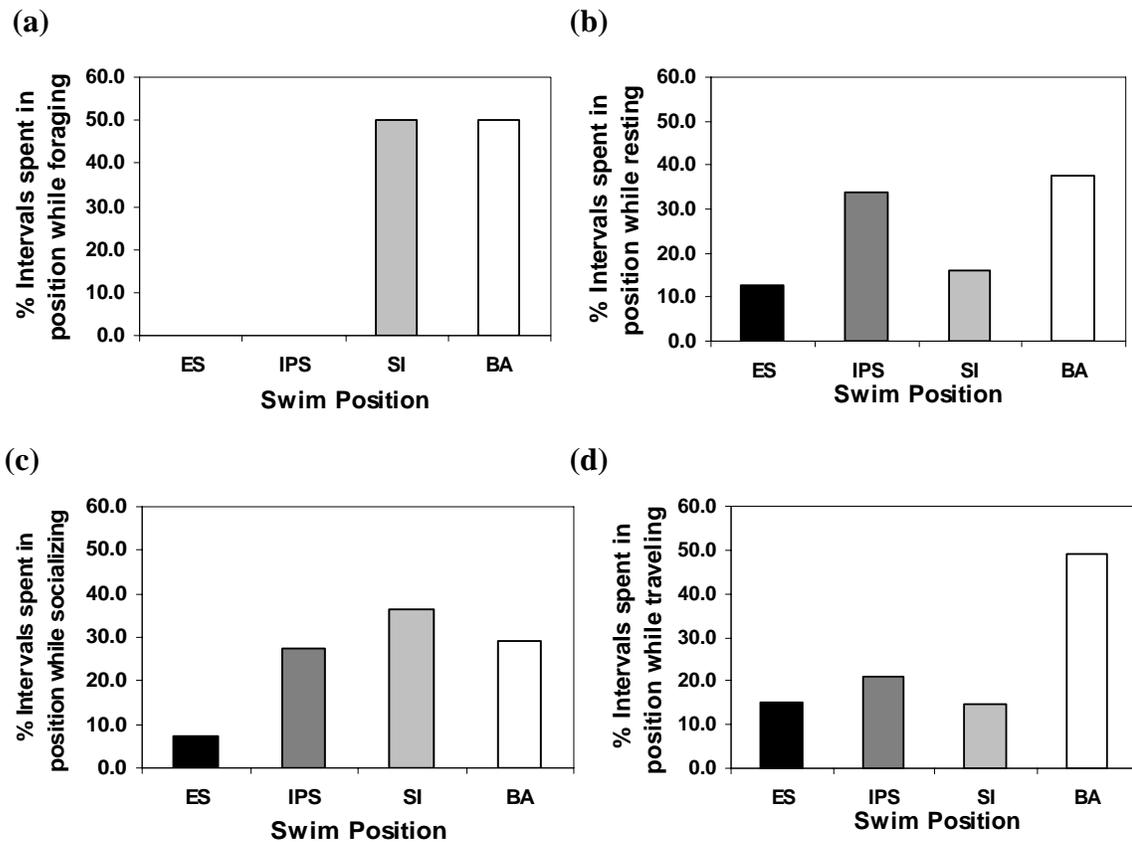


Figure 13. Calf position during (a) foraging, (b) resting, (c) socializing and (d) traveling. Swim position abbreviations are as in Figure 12.

DISCUSSION

Swim Position Preference

Dusky dolphin calf preference for swim position appears to be similar to that of bottlenose dolphins. Early infants prefer echelon, while all other age groups are less likely to swim in echelon. However, in duskies preference for infant position swim appears to remain the same for all age groups except for early yearlings.

Early age groups are less likely than late age groups to swim independently. This is as expected for early infants, as mothers may want to maintain close proximity to calves while their offspring develop motor skills. However, this trend is less expected in early yearlings who presumably have achieved some level of mastery over motor skills, and the tendency to remain close to their mothers may be an indirect effect of the peak in mating behavior October-February (Markowitz, 2004). Males are likely to be especially aggressive during this time in their attempts to copulate with females, so mothers may maintain closer proximity to their calves at all times during these months to protect them from such agonistic interactions. It follows then that early yearlings would be more likely to be near an adult, and since the echelon swim is less efficient once the calf is larger (Gubbins, McCowan, Lynn, Hooper, & Reiss, 1999), we would expect to find the calf in infant position more often instead.

Swim Position by Behavioral State

The higher energetic demands of lactating females imply that there may be more pressure for successful foraging in nursery groups. Therefore, the tendency of calves to swim independently while foraging makes sense as they are less likely to be a burden on foraging mothers. Further, calves may use these opportunities to practice foraging on their own. Bottlenose dolphins begin “practice foraging” by the end of their first month (Mann & Smuts, 1999). On several occasions, mothers and yearlings in this study chased fish in tandem. In one of these cases on November 21, 2006, a mother caught a

fish and then spit it out. A nearby yearling, presumably her calf, then pursued the fish, but it is unknown whether the mother was teaching her yearling to hunt.

While foraging was recorded for only 16 of 1380 intervals, this may in part be due to my strict definition of foraging in which birds had to be diving in the area and/or fish had to be clearly visible. The lack of observations of foraging may also reflect the time of day during which follows were conducted since little daytime foraging occurs in the Kaikoura area, where duskies rely principally on night-time feeding (Cipriano, 1992; Markowitz, 2004; Würsig et al., 1997).

The tendency of calves to be close to their mothers while resting may help them conserve energy (Fish, 1999). As well, it may function in better protection of the calf while in a more vulnerable state. Cockcroft and Ross (1990) and Gubbins et al. (1999) suggest that the white undersides of mother and calf may blend together when the calf is in infant position, making them appear as one large animal against the surface to deter potential predators, which typically attack from below.

When animals were socializing, I was better able to determine calf positions when they were near an adult. Although data on surface intervals were not collected, surface intervals appeared to be much shorter during socializing than during resting or foraging. Bassos (1993) reported that dive times of two bottlenose dolphins, reintroduced into Tampa Bay, were shortest while the animals were socializing. If this is also the case for duskies, it follows that it would be easier to keep track of the nursery group and position the boat at a better vantage point while animals were socializing than

during any other behavioral state. This may explain why it was easier to determine calf position during socializing.

Socializing often requires the calf to leave its mother's side temporarily to inspect or interact with conspecifics or other objects, so it is reasonable that they are more likely to swim independently during social interactions. Socializing calves are less likely to be in echelon swim than infant position swim. It is possible that infant position may signal a calf's affiliation to its mother to the rest of the group and it may also represent safety to the calf in stressful situations (Gubbins, McCowan, Lynn, Hooper, & Reiss, 1999; Tavalga & Essapian, 1957). However, the preference for infant position over echelon while socializing may again reflect the older age group's preference for infant position swim, together with the fact that I was able to identify positions more readily while animals were socializing.

Calves swam less in infant position while traveling than while socializing or resting, and swam independently much less while traveling than while foraging or socializing. This may occur for the following reasons:

- 1: Calf protection. Nursery groups may travel at high speeds to outrun potential threats or predators, so mothers may keep their calves close to protect them from such threats.
- 2: Prevention of a lost calf. Calves may have difficulty keeping up and keeping track of their mothers at high speeds. Therefore, it makes sense that mothers would want their calves close when traveling.
- 3: Reduction in energy costs. While results are inconclusive due to a large number of unknown positions, it is possible that calves are spending more time in echelon swim

while traveling than during any other behavioral state. Noren et al (2008) found that calves were able to increase their swim speed, while simultaneously decreasing effort by swimming in echelon. Mothers and calves spend much of their time traveling during the first few days after parturition (Mann & Smuts, 1999; Thomas & Taber, 1982), a time that coincides with high preference for echelon swim and near absence of infant position (Cockcroft & Ross, 1990; Gubbins, McCowan, Lynn, Hooper, & Reiss, 1999; Mann & Smuts, 1999).

Dolphins may receive an assisted ride by being sucked close to mother by a Bernoulli effect, and by riding the pressure wave created by the mother (Weihs, 2004). The use of formations to conserve energy is well-documented in other animals, particularly while swimming (Fish, 1995; Liao, Beal, Lauder, & Triantafyllou, 2003) or flying (Hummel, 1995; Weimerskirch, Martin, Clerquin, Alexandre, & Jiraskova, 2001). Fish (1995) found that the energy benefits of ducklings swimming in formation in a decoy's wake decreased with age. Similarly, energetic benefits of the echelon swim may decrease for dolphin calves as they grow (Norris & Prescott, 1961). However, it is possible that the energetic benefits of the echelon swim may be recovered when traveling at high speeds. Bill and Hernnkind (1976) found that energy efficiency positively correlated with travel speed of queuing lobsters. This suggests improved efficiency of formation swimming at higher speeds. Further, mothers displace more water per unit time when moving quickly through the water, and larger calves may be able to ride the mother's pressure wave more readily than when she is traveling more slowly.

Although several studies have examined energy efficiency of the echelon swim (Fish, 1995; Fish, 1999; Noren, 2008; Noren, Biedenbach, Redfern, & Edwards, 2008; Weihs, 2004; Weimerskirch, Martin, Clerquin, Alexandre, & Jiraskova, 2001), analyses of the kinematics of infant position are lacking. Closer examination of energetic differences of swimming in echelon versus infant position would help to clarify calf position preference during travel.

CONCLUSION

Dusky dolphin calves show a similar trend in position preference to that of bottlenose dolphin calves (Cockcroft & Ross, 1990; Eastcott & Dickinson, 1987; Gubbins, McCowan, Lynn, Hooper, & Reiss, 1999; Mann & Smuts, 1999), although an increase in preference for infant position swim may not be as strong in duskies as that observed in bottlenose dolphins. Further, dusky dolphin calves classified as “early” are less likely to swim independently, probably because the “early” designation coincides with a peak in mating behavior, and therefore an increase in presence of aggressive males.

The differences in preference for echelon versus infant swim during foraging, resting and socializing can be explained by overall preference of these positions in dusky dolphin calves. However, this preference appears to change when nursery groups are traveling, and this difference may be explained by examining the hydrodynamics of each position. Calves may favor echelon at higher speeds, but more data need to be gathered to investigate this suggestion. Additionally, dusky calves swim independently more

often during foraging and socializing and less often during resting and traveling. These results reflect the importance of calf position in calf protection and energy preservation for both mother and calf.

CHAPTER IV

DEVELOPMENT OF LEAPS

INTRODUCTION

Dusky dolphins, one of the most acrobatic delphinid, perform several leap types in three general categories: noisy leaps, clean head-first reentry leaps (from here on referred to as “clean leaps”), and acrobatic leaps (Markowitz, 2004; Würsig, 2002; Würsig & Würsig, 1980). I add a fourth category, coordinated leaps (Figure 14). During noisy leaps, dolphins re-enter the water with a loud splash. During clean leaps, dolphins arch in a “C” shape upon leaving the water and reenter head-first with minimal splash. A running leap, also known as porpoising, is a type of clean leap that occurs when dolphins travel at speed. This type of clean leap was not included in this analysis as the principal goal of this study was to catalogue development of leaps with social implications. Acrobatic leaps are energetic and “complicated”, such as head-over-tail flips and spins. Finally, a coordinated leap occurs when two or more dolphins perform the same type of leap at the same time. Noisy and acrobatic leaps typically occur in repeat sequences, usually with progressively less vigor towards the end of a leap bout. An individual performs the same leap, with little variation, throughout the leap bout sequence (Würsig, 2002).

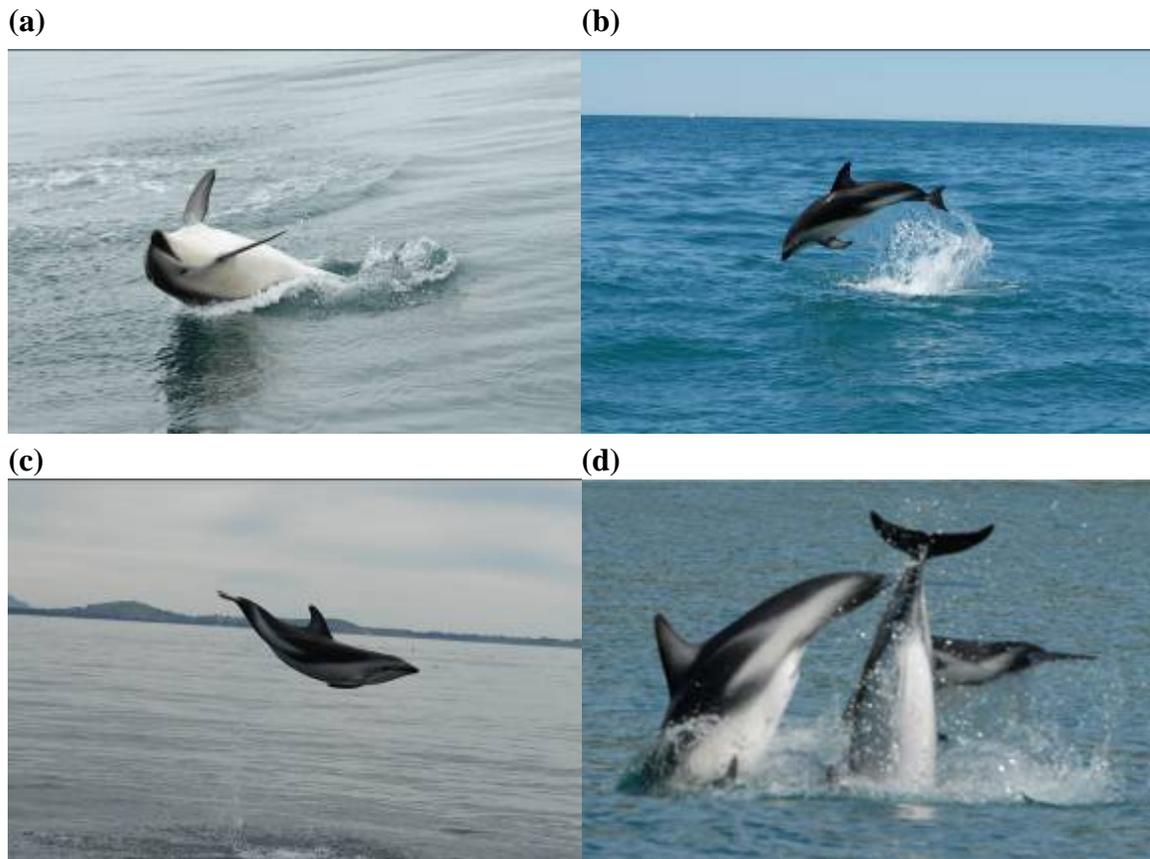


Figure 14. Four types of leaps (a) noisy, (b) clean, (c) acrobatic and (d) coordinated.

Different types of leaps may serve unique functions, but these are not clear, and may be different in different ecological settings of foraging, predator avoidance, group sizes, etc. (Lusseau, 2006; Markowitz, 2004; Norris, Würsig, Wells, & Würsig, 1994; Würsig, 2002; Würsig & Würsig, 1980). Several probable functions have been proposed, including parasite removal (Fish, Nicastro, & Weihs, 2006; Hester, Hunter, & Whitney, 1963; Norris, Würsig, Wells, & Würsig, 1994; Würsig, 2002), expeditious breathing (Markowitz, 2004; Würsig, 2002; Würsig & Würsig, 1980), energy cost

reduction (Au & Weihs, 1980; Weihs, 2002), visual assessments (Würsig, 2002; Würsig & Würsig, 1980), prey herding (Würsig, 2002; Würsig & Würsig, 1980), communication (Lusseau, 2006; Norris, Würsig, Wells, & Würsig, 1994; Würsig, 2002; Würsig & Würsig, 1980), play/fun (Würsig, 2002), and social facilitation (Lusseau, 2006; Markowitz, 2004; Norris, Würsig, Wells, & Würsig, 1994; Würsig, 2002; Würsig & Würsig, 1980).

In dusky dolphins, the main functions of noisy leaps appear to be prey herding and communication. The percussion of the splash from such leaps possibly, scares fish into aggregating more tightly (Würsig, 2002; Würsig & Würsig, 1980). Würsig and Würsig (1980) reported that feeding dusky dolphins off Argentina continually perform noisy leaps throughout feeding bouts and hypothesize that this may aid in recruiting other dolphins in the area to help herd prey into tighter balls. Dusky dolphins may also use noisy leaps to promote group cohesiveness and coordination. Markowitz (2004) found that noisy leaping occurred more in larger groups and resulted in changes in direction when the leaper was in front of the group.

Clean leaps appear to have several functions as well, and Würsig (2002) further subdivides them into three variations: stationary leaps, running leaps, and leaps designed to gain height. In stationary leaps, the dolphin is highly arched and returns to the water very near where it exited. Their principal use appears to be expeditious breathing while involved in deep water chases, such as when mating or foraging. The dolphin is able to take a breath while using its weight to plunge itself back to depth (Markowitz, 2004; Würsig, 2002; Würsig & Würsig, 1980). The function of a running leap appears to be

energy cost reduction (Au & Weihs, 1980; Weihs, 2002; Würsig, 2002), although the in-air height attained may also serve to allow enhanced forward visibility to large distance (Würsig & Würsig, 1980). The third leap, apparently designed to gain height, appears to be used for play or visual assessments (Würsig, 2002). This leap is difficult to distinguish from stationary leaps in awkward calves, and both leaps were lumped into the same category (clean leaps) for the purpose of this study.

Acrobatic leaps appear to function mainly in social facilitation and play, although it has been suggested that the spins of spinner dolphins also function in remora removal (Fish, Nicastro, & Weihs, 2006; Hester, Hunter, & Whitney, 1963). In Argentina, dusky dolphins perform acrobatic leaps most often during and after feeding, and this may help the group reestablish and enhance social bonds after social feeding (Würsig, 2002; Würsig & Würsig, 1980).

Coordinated leaps are a newly introduced category of leaps, in which two or more dolphins leap simultaneously, usually performing clean leaps (Pearson, pers. comm.). In this study, I consider coordinated leaps separately as they imply a high degree of synchronization among peers, possibly taking visual or acoustic cues from each other. Norris et al. (1994) noted that spins were preceded by short burst-pulsed sounds in a captive dolphin, and something similar may precede coordinated leaps in dusky dolphins. The possibility of pre-leap signaling is of interest in a study on development of leaps as it has implications for social influence on leap development.

A literature search revealed only one study that mentions leaps in a larger investigation of ontogeny of dolphin locomotion (Chechina, 2007). Chechina studied

four captive bottlenose mothers and their calves, with one month of observations on each pair. There thus appears to be little investigation of leap development, and the objective of my study is to provide additional data on the ontogeny of leap behavior. The specific questions are 1) Do different types of leaps occur more during different behavioral states? 2) Do dusky dolphin calves leap more often as they mature? and 3) What types of leaps do dusky dolphin calves perform, and how do these correlate with age?

METHODS

Study Area and Survey Methods were as described in Chapter II.

Behavioral Sampling

Behavioral data were collected and compiled as described in Chapter II. Additionally, all occurrences of each category of leaps were recorded by age group for each 2-min. interval. To control for overrepresentation by particular individuals, leaps were summed by follow and divided by the mean number of individuals for that follow.

Leap Type and Behavioral State

Behavioral states were defined as forage, rest, socialize, and travel (see Chapter II for definitions). To test whether different types of leaps occur during different behavioral states, I used mean number of leaps divided by number of individuals for each interval. Because behavioral states can change rapidly and all encounters were 15 intervals in length, data were analyzed by interval. Since I was exploring the correlation between leap type and behavior *when leaps occur*, zero values (i.e. intervals in which no

leaps occurred) were eliminated from analyses. Sample sizes for less frequent behaviors (e.g. forage) and leaps (e.g. acrobatic leaps) were very small, so the Kruskal-Wallis test was used on mean leap frequencies.

Leap Frequency

To test whether calves leap more often as they mature, I divided calves into four age groups including early infants, late infants, early yearlings, and late yearlings (see Chapter II for definitions) and used a Kruskal-Wallis test with the Bonferonni correction on individual Mann-Whitney U tests for post hoc analyses (Rice, 1989) to determine whether there were differences in leap frequency among these age groups. Zero values were included in the analysis of leap frequency to account for the absence of leaps. However, data were analyzed by follow, rather than by interval, to reduce the impact of ranking zero values on results.

Leap Type and Age

To examine the correlation between leap type and age, data were divided into weeks defined by follows between Sunday and Saturday, beginning with the first follow on October 27, 2006, and 52 weeks were added for yearlings. Follows with infants in week 1, 2, 3, and so on, were assigned “week 1,” “week 2,” “week 3,” and so on, while follows with yearlings in week 1, 2, 3, and so on, were assigned “week 53,” “week 54,” “week 55,” and so on. Because I was exploring the correlation between leap type and age *when leaps occur*, zero values (i.e. intervals in which no leaps occurred) were

eliminated from analyses and remaining data were analyzed using Spearman's rank-order correlation to examine the relationship between week and frequency of each type of leap.

RESULTS

Leap Type and Behavioral State

There was no significant difference between different types of leaps performed during different behavioral states (Figure 15), although this finding could be due to low sample sizes. Although calves rarely foraged, they did not perform noisy leaps or acrobatic leaps while foraging. Further, coordinated leaps were not performed by calves when foraging or traveling.

Leap Frequency

Leap frequency differed significantly by age group ($\chi^2 = 10.776$, $P = 0.013$). Early infants were less likely to leap than late infants ($Z = -3.125$, $P = 0.002$) and late yearlings ($Z = -2.511$, $P = 0.025$). To improve the power of the Bonferonni corrections on individual Mann-Whitney U tests, a comparison was not made between other age groups since they appeared very similar in their central tendencies and mean rank (Figure 16).

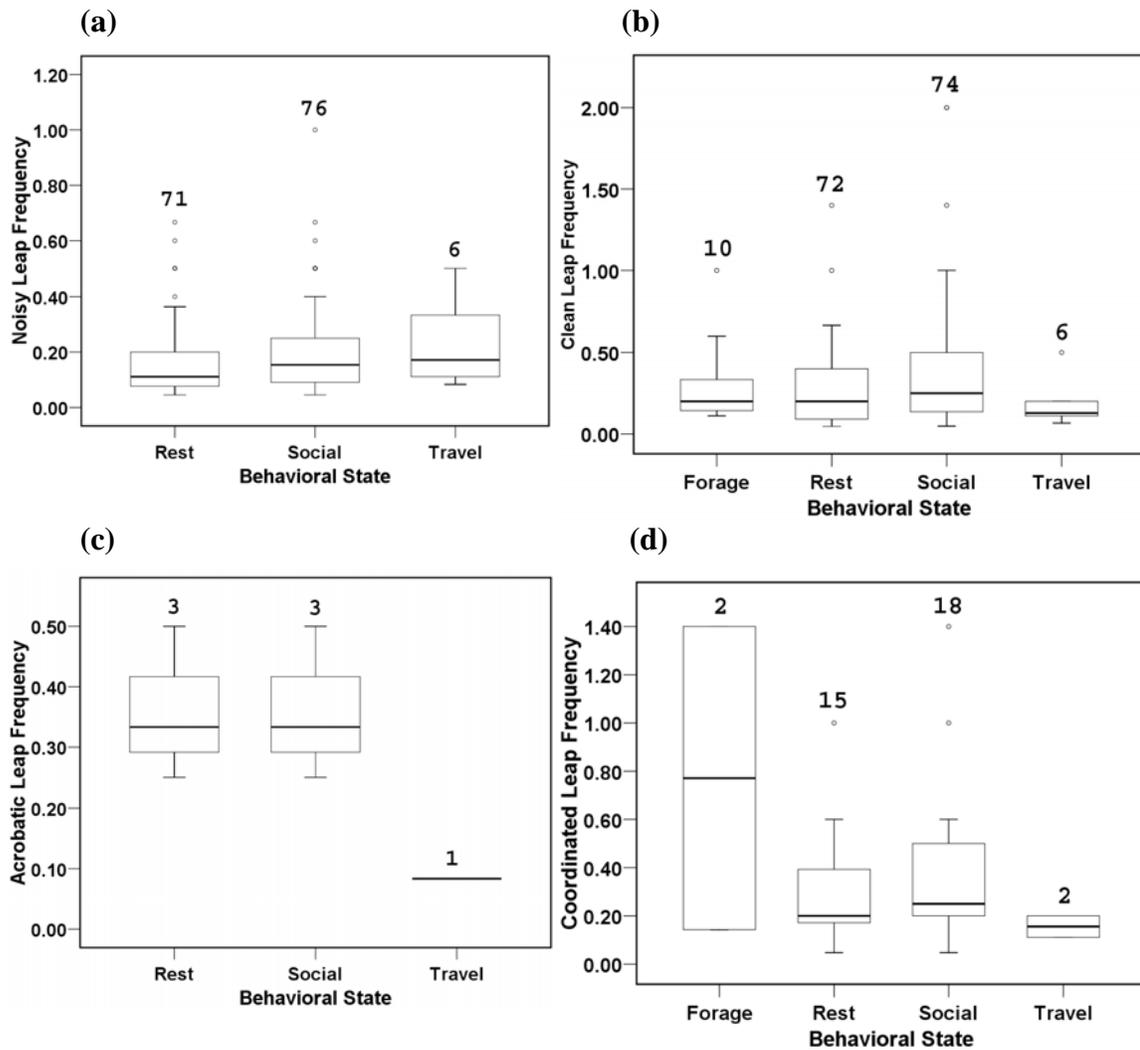


Figure 15. Leap frequency by behavioral state for (a) noisy leaps, (b) clean leaps, (c) acrobatic leaps and (d) coordinated leaps. Numbers represent sample size. Central lines represent medians and boxes contain 50% of cases. Whiskers include all other cases, excluding outliers, represented by the symbol \circ .

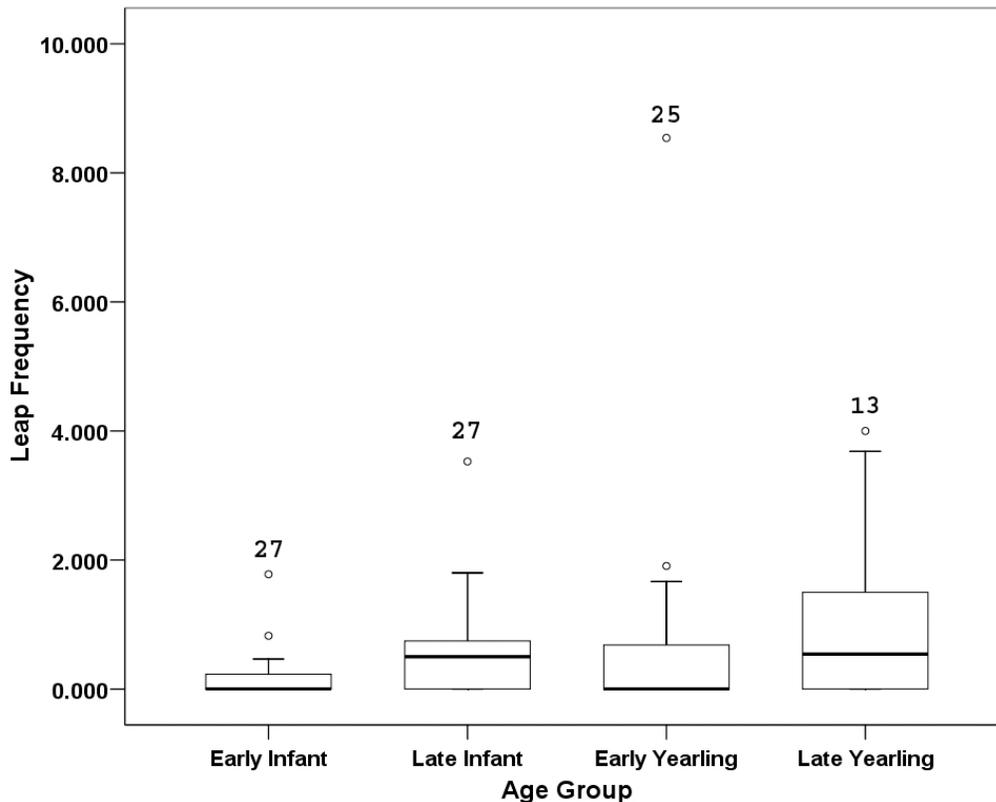


Figure 16. Overall leap frequency by age group. Display as in Fig. 15.

Leap Type and Age

Since infants and yearlings were analyzed separately (and both may be present at the same time), a total of 92 follows were included in the analyses. Noisy leaps occurred in 33 of these follows while clean leaps occurred in 35, acrobatic leaps in 4, and coordinated leaps in 12 (Figure 17). There was no correlation between noisy leap frequency and week. However, there were positive correlations between clean leap frequency and week. However, there were positive correlations between clean leap frequency ($r_s = .514$, $P = 0.002$), acrobatic leap frequency ($r_s = 1.00$, $P < 0.01$), and coordinated leap frequency ($r_s = 0.623$, $P = 0.030$) (Figure 18).

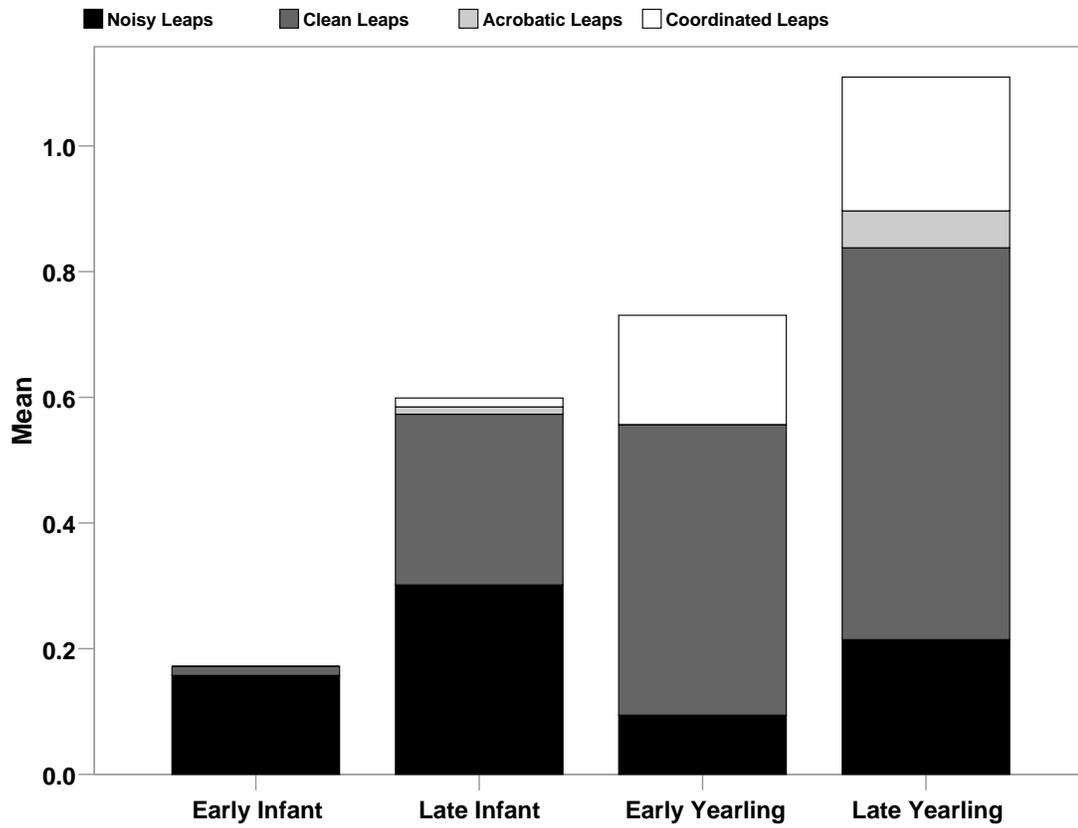


Figure 17. Mean leaps by leap type and age group.

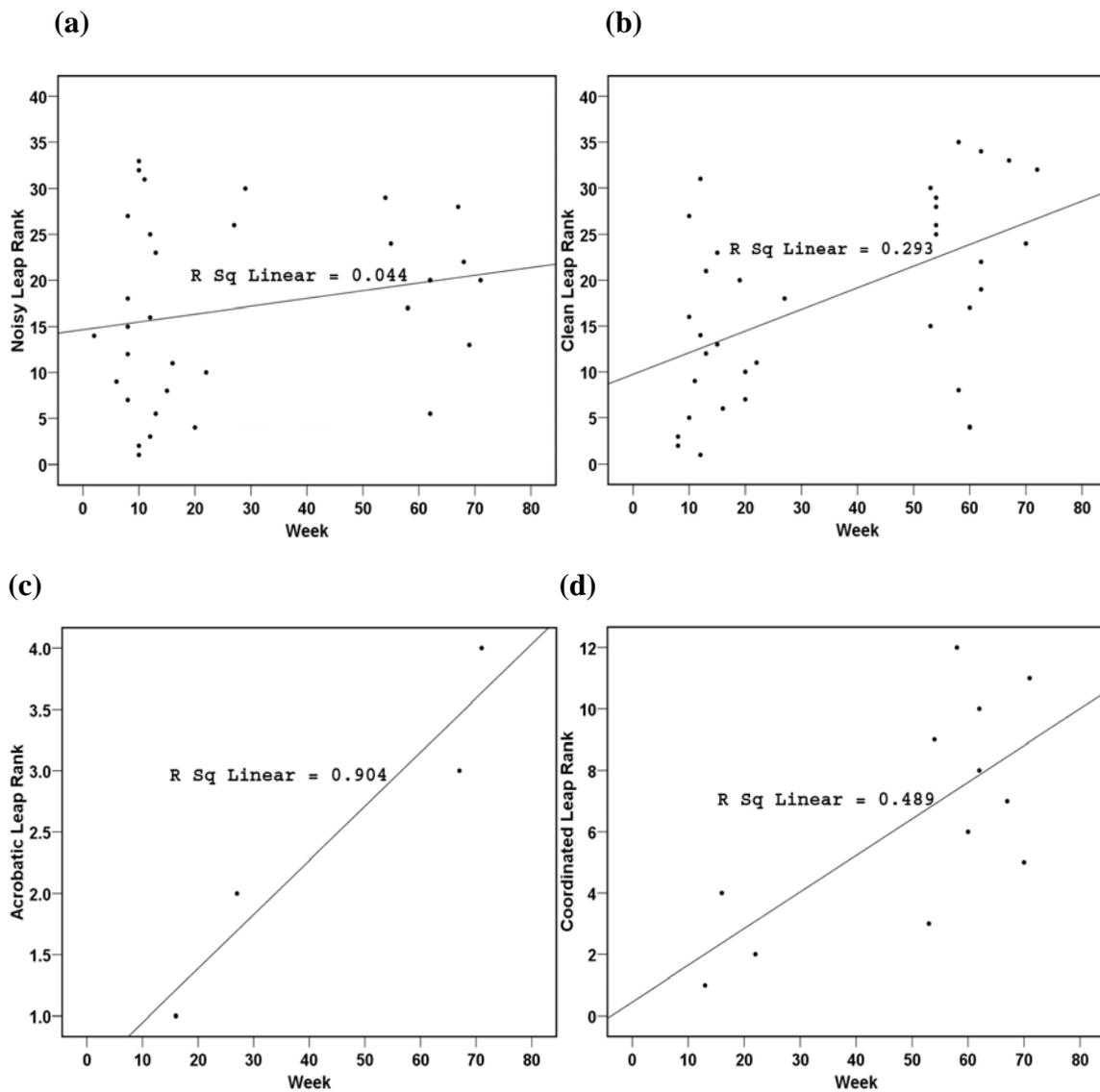


Figure 18. Leap rank vs. week for (a) noisy, (b) clean, (c) acrobatic and (d) coordinated leaps. Y values are nonparametric ranks.

DISCUSSION

Leap Type and Behavioral State

It is possible that no differences were detected in types of leaps per behavioral states due to small sample sizes. It is also possible that dusky calves do not perform

different types of leaps in the same context as adults because they rarely participate in certain behaviors compared to adults. For example, calves spend very little time foraging until their second year (see chapter II). Further, calves may be engaged in play behavior more often than adults and may exhibit different types of leaps as part of play. The lack of a strong relationship between behavioral state and leap type may also indicate that calves learn the leaps and develop the motor skills for those leaps *before* they learn the context in which to use them. This is similar to the development of hunting and stalking skills by canid cubs through play (Bekoff, 1972; Biben, 1982). Vervet monkey (*Cercopithecus aethiops*) infants learn how to produce an alarm call, but do not appear to understand its meaning until they are older (Hauser, 1989; Seyfarth & Cheney, 1986) and most species of birds are able to modify their vocalizations in certain contexts (Adret, 1992). A similar trend is also seen in some primates. For example, Tomasello et al. (1994) found that the use of gestural signals in young chimpanzees was not context dependent, and concluded that individual chimpanzees were not learning the gestures from each other, but were learning to conventionalize the gestures with each other.

Leap Frequency

Although all calves spend the majority of their time resting, it seems particularly important for early infants (see Chapter II), and this may be why they leap less frequently than other calves.

Leap Type and Age

Since overall leap frequency does not appear to increase with age, it does not seem likely that an increase in different leap types can be explained by an overall increase in leaps.

Although correlations between the various leap types and age are not very strong, when paired with frequency, they yield convincing evidence that certain leap types are more difficult than others to learn. The frequency and correlations of leap types with age indicate that leaps ranging in order from easiest to most difficult are noisy, clean, coordinated, and acrobatic leaps.

It is not clear whether leaps are learned from conspecifics or individually mastered as motor skills develop. Around week 6, while performing noisy leaps, the youngest calves would often curve their bodies in a slight “C” shape before flopping back on the water, in an apparent attempt to perform a clean leap. This continued until I saw the first obvious clean leap in this age group in week 8 and for about two weeks afterward, when this noisy-clean leap hybrid seemed to disappear from their leap repertoire. Noisy leaps are probably the easiest leap to perform, and this observation suggests that in addition to their intrinsic value in foraging and communication (Markowitz, 2004; Würsig, 2002; Würsig & Würsig, 1980), noisy leaps may be the basic blueprint from which clean and coordinated leaps develop. Further, it suggests that calves may learn clean leaps on their own as their motor skills develop.

So the pattern that seems to be emerging is that dusky calves may learn leaps on their own, but then may learn the contexts in which to use these leaps from conspecifics.

If this is the case, social learning may play a role in leap development. Similarly, young Rhesus monkeys (*Macaca mulatta*) are capable of displaying signs of fear, but may learn the contexts in which to exhibit fear. One study found that young rhesus monkeys who previously had no fear of snakes, were observed to act fearfully toward snakes after witnessing their wild-born parents exhibit fear responses when snakes were present (Mineka, Davidson, Cook, & Keir, 1984). In another example of social learning, young chimpanzees were split into two groups. Both groups had previously interacted with adults, but only one group was exposed to an adult performing food gathering with a T-bar. When subsequently reintroduced to T-bars, both groups manipulated the bars. However, only those who had witnessed an adult using the bar to obtain food were able to successfully use the bar to acquire food themselves (Tomasello, Davis-Dasilva, Camak, & Bard, 1987).

Social learning is a prerequisite for culture (Byrne, 2002; Rendell & Whitehead, 2001; Tomasello, Davis-Dasilva, Camak, & Bard, 1987; Whiten, 2000; Whiten & Ham, 1992; Yurk, Barret-Lennard, Ford, & Matkin, 2002), and cultural elements may be present in New Zealand duskie. For example, only a small proportion of dolphins in Kaikoura migrate to Admiralty Bay in winter (Markowitz, 2004). In contrast to the deep and exposed habitat off Kaikoura, Admiralty Bay is shallow and more protected. In addition, studies have shown that dusky dolphins in Admiralty Bay spend much of the day foraging (McFadden, 2003), while in Kaikoura foraging occurs mainly at night (Markowitz, 2004) and in synchrony with the ascending and descending of the deep scattering layer (Benoit-Bird, Würsig, & McFadden, 2004). Since the same duskie

found in Kaikoura in austral summers return to Admiralty Bay each austral winter, while others do not, this observed behavioral plasticity of changing habitats and foraging regimes may be learned from other duskies, and maintained as a culture in part of the population (Whitehead, Rendell, Osborne, & Würsig, 2004). However, while social learning may be a facilitator of culture, it does not necessarily follow that animals capable of social learning exhibit culture, so caution in assigning “culture” is advised.

The recent practice of identifying and using culture as a potential tool in cetacean conservation (Whitehead, Rendell, Osborne, & Würsig, 2004) may be important as human-influenced development of the natural world continues. Cultural transmission allows animals to quickly share information and adapt to rapid changes. If cultures are geographically specific, as may be the case in Admiralty Bay duskies, then it may become particularly important to protect the habitat in which cultural groups reside. If that habitat is altered or destroyed, then the species may lose the ability to exploit similar habitats.

CONCLUSION

Although adult dusky dolphins clearly use different leap types in different contexts and during different behavioral states, there does not appear to be as strong of a relationship between leap type and behavioral state in calves. This suggests that calves may learn how to use leaps from conspecifics.

With the exception of the low leap frequency in early infants, overall frequency of leaps does not appear to differ among age groups. Thus, early infants may be mainly

resting, but once slightly older they leap just as often as successive age groups, while increasing their leap repertoire as they mature.

Calves begin leap development by learning the noisy leap. While retaining its own functions of prey herding and communication, this leap also appears to be the blueprint for clean and coordinated leaps. The noisy leap is probably the easiest type of leap to learn, followed by the clean, coordinated, and acrobatic leaps.

The overall pattern in the ontogeny of dusky dolphin leaps indicates that the physical development of leaps is learned individually, while the context in which the leaps are performed is learned from conspecifics.

CHAPTER V

CONCLUSIONS

This study confirms Markowitz's (2004) and Weir's (2007) results that nursery groups rest more than other dusky dolphin groups. However, a closer examination of nursery groups revealed slight variations in behavioral state preference of different age groups. When controlling for month, calves differ in level of sociality by calf age classification (infant or yearling) and this, as well as differing energetic demands of lactating mothers, may explain the high degree of segregation seen in nursery groups by calf ages. Further, early infants spend more time resting than other calves, while late infants spend more time traveling than other calves. Early infants were not seen mouthing prey and early yearlings spend more time foraging than other calves, including late yearlings. These results indicate that dusky dolphins begin learning prey capture techniques in shallow water late in their first year, are foraging successfully in shallow waters by their second year, and are probably foraging on the DSL by the end of their second year.

With the exception of early infants, dusky dolphin calves exhibit a greater interest in boats than adults. Further, this study indicates that nursery groups represent an important setting where calves rest and develop social skills away from the chaos of the larger group and other more active small groups. Any unnecessary disturbance of nursery groups may distract calves and hinder the development of important survival skills.

Calf position in relation to the mother is probably best explained by a balance in energy cost for the mother and cost reduction for the calf. Mothers with drafting calves experience significant energy costs (Noren, 2008). However, calves swimming in close proximity to the mother reduce their cost of energy expenditure (Noren, Biedenbach, Redfern, & Edwards, 2008) and their exposure to potential predators/harassers (Cockcroft & Ross, 1990; Gubbins, McCowan, Lynn, Hooper, & Reiss, 1999). Therefore, a calf may be more likely to be found in close proximity to its mother when the added cost of drafting to the mother is less than the cost of swimming independently to the calf, such as when the calf is very small or when resting or traveling. Conversely, calves are more likely to swim independently when the cost of doing so is less than the cost of drafting to the mother, such as when foraging or socializing. Further, echelon swimming may allow calves to conserve more energy than infant position swimming, but their ability to remain in echelon may be strongly influenced by their size and the mother's speed, although more research is needed.

Several factors indicate that nursery groups are attempting to maintain a lower profile earlier in the calving season. Nursery groups are smaller in size with a smaller number of calves in the early part of the season. Additionally, nursery groups containing infants in the early part of the season spend more time resting than any other nursery groups. Finally, dusky dolphin calves are less likely to swim independently in the early part of the season.

The need for a low profile in the early part of the season indicates that risk factors for harassment or potential predation may be highest during this time. Weir

(2007) examined three hypotheses for nursery group formation, including the avoidance of predators, boats, and aggressive males. She concluded that, while boats did not appear to influence nursery group location, predators and aggressive males likely did. Killer whale researcher Ingrid Visser reported that killer whale density is highest in the austral summer during December and January (Weir 2007). The early part of the season also coincides with a peak in mating behavior (Markowitz, 2004) and testes size (Cipriano, 1992) from October to February, and males can be particularly aggressive during this time, posing a risk to young calves (Weir, 2007). So it is likely that the threat of potential predators and harassment by aggressive males are strongly influencing the behavior of nursery groups, but more research is needed.

Calves begin leaping when very young, but significantly increase the frequency of leaps in their first year at which point, although not significant, there may be a slow rise in overall leap frequency as calves continue to mature. The physical development of leaps follows the order of noisy, clean, coordinated, and acrobatic leaps. Calves appear to learn *how* to perform these leaps individually and without imitation, while they learn *when* to perform certain leaps from conspecifics.

Like many odontocetes (Whitehead & Mann, 2000), dusky dolphins spend an extended period of time with their mothers. However, to date there remain no empirical data on the length of the mother-calf bond in this species. Estimates for lactation periods range from 12 months off Peru (Van Waerebeek & Read, 1994) to 18 months off New Zealand (Leatherwood & Reeves, 1983). Although the number of yearlings in nursery groups is less than that of infants, this likely reflects high calf mortality (Herzing, 1997;

Mann, Connor, Barre, & Heithaus, 2000), as well as dispersal. During this study, a recognizable mother-calf pair, known as Cordelia and Angel respectively, were photographically recaptured on February 19, 2007, 13 months after they were last photographed on January 13, 2006 by Jody Weir. Based on this photograph and due to Angel's size, the time of year, and lack of fetal lines, I estimate its age to be a minimum of 2 months at the time of the 2006 photo. Therefore, we have new evidence that dusky calves likely stay with their mothers for a minimum of 15 months in New Zealand.

Dusky dolphins need to learn complex social, foraging, and other survival strategies from their mothers, and this would be facilitated by an extended association with her. Dusky dolphins are large-brained mammals with a highly complex social structure and recent comparisons to primates (Connor, Mann, Tyack, & Whitehead, 1998; Gowans, Würsig, & Karczmarski, 2008) have shown similar life history patterns. Primates and cetaceans are two of the few mammalian species for which we have evidence of material culture (Ducoing & Thierry, 2005; Krützen et al., 2005; Tomasello, Davis-Dasilva, Camak, & Bard, 1987; Whiten, 2000), which is acquired through some form of social learning (Rendell & Whitehead, 2001). Therefore, we should expect to see long-term bonds, such as those between mothers and young, among large-brained social mammals that would facilitate social learning.

In conclusion, nursery groups appear to represent an essential environment for normal dusky dolphin calf development. The need for reduced disturbance of nursery groups compared to larger and/or adult groups, and the higher tendency of calves than adults to be distracted by boats make nursery groups especially vulnerable to negative

impacts from tourism. New Zealand's Marine Mammal Protection Regulations of 1992 prohibit people from swimming with groups containing calves (Part III, section 20b), but not from interacting with them (i.e. viewing them from a boat). Unfortunately, calves' innate "cuteness," and relatively greater willingness to interact with boats means they may be targeted by otherwise well-intentioned tourists. I would recommend that all interactions with nursery groups be prohibited or that more stringent limits than those currently in place be imposed on interactions with nursery groups. Weir (2007) suggests higher restrictions on traffic in shallower near shore areas where nursery groups are found and I support this recommendation. Compliance with regulations is uneven, especially by operators of recreational vessels (Duprey, 2007). Therefore, as recreational boat traffic increases, so will the need for education and enforcement of current regulations around dolphin groups.

REFERENCES

- Adret, P. (1992). Vocal learning induced with operant techniques: an overview. *Netherlands Journal of Zoology*, **43**, 125-142.
- Au, D., & Weihs, D. (1980). At high speeds dolphins save energy by leaping. *Nature*, **284**, 548-550.
- Bassos, M. K. (1993). *A behavioral assessment of the reintroduction of two bottlenose dolphins*. Unpublished Thesis, University of California, Santa Cruz.
- Bearzi, M., & Stanford, C. B. (2007). Dolphins and African apes: comparisons of sympatric socio-ecology. *Contributions to Zoology*, **76**(4), 235-254.
- Bejder, L., & Samuels, A. (2003). Evaluating the effects of nature-based tourism on cetaceans. In N. Gales, M. Hindell & R. Kirkwood (Eds.), *Marine mammals: fisheries, tourism and management issues*. Collingwood: CSIRO Publishing.
- Bejder, L., Samuels, A., Whitehead, H., Gales, N., Mann, J., Connor, R., et al. (2006). Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conservation Biology*, **20**(6), 1791-1798.
- Bekoff, M. (1972). The development of social interaction, play, and metacommunication in mammals: An ethological perspective. *The Quarterly Review of Biology*, **47**(4), 412-434.
- Benoit-Bird, K. J., Würsig, B., & McFadden, C. J. (2004). Dusky dolphin (*Lagenorhynchus obscurus*) foraging in two different habitats: Active acoustic detection of dolphins and their prey. *Marine Mammal Science*, **20**, 213–231.

- Biben, M. (1982). Object play and social treatment of prey in bush dogs and crab-eating foxes. *Behaviour*, **79**, 201-211.
- Bill, R. G., & Herrnkind, W. F. (1976). Drag reduction by formation movement in spiny lobsters. *Science*, **193**(4258), 1146-1148.
- Brownell, R. L., & Cipriano, F. W. (1999). Dusky dolphins, *Lagenorhynchus obscurus*. In S. H. Ridgway & R. Harrison (Eds.), *Handbook of marine mammals (The second book of dolphins and the porpoises)* Vol. 6 (pp. 85-104). London: Academic Press.
- Byrne, R. W. (2002). Imitation of novel complex actions: What does the evidence from animals mean? *Advances in the Study of Behavior*, **31**, 77–105.
- Chechina, O. N. (2007). Dynamics of development of locomotion of the bottlenose dolphin (*Tursiops truncatus ponticus* Baravash, 1940) in early ontogenesis. *Journal of Evolutionary Biochemistry and Physiology*, **43**(4), 427-432.
- Cipriano, F. W. (1985). Dusky dolphin research at Kaikoura, New Zealand: a progress report. *Mauri Ora*, **12**, 151–158.
- Cipriano, F. W. (1992). *Behavior and occurrence patterns, feeding ecology and life history of dusky dolphins (Lagenorhynchus obscurus) off Kaikoura, New Zealand*. Unpublished Dissertation, University of Arizona, Tucson, USA.
- Cockcroft, V. G., & Ross, G. J. B. (1990). Observations on the early development of a captive bottlenose dolphin calf. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 461-478). San Diego: Academic Press, Inc.

- Connor, R. C. (2000). Group living in whales and dolphins. In J. Mann, R. C. Connor, P. L. Tyack & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 199-218). Chicago: University of Chicago Press.
- Connor, R. C., Mann, J., Tyack, P. L., & Whitehead, H. (1998). Social evolution in toothed whales. *Trends in Evolution and Ecology*, **13**(6), 228–232.
- Connor, R. C., Wells, R. S., Mann, J., & Read, A. (2000). The bottlenose dolphin: Social relationships in a fission-fusion society. In J. Mann, R. C. Connor, P. L. Tyack & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 91–126). Chicago: The University of Chicago Press.
- Constantine, R. (1999). Effects of tourism on marine mammals in New Zealand. *Science for Conservation* **106**, 60p.
- Constantine, R. (2001). Increased avoidance of swimmers by wild bottlenose dolphins (*Tursiops truncatus*) due to long-term exposure to swim-with-dolphin tourism. *Marine Mammal Science*, **17**(4), 689-702.
- Cosens, S. E., & Blouw, A. (2003). Size- and age-class segregation of bowhead whales summering in northern Foxe Basin: A photogrammetric analysis. *Marine Mammal Science*, **19**(2), 284-296.
- Dearolf, J. L., McLellan, W. A., Dillaman, R. M., Frierson, D., & Pabst, D. A. (2000). Precocial development of axial locomotor muscle in bottlenose dolphins (*Tursiops truncatus*). *Journal of Morphology*, **244**(3), 203-215.
- Ducoing, A. M., & Thierry, B. (2005). Tool-use learning in Tonkean macaques (*Macaca tonkeana*). *Animal Cognition*, **8**, 103–112.

- Duprey, N. (2007). *Dusky dolphin (Lagenorhynchus obscurus) Behavior and human interactions: Implications for tourism and aquaculture*. Unpublished Thesis, Texas A&M University, College Station.
- Dytham, C. (2003). *Choosing and using statistics: A biologist's guide* (2 ed.). Malden, MA: Blackwell Science.
- Eastcott, A., & Dickinson, T. (1987). Underwater observations of the suckling and social behaviour of a new-born bottlenosed dolphin (*Tursiops truncatus*). *Aquatic Mammals*, **13**(2), 51-56.
- Ellingson, R. J. (1972). Development of wakefulness-sleep cycles and associated EEG patterns in mammals. In C. D. Clemente, D. P. Purpura & F. E. Mayer (Eds.), *Sleep and the maturing sleep system*. (pp. 165-173). New York: Academic Press.
- Fairbanks, L. A. (1990). Reciprocal benefits of allomothering for female vervet monkeys. *Animal Behaviour*, **40**(3), 553-562.
- Fish, F. E. (1995). Kinematics of ducklings swimming in formation - consequences of position. *Journal of Experimental Zoology*, **273**(1), 1-11.
- Fish, F. E. (1999). Energetics of swimming and flying in formation. *Theoretical Biology*, **5**(5), 283-304.
- Fish, F. E., Nicastro, A. J., & Weihs, D. (2006). Dynamics of the aerial maneuvers of spinner dolphins. *Journal of Experimental Biology*, **209**(4), 590-598.
- Fisher, D. O., Blomberg, S. P., & Owens, I. P. F. (2002). Convergent maternal care strategies in ungulates and macropods. *Evolution*, **56**(1), 167-176.

- Fitzgibbon, C. D. (1990). Anti-predator strategies of immature Thomson's gazelles: Hiding and the prone response. *Animal Behaviour* **40**(5), 846-855.
- Fripp, D., Owen, C., Quintana-Rizzo, E., Shapiro, A., Buckstaff, K., Jankowski, K., et al. (2005). Bottlenose dolphin (*Tursiops truncatus*) calves appear to model their signature whistles on the signature whistles of community members. *Animal Cognition*, **8**, 17-26.
- Gowans, S., Würsig, B., & Karczmarski, L. (2008). The social structure and strategies of delphinids: Predictions based on an ecological framework. *Advances in Marine Biology*, **53**, 195-294.
- Gubbins, C., McCowan, B., Lynn, S. K., Hooper, S., & Reiss, D. (1999). Mother-infant spatial relations in captive bottlenose dolphins, *Tursiops truncatus*. *Marine Mammal Science*, **15**(3), 751-765.
- Handen, C. E., & Rodman, P. S. (1980). Social development of bonnet macaques from six months to three years of age: A longitudinal study. *Primates*, **21**(3), 350-356.
- Hass, C. C. (1990). Alternative maternal-care patterns in two herds of bighorn sheep. *Journal of Mammalogy*, **71**(1), 24-35.
- Hauser, M. D. (1989). Ontogenetic Changes in the Comprehension and Production of Vervet Monkey (*Cercopithecus-Aethiops*) Vocalizations. *Journal of Comparative Psychology*, **103**(2), 149-158.
- Herzing, D. L. (1997). The life history of free-ranging Atlantic spotted dolphins (*Stenella frontalis*): Age classes, color phases, and female reproduction. *Marine Mammal Science*, **13**(4), 576-595.

- Hester, F. J., Hunter, J. R., & Whitney, R. R. (1963). Jumping and spinning behavior in the spinner porpoise. *Journal of Mammalogy*, **44**(4), 586-588.
- Hoogland, J. L., Tamarin, R. H., & Levy, C. K. (1989). Communal nursing in prairie dogs. *Behavioral Ecology and Sociobiology*, **24**(2), 91-95.
- Hummel, D. (1995). Formation flight as an energy-saving mechanism. *Israel Journal of Zoology*, **41**(3), 261-278.
- Ioannou, C. C., & Krause, J. (2008). Searching for prey: The effects of group size and number. *Animal Behaviour*, **75**, 1383-1388.
- Jouvet-Mounier, D., Astic, L., & Lacote, D. (1970). Ontogenesis of the states of sleep in rat, cat and guinea pig during the first postnatal month. *Developmental Psychobiology*, **2**, 216-239.
- Karczmarski, L. (1999). Group dynamics of humpback dolphins (*Sousa chinensis*) in the Algoa Bay region, South Africa. *Journal of Zoology*, **249**, 283-293.
- Krasnova, V. V., Bel'kovich, V. M., & Chernetsky, A. D. (2006). Mother-infant spatial relations in wild Beluga (*Delphinapterus leucas*) during postnatal development under natural conditions. *Biology Bulletin*, **33**(1), 53-58.
- Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L., & Sherwin, W. B. (2005). Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences of the United States of America*, **102**(25), 8939-8943.
- Leatherwood, S., & Reeves, R. R. (1983). *The Sierra Club handbook of whales and dolphins*. San Francisco, California, USA: Sierra Club Books.

- Lent, P. C. (1974). Mother-infant relationships in ungulates. In V. Geist & F. Walther (Eds.), *The behaviour of ungulates and its relation to management* (pp. 14-55). Morges, Switzerland: International Union for the Conservation of Nature and Natural Resources.
- Lewis, K. B., & Barnes, P. M. (1999). Kaikoura Canyon, New Zealand: Active conduit from near-shore sediment zones to trench-axis channel. *Marine Geology*, **162**, 39-69.
- Liao, J. C., Beal, D. N., Lauder, G. V., & Triantafyllou, M. S. (2003). Fish exploiting vortices decrease muscle activity. *Science*, **302**(5650), 1566-1569.
- Loseto, L. L., Richard, P., Stern, G. A., Orr, J., & Ferguson, S. H. (2006). Segregation of Beaufort Sea beluga whales during the open-water season. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **84**(12), 1743-1751.
- Louis, J., Cannard, C., Bastuji, H., & Challamel, M. J. (1997). Sleep ontogenesis revisited: A longitudinal 24-hour home polygraphic study on 15 normal infants during the first two years of life. *Sleep*, **20**(5), 323-333.
- Lusseau, D. (2004). The hidden cost of tourism: Detecting long-term effects of tourism using behavioral information. *Ecology and Society*, **9**(1), 1-15.
- Lusseau, D. (2006). Why do dolphins jump? Interpreting the behavioural repertoire of bottlenose dolphins (*Tursiops* sp.) in Doubtful Sound, New Zealand. *Behavioural Processes*, **73**(3), 257-265.

- Lyamin, O., Pryaslova, J., Kosenko, P., & Siegel, J. (2007). Behavioral aspects of sleep in bottlenose dolphin mothers and their calves. *Physiology & Behavior*, **92**(4), 725-733.
- Lyamin, O., Shpak, O. V., & Siegel, J. M. (2003). Ontogenesis of rest behavior in killer whales. *Sleep*, **26**, A116-A116.
- Mann, J., Connor, R. C., Barre, L. M., & Heithaus, M. R. (2000). Female reproductive success in bottlenose dolphins (*Tursiops* sp.): Life history, habitat, provisioning, and group-size effects *Behavioral Ecology* **11**(2), 210-219.
- Mann, J., & Smuts, B. (1998). Natal attraction: Allomaternal care and mother–infant separations in wild bottlenose dolphins. *Animal Behaviour*, **55**, 1097-1113.
- Mann, J., & Smuts, B. (1999). Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour*, **136**(5), 529–566.
- Markowitz, T. M. (2004). *Social organization of the New Zealand dusky dolphin*. Unpublished Dissertation, Texas A&M University, College Station, USA.
- McBride, A. F., & Kritzler, H. (1951). Observations on pregnancy, parturition, and postnatal behavior in the bottlenose dolphin. *Journal of Mammalogy*, **32**(3), 251-266.
- McFadden, C. J. (2003). *Behavioral flexibility of feeding dusky dolphins (Lagenorhynchus obscurus) in Admiralty Bay, New Zealand*. Unpublished Dissertation, Texas A&M University, College Station, USA.

- Miles, J. A., & Herzing, D. L. (2003). Underwater analysis of the behavioural development of free-ranging Atlantic spotted dolphin (*Stenella frontalis*) calves (birth to 4 years of age). *Aquatic Mammals*, **29**(3), 363-377.
- Milinkovitch, M. C. (1992). DNA-DNA hybridizations support ungulate ancestry of Cetacea. *Journal of Evolutionary Biology*, **5**(1), 149-160.
- Mineka, S., Davidson, M., Cook, M., & Keir, R. (1984). Observational conditioning of snake fear in rhesus-monkeys. *Journal of Abnormal Psychology*, **93**(4), 355-372.
- Nicolson, N. (1987). Infants, mothers, and other females. In B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham & T. Struhsaker (Eds.), *Primate societies*). Chicago, IL: The University of Chicago Press.
- Noren, S. R. (2008). Infant carrying behaviour in dolphins: Costly parental care in an aquatic environment. *Functional Ecology*, **22**(2), 284-288.
- Noren, S. R., Biedenbach, G., & Edwards, E. F. (2006). Ontogeny of swim performance and mechanics in bottlenose dolphins (*Tursiops truncatus*). *The Journal of Experimental Biology*, **209**, 4724-4731.
- Noren, S. R., Biedenbach, G., Redfern, J. V., & Edwards, E. F. (2008). Hitching a ride: The formation locomotion strategy of dolphin calves. *Functional Ecology*, **22**(2), 278-283.
- Noren, S. R., & Edwards, E. F. (2007). Physiological and behavioral development in delphinid calves: Implications for calf separation and mortality due to tuna purse-seine sets. *Marine Mammal Science*, **23**(1), 15-29.

- Noren, S. R., Lacave, G., Wells, R. S., & Williams, T. M. (2002). The development of blood oxygen stores in bottlenose dolphins (*Tursiops truncatus*): Implications for diving capacity. *Journal of Zoology*, **258**, 105-113.
- Norris, K. S., & Prescott, J. H. (1961). Observations on Pacific cetaceans of Californian and Mexican waters. *University of California Publications in Zoology*, **63**, 291-402.
- Norris, K. S., Würsig, B., Wells, R. S., & Würsig, M. (1994). Aerial behavior. In *The Hawaiian Spinner Dolphin* (pp. 103-121). Berkeley: University of California Press.
- Orams, M. B. (1997). Historical accounts of human-dolphin interaction and recent developments in wild dolphin based tourism in Australasia. *Tourism Management*, **18**(5), 317-326.
- Rapaport, L., & Haight, J. (1987). Some observations regarding allomaternal caretaking among captive Asian elephants (*Elephas maximus*). *Journal of Mammalogy*, **68**(2), 438-442.
- Rendell, L. E., & Whitehead, H. (2001). Culture in whales and dolphins. *Behavioral and Brain Sciences*, **24**(2), 309-324.
- Rice, W. (1989). Analyzing tables of statistical tests. *Evolution*, **43**(1), 223-225.
- Riedman, M. L. (1982). The evolution of alloparental care and adoption in mammals and birds. *The Quarterly Review of Biology*, **57**(4), 405-435.
- Ross, C. (2001). Park or ride? Evolution of infant carrying in primates. *International Journal of Primatology*, **22**(5), 749-771.

- Seyfarth, R. M., & Cheney, D. L. (1986). Vocal development in vervet monkeys. *Animal Behaviour*, **34**, 1640-1658.
- Shane, S. H. (1990). Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. In S. L. a. R. R. Reeves (Ed.), *The bottlenose dolphin* (pp. 245-265). San Diego, CA: Academic Press.
- Smith, P. K. (1985). The reliability and validity of one-zero sampling: misconceived criticisms and unacknowledged assumptions. *British Educational Research Journal*, **11**(3), 215-220.
- Smolker, R. A., Richards, A. F., Connor, R. C., & Pepper, J. W. (1992). Part 1-2.
- Stanford, C. B. (1995). The influence of chimpanzee predation on group-size and antipredator behavior in red colobus monkeys. *Animal Behaviour*, **49**(3), 577-587.
- Stockin, K. A., Lusseau, D., Binedell, V., Wiseman, N., & Orams, M. B. (2008). Tourism affects the behavioural budget of the common dolphin *Delphinus* sp in the Hauraki Gulf, New Zealand. *Marine Ecology-Progress Series*, **355**, 287-295.
- Taber, S., & Thomas, P. (1982). Calf development and mother-calf spatial relationships in southern right whales. *Animal Behaviour*, **30**, 1072-1083.
- Tavolga, M., & Essapian, F. S. (1957). The behavior of the bottle-nosed dolphin (*Tursiops truncatus*): Mating, pregnancy, parturition, and mother-infant behavior. *Zoologica*, **42**(1), 11-31.
- Thomas, P., & Taber, S. (1982). Mother-infant interaction and behavioral development in southern right whales, *Eubalaena australis*. *Behaviour*, **88**, 42-60.

- Tomasello, M., Call, J., Nagell, K., Olguin, R., & Carpenter, M. (1994). The learning and use of gestural signals by young chimpanzees - a trans-generational study. *Primates*, **35**(2), 137-154.
- Tomasello, M., Davis-Dasilva, M., Camak, L., & Bard, K. (1987). Observational learning of tool use by young chimpanzees. *Human Evolution*, **2**, 175–183.
- Tsuji, K., & Ishikawa, T. (1984). Some observations of the caravaning behavior in the musk shrew (*Suncus Murinus*). *Behaviour*, **90**, 167-183.
- Van Parijs, S. M., & Corkeron, P. (2001). Boat traffic affects the acoustic behaviour of Pacific humpback dolphins, *Sousa chinensis*. *Journal of the Marine Biological Association of the United Kingdom*, **81**(3), 533-538.
- Van Waerebeek, K., & Read, A. (1994). Reproduction of dusky dolphins, *Lagenorhynchus obscurus*, from coastal Peru. *Journal of Mammalogy*, **75**(4), 1054-1062.
- Weih, D. (2002). Dynamics of dolphin porpoising revisited. *Integrative and Comparative Biology*, **42**(5), 1071-1078.
- Weih, D. (2004). The hydrodynamics of dolphin drafting. *Journal of Biology*, **3**(8), 8.1-8.16.
- Weimerskirch, H., Martin, J., Clerquin, Y., Alexandre, P., & Jiraskova, S. (2001). Energy saving in flight formation - Pelicans flying in a 'V' can glide for extended periods using the other birds' air streams. *Nature*, **413**(6857), 697-698.
- Weir, J. (2007). *Dusky dolphin nursery groups off Kaikoura, New Zealand*. Unpublished Thesis, Texas A&M University, College Station.

- Wells, R. S., Scott, M. D., & Irvine, A. B. (1987). The social structure of free-ranging bottlenose dolphins. In H. H. Genoways (Ed.), *Current mammalogy* Vol. 1 (pp. 247-305). New York: Plenum Press.
- Whitehead, H. (1996). Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behavioral Ecology and Sociobiology*, **38**(4), 237-244.
- Whitehead, H., & Mann, J. (2000). Female reproductive strategies of cetaceans: Life histories and calf care. In J. Mann, R. Connor, P. L. Tyack & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales*. Chicago: University of Chicago Press.
- Whitehead, H., Rendell, L., Osborne, R. W., & Würsig, B. (2004). Culture in conservation of non-humans with reference to whales and dolphins: Review and new directions. *Biological Conservation*, **120**, 431–441.
- Whiten, A. (2000). Primate culture and social learning. *Cognitive Science* **24**(3), 477–508.
- Whiten, A., & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. In *Advances in the study of behavior* Vol. 21 (pp. 239–283). New York: Academic Press.
- Würsig, B. (1989). Cetaceans. *Science*, **244**(4912), 1550-1557.
- Würsig, B. (2002). Leaping behavior. In W. F. Perrin, B. Würsig & H. Thewissen (Eds.), *The encyclopedia of marine mammals* (pp. 689-692). San Diego: Academic Press.

- Würsig, B., Cipriano, F. W., Slooten, E., Constantine, R., Barr, K., & Yin, S. (1997). Dusky dolphins (*Lagenorhynchus obscurus*) of New Zealand: Status of present knowledge. *Reports of the International Whaling Commission*, **47**, 715–722.
- Würsig, B., Dorsey, E. M., Richardson, W. J., & Wells, R. S. (1989). Feeding, aerial and play behaviour of the bowhead whale, *Balaena mysticetus*, summering in the Beaufort Sea. *Aquatic Mammals*, **15.1**, 27-37.
- Würsig, B., Koski, W. R., & Richardson, W. J. (1999). Whale riding behavior: Assisted transport for bowhead whale calves during spring migration in the Alaskan Beaufort Sea. *Marine Mammal Science*, **15**(1), 204-210.
- Würsig, B., & Würsig, M. (1980). Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the South Atlantic. *Fisheries Bulletin*, **77**, 871–890.
- Yin, S. (1999). *Movements, behavior, and whistle sounds of dusky dolphins off Kaikoura, New Zealand*. Unpublished Thesis, Texas A&M University, College Station, USA.
- Yurk, H., Barret-Lennard, L., Ford, J. K. B., & Matkin, C. O. (2002). Cultural transmission within maternal lineages: Vocal clans in resident killer whales in southern Alaska. *Animal Behaviour*, **63**, 1103–1119.

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