# DUSKY DOLPHINS IN NEW ZEALAND: GROUP STRUCTURE BY SEX AND RELATEDNESS

A Thesis

by

DEBORAH ELLEN SHELTON

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

December 2006

Major Subject: Wildlife and Fisheries Sciences

# DUSKY DOLPHINS IN NEW ZEALAND: GROUP STRUCTURE BY SEX AND RELATEDNESS

A Thesis

by

DEBORAH ELLEN SHELTON

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

Approved by:

Chair of Committee, Bernd Würsig
Committee Members, Sharon Gursky
April Harlin-Cognato
Rodney Honeycutt
Head of Department, Delbert Gatlin III

December 2006

Major Subject: Wildlife and Fisheries Sciences

# ABSTRACT

Dusky Dolphins in New Zealand: Group Structure by Sex and Relatedness.
(December 2006)
Deborah Ellen Shelton, B.S., Wake Forest University
Chair of Advisory Committee: Dr. Bernd Würsig

The sex of and genetic relatedness among interacting individuals are known to be biologically fundamental features that characterize the composition of animal groups. Current work continues to illuminate reasons for the variety of animal social patterns, including patterns in group membership. I investigated the composition of dusky dolphin groups relative to sex and relatedness at two locations in New Zealand. In Kaikoura, dusky dolphins are found year-round, foraging nocturnally on vertically-migrating prey and socializing in distinct group types (mating, nursery, and adult) during the day. By contrast, dusky dolphins use Admiralty Bay, where they feed diurnally on small schooling fishes, primarily in the winter. Molecular sexing revealed the sex of 107 dusky dolphins. The Kaikoura data support previous findings that small mating groups consist mostly of males and indicate that small adult groups can consist of either or both sexes. In Admiralty Bay, the percentage of female dolphins present during the study was estimated to be only 7.4%−22.2% (95% confidence interval, n=88). A randomization test further indicates that dusky dolphins in Admiralty Bay grouped preferentially with same-sex individuals. Nuclear and mitochondrial markers were used to investigate patterns of relatedness. Dusky dolphins sampled in Kaikoura (n=17) and Admiralty Bay (n=47) were genotyped at seven microsatellite loci, and genetic relatedness among all genotyped pairs was estimated. A randomization test indicates that dusky dolphins did not group preferentially by relatedness in Admiralty Bay. Grouping history for 13 genotyped samples was also known from a multi-year photographic record of individually distinctive dusky dolphins. No relationship was found between these longer-term grouping patterns and genetic relatedness. The d-loop region of the mitochondrial DNA (mtDNA) was sequenced for 197 dusky dolphins. The pattern of grouping among dolphins with different haplotypes indicates that dusky dolphin groups are not strongly structured by maternal lineages. However, data from eight individual dusky dolphins hint that nursery groups in Kaikoura tend to consist of dolphins that share a maternal ancestor. This investigation raises many questions about the nature of dusky dolphin social organization and suggests promising avenues for finer-grained investigations into the causes and consequences of dusky dolphin group structure.

*To my parents*

# ACKNOWLEDGEMENTS

I owe thanks to many people and organizations for supporting this work in various ways. My advisory committee—Bernd Würsig, Rodney Honeycutt, Sharon Gursky, and April Harlin-Cognato—has guided me through the many aspects of work on this project, and this thesis is the product of their dedication and advice. I especially thank the chair of my committee, Bernd Würsig, for sharing his considerable (to say the least!) knowledge and skills; Rodney Honeycutt for his generosity with lab equipment, space, and advice; Sharon Gursky for her input on the behavioral aspects and comparative implications of the project; and April Harlin-Cognato for the countless hours of work she contributed to this project and for her positive attitude and determination. Adam Jones also deserves special thanks for being so generous with lab space and equipment and for including me in lab meetings and offering microsatellite advice. I also am grateful to Terry Thomas for the use of lab equipment. This project builds on the works of many people, but benefited most directly from the works of April Harlin-Cognato and Tim Markowitz; their generosity in sharing data, ideas, and advice made this project possible.

I am thankful for the company, insight, and encouragement that stemmed from my interactions with many Texas A&M graduate students and post-docs., especially Robin Vaughn, Cindy McFadden, Heidi Pearson, Glen Proudfood, Jan Janeka, Orie Gilad, Amanda Crouse, Igor Vilchez, Jason Sumners, Michael Parks, Nicole Smolensky, Amanda Subalusky, Brad Johnson, Clay Small, and Catherine Engelman.

Bernd's recognition of the importance of a first-hand perspective on an animal's behavior allowed me to gain valuable experience with dusky dolphin field work. This work was interesting and productive, thanks to the hard work and good spirits of Robin Vaughn, Heidi Pearson, Lori Timm, and Leslie Watson. Danny and Lynn Boulton were kind hosts, full of knowledge and enthusiasm for the local region. Robin and Lori also deserve thanks for reviewing an early version of this thesis.

The money that made this project possible came from many sources. I was supported by a Texas A&M Graduate Merit Fellowship, Erma Lee and Luke Mooney

Travel grants, Texas A&M Department of Marine Biology mini-grants, a teaching position under Roel Lopez, and gifts and loans from my parents. Money for the project came from National Fish and Wildlife Services, the National Geographic Society, Earthwatch, Texas A&M Department of Marine Biology, and the Würsig gift fund.

Many thanks to Devin Taylor for his support and encouragement over the past 2+ years. I will remember many good moments that we shared in the lone star state. Finally, I could never thank my parents, Bob and Tina, or my siblings, Kathryn and Kevin, enough for their support. How ridiculously lucky I am to have family members who not only offer love, support, and comic relief, but even edit drafts and provide advice on technology!

## TABLE OF CONTENTS

# LIST OF TABLES

# LIST OF FIGURES

# CHAPTER I

# INTRODUCTION

## Structured groups

A necessary step for discovering the ultimate (i.e. evolutionary) reasons why a species socializes requires an understanding of the context in which social interactions occur. A group, or a spatially discrete set of interacting organisms that persists for some time, is a basic unit of social life. Animal groups are not comprised of identical units and, therefore, can consist of individuals who are distinct from the general population (Krause & Ruxton 2002). Empirical evidence indicates that groups can be defined on the basis of one or more characteristics (e.g. age, size, sex, dominance, relatedness, familiarity, level of parasitism) and that the composition of groups often, but not always, is the result of individuals actively asserting social preferences (Krause & Ruxton 2002). Experiments with fish have illuminated the role of individual preferences in creating structured groups. For example, chub (*Leuciscus cephalus*) prefer to shoal with familiar individuals, and this preference, when experimentally manipulated, swamped their usual preference for shoaling with conspecifics (Ward *et al.* 2003). Species and parasite load were both shown to be important factors influencing shoaling decisions in sticklebacks, *Gasterosteus aculeatus* (Barber *et al.* 1998). Theoretical work on the costs and benefits of group foraging (Ranta *et al.* 1993) and on optimal time budgets (Conradt & Roper 2000) suggested mechanisms by which group composition can become structured by factors such as individual rank, size, or sex.

Dusky dolphins (*Lagenorhynchus obscurus*) maintain individualized networks of social relationships; thus, groups are structured by individual social preferences (Markowitz 2004). This fact, though difficult to demonstrate in large-group-living dolphins, is consistent with what is known from detailed studies of social life in less

---

This thesis follows the style and format of *Molecular Ecology*.

gregarious species of dolphin (e.g. Baird 2000; Connor *et al.* 2000). Social preferences are often manifestations of differential allocation of benefits among individuals interacting in a particular way (Connor 2000). For example, altruists may prefer to partner with close relatives (Hamilton 1964a,b), and reciprocal altruists are expected to value partners differentially based on qualities such as tendency to reciprocate or gullibility (Trivers 1971). In by-product mutualisms, individual variation in the ability to either dispense or utilize by-products could also lead to individualized partner preferences (Wrangham 1982). Thus, in addition to the factors that can create structured groups in the absence of individualized relationships, social partner preferences (and thus group structure) can be strongly influenced by the type of social interactions that occur.

The game-theoretic concept of an evolutionarily stable strategy (ESS), a state that cannot be invaded by rare mutants, is often used to predict the long-term outcome of the evolution of social interactions (Maynard Smith 1982; Maynard Smith & Price 1973; Michod 1999). This approach captures the frequency-dependent nature of the fitness consequences of social interactions, but often ignores the important question of whether an ESS is dynamically achievable (Michod 1999; Nowak 1990). Add to this issue the likelihood that non-genetic replicators (i.e. “memes”: Dawkins 1976; 1982) are concurrently affecting the evolution of behavior (Dugatkin 2000), at times with potential genetic consequences (e.g. Whitehead 1998; 2005a), and it is no small wonder that patterns in animal social behavior, including group structure, are ever understandable! In spite of this complexity, much is known about how and why animals interact (Alcock 2001b; Trivers 2002; Wilson 2000); because of it, much remains to be learned, and the ultimate goal—integrated and cohesive knowledge (Wilson 1998)—remains unattained.

## Research objectives

The purpose of this research is to describe the composition of New Zealand dusky dolphin groups. Two aspects of group composition, sex ratio and relatedness, were examined at two scales, within various types of small groups and within sampling locations. Group types included feeding, mating, nursery, and restful adult groups. The sampling locations—Kaikoura and Admiralty Bay, New Zealand—are distinct habitats within which dusky dolphins show different feeding behavior and social patterns.

## Grouping patterns in dolphins

### *Model species*

Aspects of the oceanic environment, including the relatively low cost of locomotion in water (Williams 1999) and the relative lack of spatial refuges from predation, may have influenced the evolution of sociality in delphinids—a taxon which shows a remarkable tendency for living and cooperating in groups (Connor 2000; Norris 1994). However, researchers have accomplished detailed, long-term studies of social structure in only a few delphinid species (Connor 2000). Thus, delphinid types, causes, and implications of structure in group composition are largely unknown. Bottlenose dolphins (*Tursiops* spp.), killer whales (*Orcinus orca*), and spinner dolphins (*Stenella longirostris*) are among the better-studied delphinids, and research into grouping patterns in these and other delphinid species provides a context within which dusky dolphin group composition can be examined.

Social life for most populations of bottlenose dolphin is characterized by small groups with frequent changes in group size and turnover of individuals (Connor *et al.* 2000). Considerable variation in social structure exists, however, and at least one relatively closed bottlenose dolphin population, in which community membership is constant over time, has been documented (Lusseau *et al.* 2003). Additionally, long-term studies have revealed that among the frequent shuffling of social partners, inshore bottlenose dolphins characteristically form strong social bonds, as indicated by levels of association (Connor *et al.* 2000; Shane *et al.* 1986). In contrast, bottlenose dolphins off the coast of southern California have home ranges spanning hundreds of kilometers and show weak levels of association (Defran & Weller 1999; Defran *et al.* 1999). Levels of association are also weak in the resident population of Moray Firth, Scotland (Wilson 1995).

In two locations, Sarasota Bay, Florida and Monkey Mia, Australia, association patterns of bottlenose dolphins have been analyzed separately by sex.[1] In both locations, females maintain large networks of associations, with most, but not all, females associating in "bands" (i.e. subsets of individuals that preferentially associate with one another) (Connor *et al.* 2000). In Sarasota, at least some females within bands are closely related (Duffield & Wells 1991). Variation in sociability among different females is also notable (Smolker *et al.* 1992; Wells *et al.* 1987). A relationship between sex differences in both sociability and foraging tactics has been detailed in chimpanzees, *Pan troglodytes*, (termite fishing: Pandolfi *et al.* 2003) and, in one case, it appears that female dolphin sociability is also closely linked to a foraging specialization (sponge-foraging: Smolker *et al.* 1997). Males in both Sarasota and Monkey Mia form strongly bonded pairs or trios (Connor *et al.* 1992b; Wells 1991b; Wells *et al.* 1987). In Monkey Mia, members of these "first-order alliances" cooperate to aggressively maintain consorts with a female (Connor 1996; Connor *et al.* 1992a; Connor *et al.* 1992b). Cooperation among first-order alliances (i.e. "second-order alliances") has been documented, as has an alternate "super-alliance" social strategy for gaining access to females (Connor *et al.* 1999; Connor *et al.* 1992b). First- and second-order alliances in Monkey Mia tend to consist of close relatives, while super-alliance members are not closely related (Krützen *et al.* 2003). Male pairs in Sarasota Bay tend not to be closely related (Connor *et al.* 2000). Bottlenose dolphins in other locations have also revealed variety in the extent to which male association patterns are nepotistic (Möller *et al.* 2001; Parsons *et al.* 2003). Male-female associations are strongly influenced by the female's reproductive state. Between-sex levels of association are relatively low, indicating that between-sex individualized relationships are uncommon. Nevertheless, mixed-sex groups are relatively common in Monkey Mia and are not observed exclusively in a mating context (Connor *et al.* 2000).

---

[1] Comparisons between the locations are interspecific. The common bottlenose dolphin (*Tursiops truncatus*) is found in Sarasota Bay, while the Indian Ocean bottlenose dolphin (*Tursiops aduncus*) is found in Monkey Mia.

Social life in the largest delphinid, the killer whale, is generally characterized by long-term associations between individuals and limited dispersal from maternal groups (Baird 2000). Although they can be found in groups of up to hundreds of individuals, larger groups of killer whales often appear to be temporary associations of smaller, more stable groups (Baird 2000). In the eastern North Pacific, researchers have identified sympatric populations, labeled “residents” and “transients,” that differ in morphology, behavior, and social organization. Neither male nor female offspring disperse from their natal pods in resident killer whales (Bigg *et al.* 1990). In contrast, transient killer whales typically maintain group sizes of four or fewer individuals, and females disperse upon reaching sexual maturity (Baird & Dill 1995). The populations differ markedly in foraging specializations (residents are fish-eaters and transients are mammal-eaters), a fact that seems to drive differences in group size and dispersal patterns (Baird 2000). However, not all populations follow the pattern of strict foraging specialization, and data from animals that frequent offshore waters are lacking (Baird *et al.* 2006).

Morphological data indicate that the mating system differs between subspecies of spinner dolphin (Perrin & Mesnick 2003), but grouping patterns have been detailed only in the Gray’s (or long-beaked) spinner dolphin (*Stenella longirostris longirostris*). Off the Big Island of Hawaii, the social organization of spinner dolphins is fluid (i.e. individuals maintain large networks of loose associations) (Norris *et al.* 1994), with animals typically resting in smaller groups in shallow inshore habitats during the day and moving further offshore in larger groups to feed at night (Benoit-Bird & Au 2003; Norris & Dohl 1980; Würsig *et al.* 1994). Strong social bonds (i.e. high levels of association) have been documented for several groups of five to six males, as has relatively frequent associations between adult males and calves (Östman, 1994). In northwestern Hawaii, spinner dolphins at Midway Atoll do not show fission-fusion grouping patterns, but instead live in relatively stable, closed societies (Karczmarski *et al.* 2005). Karczmarski *et al.* (2005) suggested that the relative isolation of patches of suitable (i.e. safer, shallow-water) habitats in northwestern Hawaii accounts for this pattern. The unusual stability of these groups is similar to that of the bottlenose dolphins of New Zealand's fjords (Lusseau *et al*. 2003), and isolation may be an explanation for both.

Observations of delphinids—notably killer whale bisexual philopatry (Bigg *et al.* 1990) and bottlenose dolphin second-order alliances (Connor *et al.* 1992b)—have widened the scope of documented social phenomena. Yet, the overall picture of delphinid grouping patterns remains relatively sparse. For the better-studied species, knowledge of the intraspecific range of grouping patterns continues to expand (e.g. Baird *et al.* 2006; Karczmarski *et al.* 2005). Knowledge of social life in some dolphin species relies largely on the limited evidence available from animals killed in drive fisheries. Such data indicate, for example, lifelong mother-son bonds in long-finned pilot whales, *Globicephala melas*, (Amos *et al.* 1993) and a social function for post-reproductive female short-finned pilot whales, *Globicephala macrorhynchus*, (Marsh & Kasuya 1984). Little is known about social life in other species (e.g. the rough-toothed dolphin, *Steno bredanensis*). Much also remains to be learned from dolphins that live in large societies and those that tend to move over large distances, two factors that characterize dusky dolphins and add to the challenge of describing and understanding grouping patterns.

## New Zealand dusky dolphins

With an asymptotic length of 1.7−1.8 m, New Zealand dusky dolphins are small, even compared to conspecifics from other regions (Cipriano 1992; Würsig *et al.* 1997). The sexes are dimorphic for relatively subtle characters, including the length of the dorsal fin base and the positioning of dorsal fin and flipper insertions, but size dimorphism (i.e. overall weight or length) is virtually non-existent (Cipriano 1992; Van Waerebeek & Read 1994). Females provide parental care to singleton calves, born after about 11.4 months of gestation (Cipriano 1992). Early in life, calves remain tightly associated with their mothers, but they are weaned by the relatively young age of approximately one and a half years (Leatherwood & Reeves 1983). Conceptions and calving occur seasonally,[2] with nearly all births occurring in November through January (Cipriano 1992). Age at first reproduction is roughly seven to eight years for both males and females (Cipriano 1992). The mating system appears to be polygynandrous (i.e. promiscuous; males and females mate multiple times within a season) (Cipriano 1992). Thus, male parental investment likely ends at conception, and individuals are unlikely to be able to discriminate paternal relationships (Alcock 2001a). In spite of seasonal breeding, sexual behavior occurs throughout the year (Cipriano 1992). The average inter-birth interval is not known, though due to the lengths of gestation and nursing, at least two or three years probably pass between births. Thus, the overall operational sex ratio is likely male-biased, inducing male intrasexual competition. That males compete for access to females and for conceptions is evident in behavioral observations of frequent chases and in the remarkably large size of dusky dolphin testes (Cipriano 1992). Dusky dolphins live up to 35−36 years, making them relatively long-lived for their size (Cipriano 1992; Leatherwood & Reeves 1983).

Dusky dolphin populations occur in the Southern Hemisphere, off the coasts of South America, southwestern Africa, New Zealand, and some oceanic islands (Jefferson *et al.* 1994; Van Waerebeek *et al.* 1995; Würsig *et al.* 1997). Populations separated by open ocean are relatively discrete, as dusky dolphins are rarely observed in waters deeper than 2000 meters (Jefferson *et al.* 1994). In spite of this, genetic differentiation of dusky dolphin populations within oceans is remarkably low (Cassens *et al.* 2003). Cassens *et al.* (2005) analyzed the variation in mitochondrial DNA (mtDNA) and nuclear markers (microsatellites) in dusky dolphins from Peru, Argentina, southern Africa, and New Zealand. They concluded that male-specific gene flow occurs between Peruvian and Argentine populations, while little gene flow occurs between the Argentinean and African populations. Only the Peruvian population was highly differentiated, possibly due to historic population fluctuations and genetic drift. New Zealand dusky dolphins were not highly differentiated, indicating that the population

---

[2] The order Cetacea is not among the mammalian orders in which embryonic diapause is common (Renfree & Shaw 2000).

may have originated from multiple migration events from Atlantic waters. Within New Zealand, Harlin *et al.* (2003) analyzed the mtDNA haplotype distribution among dusky dolphins found in discrete areas of relative abundance. Nested-clade analyses indicated geographic structure, but the extent to which this is a result of historical processes or contemporary seasonal migrations is not known (Harlin *et al.* 2003). The inferred absence of strong genetic differentiation among dusky dolphin populations is consistent with radio-tracking and photo-identification data in demonstrating that dusky dolphin individual vagility is high, at least at times (Markowitz 2004; Würsig *et al.* 1991).

In New Zealand, dusky dolphins use areas off the coasts of the southern North Island, much of the South Island, Campbell and Auckland Islands, and over the Chatham Rise, east of the South Island (Würsig *et al.* 1997). Sighting records indicate a seasonal shift in distribution, possibly linked to changes in water temperature and prey distribution (Gaskin 1968; Webb 1973; Würsig *et al.* 1997). Two areas of the South Island of New Zealand— Kaikoura on the east coast and Admiralty Bay in the Marlborough Sounds —have produced particularly consistent sightings of dusky dolphins, year-round in Kaikoura and during winter in the Marlborough Sounds (Cipriano 1992; Gaskin 1968; Markowitz 2004). This study utilizes dolphin tissue collected from these two locations, which are distinct habitat types. Individual dusky dolphins are known to move between the two sites, yet feeding behavior and grouping patterns differ dramatically between the two areas (Markowitz 2004).

The waters near Kaikoura, on the east coast of the South Island, are dominated by the effects of the more than 1000-meter-deep submarine Kaikoura Canyon, which comes within 500 meters of shore (Lewis & Barnes 1999) and by the mixing of Antarctic and tropical waters in the subtropical convergence (Boyd *et al.* 1999). These features create an area that supports high primary productivity and a rich food web (Boyd *et al.* 1999). The Kaikoura area is relatively open and influenced by oceanic swell. Dusky dolphins are observed in Kaikoura in large numbers year-round (Cipriano 1992; Gaskin 1968). They tend to use the area just south of the Kaikoura peninsula (Würsig *et al.* 1997), and at times may enjoy some protection from prevailing weather by congregating in the lee of Haumuri Bluffs (Markowitz 2004). The dusky dolphins in this area support a tourism industry, which potentially affects their behavior (Bar & Slooten 1998).

In Kaikoura, dusky dolphins feed nocturnally, exploiting the shallower night-time depths of fishes and squids associated with a deep sound-scattering layer (DSL) (Benoit-Bird *et al.* 2004; Cipriano 1992; Cipriano *et al.* 1989; Würsig *et al.* 1989). Gut-content analysis revealed that prey items included lanternfishes (Myctophidae), hoki (*Macruronus novaezelandie*), red cod (*Physiculus bacchus*), hake (*Merluccius australis*), and squids (*Nototodarus* sp. and *Todaroides* sp.) and that diet composition shifted seasonally (Cipriano 1992). It is likely that the length of time during each night that the DSL is shallow enough to be exploited by dusky dolphins also changes seasonally, reaching a maximum in winter (Benoit-Bird *et al.* 2004; Clarke 1970). During a winter-time study, Benoit-Bird *et al.* (2004) observed that dusky dolphins fed in Kaikoura when the DSL rose to within 130 meters of the surface, between 2000 and 0500 local time. Before feeding, nearly all dolphins swam individually, but during feeding coordinated subgroups of up to five individuals were observed. Foraging subgroups did not coordinate movement with nearby groups, and subgroup size increased as the depth of the DSL decreased (Benoit-Bird *et al.* 2004). Although spinner dolphins feed on similar prey off Hawaii, they forage almost exclusively in pairs that are part of larger coordinated groups (Benoit-Bird, Au 2003). Spinner dolphins off Hawaii (Benoit-Bird, Au 2003) and dusky dolphins off Argentina (Würsig & Würsig 1980) actively aggregate their prey, but this does not seem to be the case for dusky dolphins in Kaikoura (Benoit-Bird *et al.* 2004).

Although dusky dolphins are present in Kaikoura year-round, photo-identification (Würsig & Jefferson 1990; Würsig & Würsig 1977) indicates that most individuals stay in the area for only a few months at a time (3.4 ±1.27 months, mean ± s.e.) and that some tend to return at roughly yearly intervals (Markowitz 2004). Over 1000 dusky dolphins of a population numbering over 10 000 may be found off Kaikoura at any one time (Markowitz 2004). Dusky dolphins off Kaikoura are often found in a large (100s to over 1000 individuals) group, with some smaller “satellite” groups nearby. In winter, groups tend to be larger, farther offshore, and farther north (Markowitz 2004; Würsig *et al.* 1997). Non-random associations among Kaikoura individual dusky dolphins persist for over half a year on average (Markowitz 2004).

Some dolphins identified in Kaikoura (n=37) are known to travel roughly 160 km north to winter at the other study site, Admiralty Bay in the Marlborough Sounds (Markowitz 2004). The Marlborough Sounds are in the northernmost part of the South Island and are characterized by many relatively warm, shallow, and protected bays and inlets. Dusky dolphins use several areas within the Marlborough Sounds sporadically throughout the year, but they are seen in the greatest numbers and with greatest consistency in Admiralty Bay during the winter (Markowitz 2004). Admiralty Bay is about 7 km long and 4.5 km wide at its widest, with a mouth that opens towards the north-northeast. It is a relatively enclosed area that is not affected much by oceanic swell. On the western side of the bay, the narrow French Pass provides a connection between the waters of Cook Straight and the Tasman Bay.

In sharp contrast to feeding behavior in Kaikoura, dusky dolphins in Admiralty Bay feed diurnally on small schooling fishes, including pilchard (*Sardinops neopilchardus*), sprat (*Sprattus antipodum*), yellow-eye mullet (*Aldrichetta forsteri*), and anchovy (*Engraulis australis*) (Benoit-Bird *et al.* 2004; Markowitz 2004; Markowitz *et al.* 2004; McFadden 2003). In Admiralty Bay, dusky dolphin spend much of the day searching for food and feeding (Markowitz 2004; McFadden 2003). Unlike in Kaikoura, dusky dolphins in Admiralty Bay do not experience large-scale, daily tourism. However, the presence in the area of green-lipped mussel (*Perna canaliculus*) farms, which the dolphins avoid, is a conservation concern (Markowitz *et al.* 2004; Whitehead *et al.* 2004).

Würsig and Würsig (1980) detailed the patterns in movement, grouping, and behavior of dusky dolphins in a similar shallow-bay habitat (Golfo San José, Argentina) that also prey on a small schooling fish (southern anchovy, *Engraulis anchoita*). They found that the dolphins typically started the day resting in small groups (<20 individuals) and that groups spread out in search of prey as the morning progressed. Often by late morning or early afternoon, a small dolphin group would encounter prey and, at times, a large aggregation of highly surface-active feeding dolphins would ensue. Feeding could last for hours, with the school of fish maintained in a dense formation just under the surface of the water by the coordinated herding efforts of the dolphins. After feeding, the dolphins tended to socialize, maintaining a relatively large group size (Würsig & Würsig 1980).

Like their counterparts in Argentina, Admiralty Bay dusky dolphins often work together to herd small schooling fishes just under the surface (Benoit-Bird *et al.* 2004; Markowitz 2004; Markowitz *et al.* 2004; McFadden 2003). However, the feeding and grouping behavior of dusky dolphins in Admiralty Bay is not altogether similar to the Argentinean situation observed by Würsig and Würsig (1980). In Admiralty Bay, McFadden (2003) found that group size tended to remain relatively small throughout feeding bouts, and coordinated, prolonged surface feeding appeared to be one of several feeding tactics employed by dusky dolphins.

Photo-identification of Admiralty Bay dusky dolphins revealed that, in spite of frequent changes in group size and composition, individuals maintain preferred associations during and between winter seasons (Markowitz 2004). A total of 983 individuals were estimated to have used Admiralty Bay during the winters of 1998−2002 and 2004, with per-season estimates ranging from 122 to 272 individuals (in 2003 and 2001) (Markowitz & Würsig 2004).

## Completed research

The work reported here considers the social context of genetically sampled individuals, building directly on the behavioral results of Markowitz (2004).[3] The results can also be readily integrated with a suite of ongoing investigations into New Zealand dusky dolphin social behavior, feeding ecology, and habitat use (unpublished research proposals at Texas A&M University: A. Dahood, Dusky dolphin seasonal

---

[3] The results reported by Markowitz (2004) include, but are not limited to, groups from which tissue samples were taken.

habitat use; S. Deutsch, Dusky dolphin social learning; N. Duprey, Dusky dolphin interactions with boats; H. Pearson, Dusky dolphin and bottlenose dolphin sociality compared with select primates; M. Srinivasan, Influence of predators on dusky dolphins; R. Vaughn, Dusky dolphin feeding interactions with other marine predators; and J. Weir, Dusky dolphin nursery group behavior).

## *Methods*

### *Sample collection and preservation*

Dusky dolphins often approach small boats and ride the bow wave. For this study, skin from bow-riding dusky dolphins was collected using a sterilized nylon scrub pad affixed to a wooden dowel (Harlin *et al.* 1999). Harlin *et al.* (1999) found that the dolphins' behavioral response to this method was generally mild and that the tissue collected with this method is suitable for the amplification and sequencing of mtDNA *via* the polymerase chain reaction (PCR). For this study, the skin-swabbing technique was used to collect tissue samples from dusky dolphins in Kaikoura between February 1998 and May 2000 and in Admiralty Bay between June 1999 and July 2001 (Harlin-Cognato, personal communication). The tissue samples were fixed in either 20% dimethylsulfoxide or in ethanol and stored in a standard freezer. Two hundred skin samples were collected from individuals in 54 distinct small groups of four types: mating, nursery, adult, and feeding. Calves were used to classify a group as a "nursery" but were not sampled. Researchers identified distinctive marks of sampled individuals and moved the vessel position within the group in order to avoid sampling the same individual more than once within a sampling bout.

### *Group and behavior definitions*

For the dolphins from which tissue samples were taken, Markowitz (2004) collected and analyzed behavioral data. Dolphin groups were defined by spatial proximity according to the "10-m chain rule" (Smolker *et al.* 1992), meaning that dolphins were considered part of the same group if they were within 10 meters of another dolphin. This definition was chosen for simplicity and because it does not require any assumptions about the dolphins' behavior (Markowitz 2004).

Experienced observers estimated group size by reaching a consensus. For "smaller" groups (i.e. those with < 50 individuals), group size was estimated by noting the maximum number of animals simultaneously observed at or near the surface and also by taking into account distinctly marked individuals that were not seen during the largest simultaneous surfacing (Markowitz 2004).

In Kaikoura, smaller groups were classified into three categories—mating, nursery, and adult—based on the behavior and age class of group members (Harlin *et al.* 1999; Markowitz 2004). Mating groups consisted of fewer than 50 individuals with confirmed sexual activity. Nursery groups were those with fewer than 50 individuals and with neonatal calves or those up to about one year of age present. Calves were identified as smaller individuals that consistently swam in close proximity to an adult. Fetal folds (white, vertical markings) distinguished neonatal calves. Adult groups had fewer than 50 individuals without calves or sexual activity. In Admiralty Bay, samples were collected predominantly from small feeding groups. Feeding was noted if dolphins were apparently "pursuing fish or holding fish in their mouths" (Acevedo-Gutiérrez & Parker 2000; Markowitz 2004). Occasionally, pairs of dolphins (dyads) were also sampled at both locations. For all groups, behavioral observations were recorded at 2-minute intervals during focal group follows (Markowitz 2004).

## ***Behavioral results and discussion***

### *Mating groups*

Markowitz (2004) observed that mating groups consisted of mostly adults, although juveniles, as distinguished by their smaller size, were occasionally group members. The number of adults ranged from three to 35, with a median group composition of one female and six males. Rubbing, ventral presentation, and sexual approach (approaching another dolphin with the penis out) often preceded intromission (Markowitz 2004). A mother-calf pair was the subject of a chase in sexual groups on three separate occasions, and in all cases both the mother and calf showed signs of distress (Markowitz 2004). Social and high-speed activities were common in mating groups, as were extremely close inter-individual distances. Coordinated swimming formation was observed less often in mating groups than in other types of groups.

Competition between males for access to females, as the result of the inexpensiveness of male paternal investment (Alcock 2001a), is the likely case in dusky dolphins. In addition to competition among males, the dynamics of mating group interactions could be affected by cooperative coalitions among males (e.g. Connor *et al.* 1992b; Harcourt & de Waal 1992; Parsons *et al.* 2003), choosiness of females, and inbreeding avoidance by either sex (Trivers 1985). For mating groups of dusky dolphin, evidence relative to these possibilities is limited.

Markowitz (2004) interpreted mating groups as arenas in which male intrasexual competition takes the form of physical chasing; observations of quick speeds, lack of coordination between individuals, and successful female evasive maneuvers all support this interpretation. Dusky dolphins' large testes size (Cipriano 1992) further indicate the importance of sperm competition rather than pre-copultory male-male competition (Birkhead & Møller 1992). Thus, it seems likely that dusky dolphin males—alone or together—are unable to control access to females and seems unlikely that cooperation among males plays an important role in this context. However, coalitions, or "coordinated attacks by at least two individuals on one or more targets, often preceded by signaling between attackers," occur between adults in some carnivores, cetaceans, and primates (Harcourt 1992; Van Schaik *et al.* 2006), so the possibility of this type of social interaction cannot be discounted for dusky dolphins without further evidence.

### *Nursery groups*

Markowitz (2004) found that small nursery groups consisted of a mean of 13 adults, one juvenile, four older calves, and one neonatal calf. Nursery groups were observed resting more often, swimming more slowly, maintaining closer inter-individual distances, swimming more often in parallel formation, and engaging in minimal boisterous social activity and leaping when compared to other types of groups.

Würsig & Würsig (1980) observed rather large (10−20 adults and as many calves) nursery groups of dusky dolphins on the periphery of large, highly active feeding groups in Golfo San José, Argentina. They suggested that physical separation of calves could serve to protect them from aggression and competition among conspecifics and from larger predators attracted to the feeding activity. In Kaikoura, however, feeding is nocturnal, so in this location, the "nursery" grouping pattern (which consists of smaller groups that also contain non-mothers) is apparently not a result of feeding behavior in the larger group.

Current data leave the Kaikoura nursery group pattern open to many possible functional interpretations. For example, mother-calf pairs could segregate due to an activity synchrony effect (Conradt & Roper 2000) or due to the fact that calves would not benefit from the dilution of predation risk in a larger group that consists mostly of quicker (i.e. less at-risk) adults (Krause & Ruxton 2002). Dusky dolphin mother-calf pairs in Kaikoura could also be avoiding some aspects (e.g. aggression, high-level activity) of the behavior of conspecifics. Evidence exists for alloparental care in other cetaceans (e.g. Mann & Smuts 1998; Whitehead 1996), and this phenomenon could occur as well in dusky dolphin nursery groups. However, because foraging occurs at night and nursery groups are observed during the day, dusky dolphin mothers have relatively little to gain from alloparents in comparison to situations in which feeding mothers must accelerate or dive in a way that exceeds the ability of the calf to maintain contact (Mann 2002).

The presence of full-grown non-mothers in the nursery groups has been documented, but data relevant to explaining their presence is lacking. It is not known to what extent or in what ways they interact with calves. They could be older offspring that are showing delayed "social dispersal"; they could be adults that are motivated to join the group because of an interest in infants. Such an interest could have an adaptive explanation (e.g. learning to parent, establishing relationships with new members of the society) or it could be mal- or non-adaptive (e.g. Anderson *et al.* 2004; Silk 1999).

### *Adult groups*

Small adult non-mating groups were observed to be generally restful and engaged in few high-speed activities (Markowitz 2004). The existence of small non-mating adult dusky dolphin groups is intriguing because no overt social behaviors suggest a clear reason for the grouping pattern.

Markowitz (2004) suggested that these groups may serve to form or maintain social bonds that are important in other settings (e.g. mating, foraging, and rearing young). I suggest that that the grouping pattern could also result from the combination of three hypothetical conditions: (1) the difficulty of resting within a large group of active conspecifics, (2) the benefits of resting in a small group as opposed to alone (e.g. increased predator awareness), and (3) the lack of tight synchronization of the resting needs of all the individuals in a large dusky dolphin group. However, resting is known to peak at mid-day in Kaikoura, so resting behavior is at least somewhat synchronized (Bar & Slooten 1998).

### *Feeding groups*

In Admiralty Bay, feeding groups predominated, making up 72% of the groups observed by Markowitz (2004). Although swimming speeds were generally slow for Admiralty Bay feeding groups, synchronous bursts of rapid swimming, during which dolphins were apparently chasing fish, were often noted. Admiralty Bay feeding groups were also characterized by a high proportion of head-first re-entry leaps and by the presence of other predators, including seabirds, sea lions, and sharks (Markowitz 2004).

Feeding behavior of dusky dolphins in Admiralty Bay appears to be similar in many respects to that observed by Würsig & Würsig (1980) in Golfo San José, Argentina (Markowitz 2004; McFadden 2003). In both locations, dusky dolphins coordinate foraging efforts and actively aggregate a school of prey into a dense formation just under the surface of the water. This type of feeding is likely cooperative, in the sense that the dolphins work in tandem and individuals benefit from foraging together as opposed to foraging alone. However, given current data, the nature of social interactions in feeding groups is open to speculation, particularly concerning whether this type of foraging is properly described as a by-product mutualism or whether altruistic behaviors (e.g. individual temporary restraint from feeding) are involved. As discussed previously, the nature of social interactions has implications for what one would expect in terms of group structure relative to individual social preferences.

Cooperative feeding behavior is relatively common on land and in the sea (e.g. African wild dogs, *Lycaon pictus*: Creel & Creel, 1995; bottlenose dolphins: Acevedo-Gutiérrez & Parker 2000; chimpanzees: Boesch & Boesch 1989; Goodall 1990; killer whales: Hoelzel 1993; lions, *Panthera leo*: Schaller 1972). Interspecific cooperative hunting between giant moray eels (*Gymnothorax javanicus*) and red sea coral groupers (*Plectropomus pessuliferus*) or lunartail groupers (*Variola louti*) has even been described (Bshary *et al.* 2002). More specifically, the strategy of somehow herding schooling fish into tight aggregations is employed by a variety of species in addition to dusky dolphins, including humans (Parrish 1999), killer whales (Similä & Ugarte 1993), humpback whales, *Megaptera novaeangliae*, (Jurasz & Jurasz 1979), minke whales, *Balaenoptera acutorostrata*, (Kuker *et al.* 2005) and several species of mackerel (Carangidae) (Bshary *et al.* 2002; Hiatt & Brock 1948; Hobson 1968; Schmitt & Strand 1982). Coordinated herding exploits the behavioral tendencies of the prey and seems to be a robust solution to the problem of how to successfully feed on small schooling fish. Fish herding by dusky dolphins, then, may be a by-product mutualism, requiring no further explanation in terms of kin selection, reciprocity, or any other mechanism of inter-individual conflict mediation. Nevertheless, the commonness of the general behavioral strategy (actively herding schooling fish) gives relatively little information about its nature or historical (i.e. evolutionary) origins in this particular case; clearly, more data are needed to fully appreciate the role of cooperative foraging in dusky dolphin social life.

## Molecular methods in social analyses

In essence, the study of social behavior concerns how and why individual animals interact (Tinbergen 1953). Observations of individual animals are invaluable to the researcher interested in social behavior, but discovering meaning behind the observations often requires combining information gleaned from a variety of methods.

Advances in the number and types of genetic markers, the automation of laboratory methods, and the development of analytical methods continue to increase the power and practicality of applying molecular methods to the study of wildlife (DeYoung & Honeycutt 2005). Molecular methods have proved useful in determining information relevant to social behavior, and at times have provided surprising results, spurring further research and ultimately a deeper understanding of social behavior (Hughes 1998).

Molecular methods have revealed patterns of group structure for a range of systems. Leks of unrelated individuals in the greater sage grouse, *Centrocercus urophasianus* (Gibson *et al.* 2005); kin-based social groups in common eiders, *Somateria mollissima* (McKinnon *et al.* 2006); "nuclear" families of black rock skinks, *Egernia saxatilis* (O'Connor & Shine 2003); closed societies of Bechstein's bats, *Myotis bechsteinii* (Kerth *et al.* 2000); matrilineal social structure in sperm whales (*Physeter macrocephalus*) (Lyrholm & Gyllensten 1998); large maternally related pods of long-finned pilot whales (Amos *et al.* 1993); and lack of relatedness structure in groups of migrating humpback whales (Valsecchi *et al.* 2002) are only a few examples of social grouping patterns that have been described based on molecular information.

By implementing molecular methods, the current study describes aspects of group composition in dusky dolphins that have been largely hidden from researchers using traditional field observation methods. Chapter II describes the sex of small group members in Admiralty Bay and Kaikoura, New Zealand. The data were checked for evidence of sexual segregation at two spatiotemporal scales. Large-scale "habitat" segregation was investigated by estimating the sexual composition of animals sampled at each of the two locations. For group types in which sample size allowed, smaller-scale "social" segregation was also investigated. Chapter III describes the genetic relatedness within small groups of New Zealand dusky dolphins. Evidence from nuclear and mitochondrial DNA markers was considered. Pairwise relatedness was estimated and examined relative to the observed grouping patterns. Chapter IV summarizes the findings of this study and outlines some possible causes and implications of the results.

# CHAPTER II

# SEX OF GROUP MEMBERS

## Introduction

A 1:1 primary sex ratio is common in mammals (Trivers 1985), and dusky dolphins are likely no exception to this pattern.[4] Assuming roughly similar mortality rates between the sexes, deviations from a 1:1 sex ratio within groups would indicate that sex is a factor by which groups are structured. A 1:1 ratio is also expected at a larger (habitat) scale if there is no difference between males and females in habitat use.

In natural populations, each sex often faces distinct selective pressures. A difference between the sexes in the amount of investment in offspring can induce sexual selection, a process that has intrigued scientists since Charles Darwin (Darwin 1981; 1999) and that can result in dramatic sex differences in form and behavior (Trivers 1985). Sexual dimorphism and differential parental investment also cause distinct costs and benefits—and thus selective pressures—in contexts other than mating (Trivers 1985). Because selection is so often distinct for males and females, one would expect —and it is the case—that the sexes often separate along a behavioral or ecological dimension, a phenomenon known as sexual segregation (MacFarlane & Coulson 2005). Three spatiotemporal "levels" of sexual segregation have been described (Bon & Campan 1996; Bon *et al.* 2001; Conradt 1998; Conradt 1999): (1) Inter-habitat (segregation into to different habitats); (2) Intra-habitat (spatial segregation between ranges or areas within a habitat); and, (3) Social (segregation of the sexes into distinct

---

[4] Fisher (1930) proposed a now well-supported explanation of how the primary sex ratio could be an adaptive result of natural selection and why it is so often 1:1 (Trivers 1985). Nevertheless, a recent study demonstrated evolutionary constraints on the primary sex ratio in vertebrates (Toro *et al.* 2006), so the assumption that an observed 1:1 primary sex ratio is adaptive cannot be taken for granted.

groups).[5] The data presented here allow investigation into habitat and social sexual segregation in dusky dolphins.

Sexual segregation—at one or more levels—has been noted in a variety of animals; examples include fish, birds, and mammals. Male Trinidadian guppies (*Poecilia reticulate*) are more vulnerable to predation and thus prefer "safer" habitats, whereas females enjoy reduced harassment from males in relatively riskier (deeper) waters (Croft *et al.* 2006). In the sexually dimorphic northern giant petrel (*Macronectes halli*), the sexes employ distinct foraging strategies that result in differential habitat use. Females (the smaller sex) typically forage at sea, while males tend to feed on carrion on shore (Gonzalez-Solis *et al.* 2000). Differences between "nursery" and "male-only" roost site characteristics have been documented in Daubenton's bats, *Myotis daubentonii*, an effect that could be due to sex differences in the benefits of competing with conspecifics for the better sites (Encarnacao *et al.* 2005). In the Galápagos sea lion (*Zalophus californianus wollebaeki*), males were found disproportionately more often in "suboptimal" inland habitats, a result that Wolf *et al.* (2005) attributed to male displacement from preferred sites due to male-male aggression during the mating season and to "social" preferences for forming single-sex groups. Sexual segregation is particularly common in polygynous ungulates (Main *et al.* 1996) and has also been documented in an ecologically similar group, kangaroos (MacFarlane & Coulson 2005).

The topic of sexual segregation in polygynous ungulates has been addressed extensively, and Bon *et al.* (2001) reviewed and categorized explanations that have been proposed for this taxon. Several hypotheses hinge on sexual dimorphism in size or foraging abilities, and thus are not likely to be applicable to dusky dolphins. These include the "sexual dimorphism-body size/forage selection/indirect competition" hypothesis (Main *et al.* 1996), the "activity budget/energetic demands" hypothesis (Ruckstuhl 1998), and the "weather sensitivity" hypothesis (Bon *et al.* 2001; Conradt *et al.* 2000). Proposed explanations that concern sexual differences in parental care or

---

[5] Further indication that the sexes often respond to distinct selective pressures comes from evidence in mixed-sex groups for strong sex biases in the active coordination of group movement (Boinski 2000).

social behavior, such as the “reproductive strategy/predation risk” and “social affinity/social preference” hypotheses, are more likely to be relevant to dusky dolphins. The “reproductive strategy/predation risk” hypothesis proposes that female care for vulnerable offspring lead them to select habitats with lower predation risks, even if there are costs in terms of foraging opportunities, while males give more importance to the quality of foraging opportunities when choosing habitats (Bon *et al.* 2001; Main *et al.* 1996). According to the “social affinity/social preference” hypothesis, spatial and habitat segregation could be by-products of social segregation, resulting ultimately from “behavioral incompatibility” between the sexes (Bon & Campan 1996; Conradt 1999). Bon *et al.* (2001) described behavioral compatibility as “a set of behaviours allowing lasting interactions between partners sharing similar social motivation,” and defined behavioral incompatibility, after Legault and Strayer (1991), as “a set of differences in the behavioural repertoire.” For the alpine ibex, *Capra ibex ibex*, Bon *et al.* (2001) proposed that two factors, higher motivation for males to interact socially and avoidance by females of some components of male behavior, contribute to sexual segregation *via* behavioral incompatibility.

Varying levels of sexual segregation have been described in cetacean species, and hypothesized explanations are similar to those that have been explored more thoroughly in ungulates. In humpback whales (*Megaptera novaeangliae*) (Smultea 1994) and botos (*Inia geoffrensis*) (Martin & da Silva 2004), sexual segregation is thought to result from female avoidance of male harassment (i.e. a “social affinity” hypothesis). A variation of the “sexual dimorphism-body size” hypothesis would account for the large-scale separation of adult male sperm whales if they are indeed taking advantage of rich high-latitude food sources that are inaccessible to the much smaller, thermally vulnerable, females and young (Whitehead & Weilgart, 2000).

Both the “predation risk/reproductive strategy” and the “social affinity” hypothesis categories have been discussed relative to bottlenose dolphins. Bottlenose dolphin males are often more motivated to interact socially than females and are often aggressive (Connor *et al.* 2000), factors which could cause behavioral incompatibility and social segregation (see Chapter I for a further discussion of sex differences in bottlenose dolphin grouping patterns). Differences between the sexes in ranging patterns (e.g. Wells 1991b) could result in intra-habitat sexual segregation in bottlenose dolphins, and predation risk is thought to be particularly high for young calves and their mothers (Connor *et al.* 2000). Sex-specific affiliative behavior (Connor *et al.* 2006) and learning (Krützen *et al.* 2005), both mechanisms that could contribute to sexual segregation, have been documented in Indian Ocean bottlenose dolphins.

Social segregation by sex is also apparent in some of the less-often-studied cetacean species, though potential causes of the patterns are more difficult to evaluate given sparser information regarding social life in these species. The distinct and synchronized sub-groups of male spotted dolphins (*Stenella attenuata*) found within a larger school (Pryor & Shallenberger 1991) are a clear example of sexual segregation at the social level. Blainville's beaked whales (*Mesoplodon densirostris*) in the Bahamas segregate by age at the social and habitat level and, among juveniles, by sex at the social level (Claridge 2005).

Dusky dolphins are not sexually dimorphic for size, contraindicating several hypotheses proposed to explain sexual segregation in other species. However, other factors that are known to influence the phenomenon—seasonal breeding, uniparental care, and sex differences in social strategies and behavioral repertoire (Bon *et al.* 2001; Main *et al.* 1996; Trivers 1985)—are either known or suspected to occur in dusky dolphins (see Chapter I for further discussion of what is known about these factors relative to dusky and other dolphin species). Thus, the nutritional demands of lactation, the relatively high vulnerability of young dolphins to predation by large sharks and killer whales and to harassment by conspecifics, and the potential for females to be less motivated to socialize could affect grouping and migration decisions in female dusky dolphins. Conversely, grouping and migration decisions in males are presumably more influenced by factors related to mating success.

## Materials and methods

### *DNA extraction and sex determination*

Total genomic DNA was isolated using a DNeasy kit (Qiagen, Valencia CA). DNA was suspended in water, and negative controls were included for all extractions. For some samples, DNA template amount was increased by using a Genomiphi whole-genome amplification kit (GE Healthcare, Chalfont St. Giles, United Kingdom). Sex was determined by the simultaneous polymerase chain reaction (PCR) amplification of the zinc-finger protein on the X-chromosome (ZFX) and the sex-determining region on the Y-chromosome (SRY). This was accomplished by following either standard protocol with primers designed for sexing mammals (Harlin-Cognato, personal communication; Banks *et al.* 1995) or the odontocete-specific protocol and primers described in Rosel (2003).

### *Analytical methods*

Sexual segregation at the habitat level was investigated by estimating the proportion of females in the population (in the statistical, not biological, sense), $\pi$, at each sampling location. As described in Ott and Longnecker (2001), the population proportion was estimated according to the formula: $\frac{y}{n}$, where *y* is the number of females sampled and *n* is the total number of animals sampled. If $n\hat{\pi} \geq 5$ and $n(1-\hat{\pi}) \geq 5$, then $\pi$ was assumed to have a mound-shaped distribution with a standard error approximated by the equation $\hat{\sigma}_{\hat{\pi}} = \sqrt{\frac{\hat{\pi}(1-\hat{\pi})}{n}}$. Ninety-five percent confidence intervals for the estimated proportion of females in the population ($\hat{\pi} \pm z_{\alpha/2}\hat{\sigma}_{\hat{\pi}}$) were calculated.

The distribution of the sexes among group types was also examined. The proportion of females in the statistical populations were again estimated, but with individuals pooled according to the type of group, rather than the habitat, in which they were found.

Finally, patterns of sexual composition within group types were examined. For group types that were sampled multiple times, the frequency, within each group, of males, females, and unsexed individuals was plotted. The number of individuals of unknown sex was based on field estimates of group size. If a group size range was noted, the average was used, if a minimum number of individuals was noted, then the minimum was used. A randomization test (Manly 1997), specifically the "category membership" procedure in the program PERM (Duchesne *et al.* 2006) was employed to address the question of whether groups are structured by attraction of same-sex individuals (or, equivalently, avoidance of different-sex individuals). This program was used to calculate a homogeneity statistic, H, for each of the observed groups. H is the sum of hG over all groups, where hG is the number of specimens belonging to the most frequently identified category within group G. For example, in a group of four males and three females, hG would be four, whereas in a group of one male and six females, hG would be six. The more clumped the categories (i.e. sexes) are in terms of group membership, the higher H, the sum of hG, will be. "P-values" were estimated by comparing the observed H value to a null distribution of values generated from 10 iterations of 1000 random permutations of the data (i.e. the observed sexes), in which the observed number and sizes of groups were kept constant (Duchesne *et al.* 2006). Each type of group was tested separately. This procedure thus tests the degree to which groups are structured by sex relative to the overall sex ratio for that group type.

## Results

Sex was determined for 107 dusky dolphin samples (Table 1). A total of 20 females and 87 males were identified. The large-scale question of the overall sex ratio at each study site was addressed by calculating confidence intervals for the proportion of females identified at each site, regardless of small group membership. The 95% confidence interval for the proportion of females in Admiralty Bay (n=88) is 0.074−0.222; for the proportion of females in Kaikoura (n=19), it is 0.152−0.585 (Figure 1).

**Table 1** Proportion, by location and group type, of observed sexes.

| Location | Group type | Proportion female ( $\hat{\pi}$ ) | Individuals sampled ( $n$ ) | Number of groups |
|---|---|---|---|---|
| Kaikoura | Mating | 0.250 | 8 | 5 |
| | Nursery | 0.000 | 1 | 1 |
| | Adult | 0.444 | 9 | 5 |
| | Dyad | 1.000 | 1 | 1 |
| | *Sub-total* | *0.368* | *19* | *12* |
| Admiralty Bay | Feeding | 0.159 | 82 | 38 |
| | Adult | 0.000 | 5 | 2 |
| | Dyad | 0.000 | 1 | 1 |
| | *Sub-total* | *0.148* | *88* | *41* |
| Grand total | | | 107 | 53 |

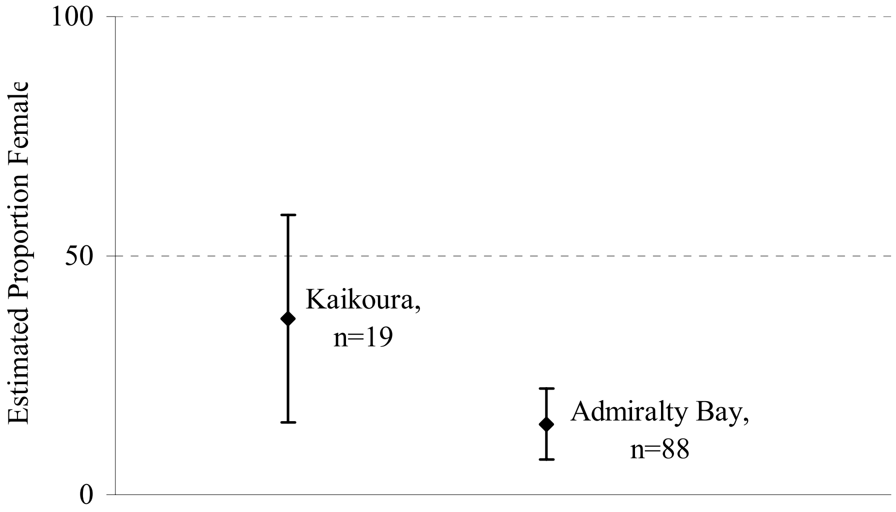

**Figure 1** Estimated proportion of females identified, with individuals pooled by sampling location.

At a smaller scale, the proportion of females sampled within each group type ( $\hat{\pi}$ ) was also estimated (Table 1). Most group types did not meet the conditions necessary for calculating a confidence interval on this estimate. The only exception was Admiralty Bay feeding groups, which have a 95% confidence interval of 0.0795−0.237 for $\hat{\pi}$.

At a still smaller scale, the distribution of the sexes among groups within a group type was investigated. Three group types (Kaikoura mating, Kaikoura adult, and Admiralty Bay feeding) were sampled in more than two distinct groups (Figure 2, Figure 3, and Figure 4). The null hypothesis that groups are not structured by sex was tested with permutation tests. Admiralty Bay feeding groups showed evidence of group structure *via* positive assortment, while Kaikoura mating and adult groups did not (Table 2).

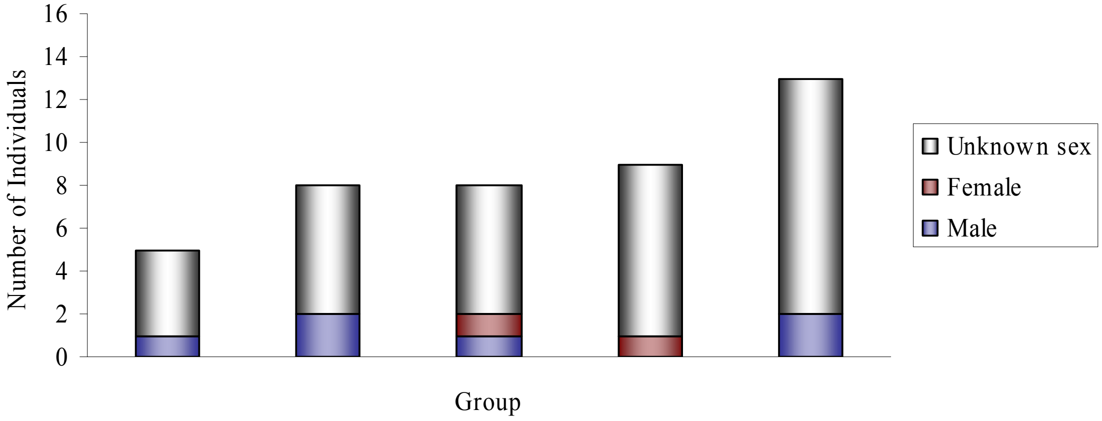

**Figure 2** Sexual composition of Kaikoura mating groups.

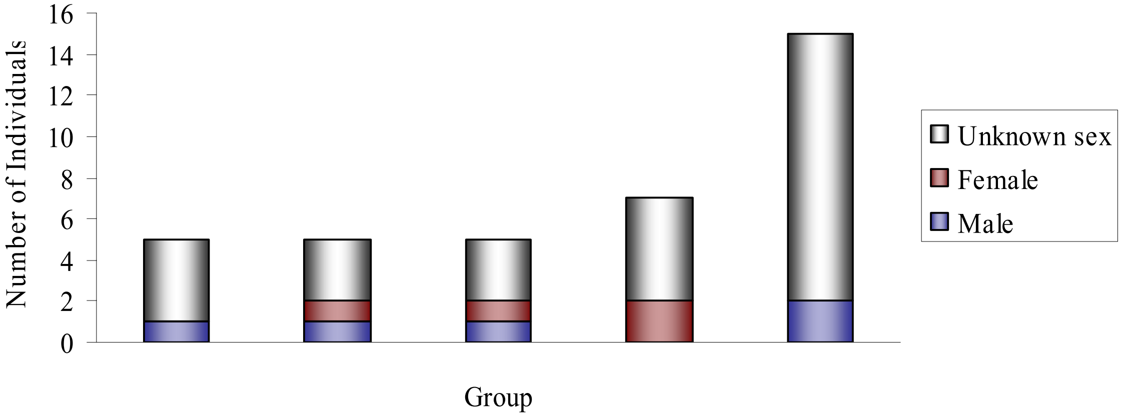

**Figure 3** Sexual composition of Kaikoura adult groups.

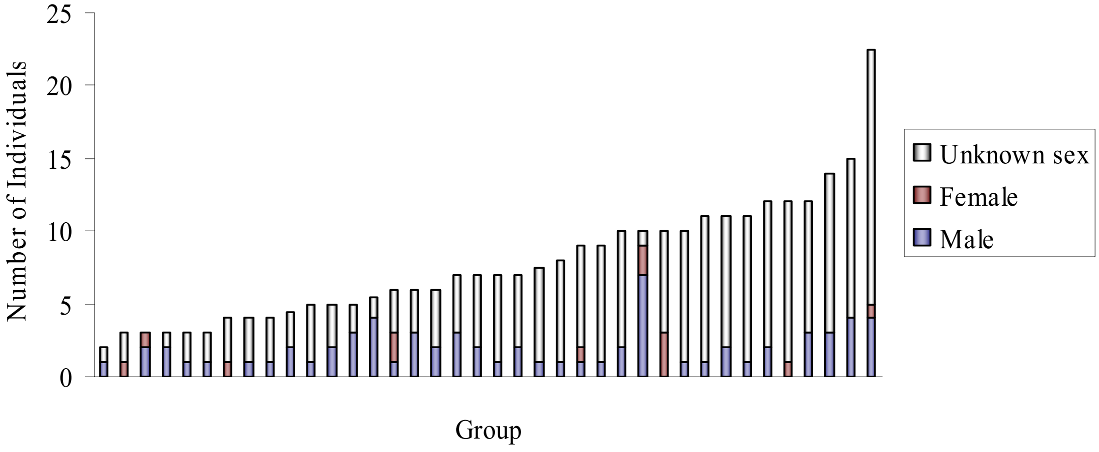

**Figure 4** Sexual composition of Admiralty Bay feeding groups.

**Table 2** Results of a randomization test of group homogeneity in sexual composition. The null hypothesis that individuals group randomly with respect to sex was tested.

| Type of group | Location | Global p-value |
|---|---|---|
| Mating | Kaikoura | 0.564 |
| Adult | Kaikoura | 0.616 |
| Feeding | Admiralty Bay | 0.030 |

## Discussion

### *Habitat-level sexual segregation*

Overall, several sources indicate that the dusky dolphin population off Kaikoura has a relatively even sex ratio. This study indicates that the population consists of between 15% and 58% females (Figure 1). However, this result is based on samples that were collected from small groups (which were not expected to be representative of the general population of dolphins present), and therefore is not particularly relevant to the question of the overall sex ratio in the area. In examining samples from the presumably more representative larger groups, Harlin (2004) observed a 1:1 sex ratio off Kaikoura. In the same area, Cipriano (1992) observed a potentially male-biased adult population (4 adult females and 9 adult males). However, sample size (for Kaikoura) in this study was small, and the pattern may be influenced by a sex bias in the likelihood of stranding.[6]

In contrast to the situation in Kaikoura, the data reported here clearly indicate habitat-level sexual segregation in Admiralty Bay, where the population of dusky dolphins was estimated to consist of only 15% females (Table 1; Figure 1). The seasonality of dusky dolphin breeding (Cipriano 1992) indicates that males do not suffer reduced opportunities to sire offspring by choosing to winter with (mostly) other males in Admiralty Bay. What benefits either sex gains from the pattern is not clear. Because dusky dolphins are not sexually dimorphic and because females invest heavily in parental care, the "reproductive strategy/predation risk" and "social affinity/social preference" hypothesis categories (Bon *et al.* 2001) encompass most of the potential adaptive explanations for dusky dolphin sexual segregation. However, considering adaptive explanations is only a starting point for exploring possible causes of the pattern. Many constraints (e.g. pleiotropic effects, functional trade-offs, local maxima in the fitness landscape, multilevel selection) can limit the potential for natural selection to optimize individual inclusive fitness (Sober 2006). Furthermore, simple adaptive hypotheses tend not to incorporate the idea that behavioral patterns can result from evolution within genetic or non-genetic (i.e. "cultural") inheritance systems or from the interaction of the two (e.g. Dugatkin 2000; Grant & Grant 1996; Schlupp *et al.* 1994; Whitehead 1998). To assume that individuals maximize inclusive fitness is a good starting point, but it is nonetheless an assumption and a starting point. Clearly, much detailed knowledge about a system is required to evaluate the causes of an observed behavioral pattern, particularly in order to replace the assumption of overall adaptedness of animal behavior with details about how a particular system actually evolves and functions. For the dusky dolphin system, knowledge has been accumulating through

---

[6] Samples reported by Cipriano (1992) were either netted (in fishing operations) or stranded. Overall, 11 of the 11 stranded samples were male, while 11 of the 20 netted samples were male.

past and ongoing studies, so there is information relevant to potential causes of sexual segregation.

Sex differences in the likelihood of migrating to Admiralty Bay for the winter season underlie the observed dusky dolphin sexual segregation. Dusky dolphins primarily use Admiralty Bay in the winter, many individuals return to Admiralty Bay in multiple years, and at least some of these individuals can be found off Kaikoura at other times of the year (Markowitz 2004). The seasonality, reliability, and distance between of food sources, as well as the social dynamics involved in foraging for different types of prey are all factors that could affect dusky dolphin migration. The pattern of habitat-level sexual segregation could be a by-product of sex differences in the ecological (i.e. non-social) costs and benefits influencing migration. This could stem, for instance, from calves being less adept long-distance travelers (due to swimming ability or predation risk on the migration route) or from differences in fasting tolerance between males and lactating females. Alternately, sexual segregation at the social level could be driving larger-scale habitat segregation.

Both this study and Würsig and Würsig (1980) reported social-level sexual segregation in conjunction with dusky dolphin feeding groups, supporting the idea that social factors could play a role in the habitat-level pattern. In Golfo San José, Argentina, Würsig and Würsig (1980) observed that dusky dolphin mother-calf pairs tended to separate from fish-herding groups of conspecifics, and they noted that two aspects of fish-herding—boisterous or competitive interactions among feeding dusky dolphins and the conspicuousness of such groups to dusky dolphin predators—could drive mother-calf pairs to separate. The same factors—"social affinity" and "predation risk" hypotheses—could be causing females to avoid the fish-herding feeding mode, and thus Admiralty Bay. However, while these proposed explanations are rather satisfying at the social scale described by Würsig and Würsig (1980), the "predation risk" hypothesis is less satisfying at the habitat scale described in this study. Some characteristics of Admiralty Bay (e.g. the shallow depth and sheltering land forms) and some aspects of Kaikoura DSL feeding behaviors (e.g. movement to a deep-water habitat at dusk) make Admiralty

Bay/fish-herding seem *less* risky, in terms of predation on calves, than Kaikoura/DSL-feeding. However, extensive data relative to predation risk in different habitats and during different feeding modes do not exist for dusky dolphins. Additional "social affinity" hypotheses that could cause habitat segregation *via* social segregation include the ideas that females avoid harassment by male conspecifics (i.e. that they avoid the behaviors characteristic of males rather than characteristic of fish-herding dolphins) or that males avoid profitable, but relatively asocial, feeding modes (i.e. DSL feeding) due to a high motivation to socialize.

The effect of social learning on the evolution of behavior is another social-level factor that could play a role in causing sexual segregation. Whitehead *et al.* (2004) suggested that dusky dolphin use of the Marlborough Sounds (including Admiralty Bay) is a likely candidate for a "cultural" behavior. Habitual preference of a particular wintering ground, as is seen in this case, could result from dolphins employing a genetically adaptive behavioral heuristic (e.g. "find a good place, by any learning method, and return there every year"). Depending on the scale of variability in the environment, social learning could be a particularly effective way to "find a good place" (Whitehead 2005b). This mechanism could be acting in concert with any of the previously-discussed adaptive hypotheses to produce the observed sexual segregation. Alternately, a sex bias in social learning could be the root cause of the pattern. If (for any reason) individuals are more likely to learn from same-sex conspecifics, then a scenario in which a (chance) male bias in the initial group that learned how and when to use Admiralty Bay was magnified through sex-biased social learning, creating non-adaptive sexual segregation, is plausible.

The importance of social learning in dusky dolphin winter use of Admiralty Bay is hypothetical, but the idea resonates with evidence for social learning in many aspects of cetacean behavior (Rendell & Whitehead 2001) and for social learning of migratory routes and destinations in other species. Helfman and Shulz (1984) used translocations to demonstrate that social learning causes French grunts, *Haemulon flavolineatum*, to use specific daytime schooling sites and twilight migration routes. Similarly, the blueheaded wrasse, *Thalassoma bifasciatum*, uses traditional mating sites (Warner 1988; 1990). In guppies, *Poecilia reticulata*, laboratory experiments demonstrated social learning of a circuitous (i.e. energetically costly) route to a food source, indicating that social learning of maladaptive behaviors is possible (Laland & Williams, 1998). Observations of cetacean movements have also indicated the likelihood that social learning plays an important role. Remarkably strong fidelity to particular wintering grounds, in which different foraging tactics are employed, has been observed in distinct sub-populations of narwhal (*Monodon monoceros*) (Laidre *et al.* 2003). Loss of the whales' traditional knowledge has been proposed to explain the lack of re-establishment of North Atlantic right whales, *Eubalaena glacialis*, in Labrador waters after large-scale whaling ended (Katona & Kraus 1999; Whitehead *et al.* 2004). Further, studies of captive dolphins have demonstrated that the ability to imitate—an integral part of social learning—is a sophisticated and readily expressed faculty in dolphins (Pryor 2001).

We have identified factors that are important to consider as possible causes of habitat sexual segregation in Admiralty Bay dusky dolphins. Most potential adaptive explanations ultimately rely on the idea that sex differences in investment in offspring leads to sex differences in reproductive strategies and sex-specific behavioral repertoires. The evolutionary effects of these sex differences are influenced by many factors—the nature of prey resources and predators in an area, the age and parturitional status of individuals, and the nature of learning mechanisms, to name only a few. Additionally, because there are evolutionary constraints on the optimization of individual inclusive fitness and because "cultural" inheritance systems are clearly capable of producing non- or mal-adaptive behavioral patterns, adaptive explanations should not be considered exclusively. Teasing apart the influence of diverse but interrelated factors on the evolutionary dynamics of dusky dolphin behavior remains a daunting task, but already knowledge of dusky dolphin biology has narrowed the field of possible causes for habitat-level sexual segregation.

### ***Distribution of the sexes between and within group types***

The distribution of the sexes among the different group types was examined by pooling individuals according to group type (Table 1). In Kaikoura, more than one individual was sampled for two group types (mating and adult). In Admiralty Bay, one group type (feeding) predominated the samples, so the distribution of sexes among group types was not addressed in this location. Markowitz (2004) observed a median proportion of 14% females in Kaikoura small mating groups. The results of this study (25% females in mating groups, when individuals are pooled), generally concur with the finding that mating groups consist of mostly males. The results are, therefore, also consistent with Markowitz's (2004) interpretation of mating groups as arenas in which males compete amongst themselves for access to female(s). The estimation of the proportion of females in Kaikoura small adult groups (44% when individuals were pooled across groups) showed a trend towards more even sexual composition, indicating that both males and females form adult groups.

The distribution of sexes among the group types leaves unanswered the important question of the homogeneity, relative to sex, of individual groups within each group type. Graphical representation of each group (Figure 2; Figure 3; Figure 4) and randomization tests (Duchesne *et al.* 2006) (Table 2) addressed the question of group homogeneity. The randomization tests indicated that the mating and adult groups in Kaikoura do not tend to be homogeneous relative to sex, given the overall sex ratio of each group type. That is, although mating groups consist mostly of males and are thus homogeneous relative to the presumed 1:1 sex ratio in the area, the distribution of the sexes among particular groups within the mating group type is relatively even. However, small samples size (n=9 for mating and n=8 for adult) likely caused a lack of power for these tests to discriminate group homogeneity. In contrast, the few females that were observed in Admiralty Bay (n=13) tended to co-occur within a group more often than you would expect if sex were not a factor by which the dolphins were grouping. Possible adaptive reasons for social-level sexual segregation (e.g. “reproductive strategy” and “social affinity” hypotheses) were detailed in the discussion of habitat-level sexual segregation. The observation that social-level segregation occurs in Admiralty Bay lends credence to the idea that social factors could be driving the habitat-level pattern.

That these results—in particular, the uneven sex ratio in Admiralty Bay—reflect reality, rather than biases inherent in the sampling procedure, is supported by Harlin's (2004) observations of a 1:1 sex ratio of dusky dolphins (off Kaikoura) and two primarily female dusky dolphin populations (off Otago and off the west coast of the South Island) using the same procedures followed in this study. Nevertheless, a bias in the "catchability" of the sexes during sample collection from bow-riding dolphins is a potential concern that should be considered when interpreting these data. Fortunately, this consideration does not detract significantly from the major finding that Admiralty Bay is used primarily by males. Even if males were three times as likely as females to be sampled, the conservative conclusion that most (i.e. >50%) of the dolphins using Admiralty Bay in the winter are males would be supported by the data reported here.

# CHAPTER III

# RELATEDNESS WITHIN GROUPS

## Introduction

### *Animal kin groups*

Mammals, including cetaceans, often associate in kin groups. For example, yellow-bellied marmots, *Marmota flaviventris* (Armitage & Schwartz 2000), grey squirrels, *Sciurus carolinensis* (Gurnell *et al.* 2001), and wild boars, *Sus scrofa* (Kaminski *et al.* 2005) associate in groups of closely related females with their offspring. Sperm whale societies consist of associations among related matrilines, and some populations of killer whales maintain parent-offspring relationships throughout life (Baird 2000; Whitehead & Weilgart 2000). Bottlenose dolphins in Sarasota Bay associate in “bands” comprised in part of female relatives, and in Monkey Mia, some males associate preferentially and cooperate with close relatives (Connor *et al.* 2000). It is reasonable to suspect that grouping patterns in dusky dolphins could also be influenced by kin relationships. This chapter describes the relationship between genetic relatedness, grouping patterns, and behavior in dusky dolphins. This description is relevant to several interrelated topics, including the role of proximate mechanisms in producing or limiting patterns of relatedness, the role of kin selection in the evolution of behaviors and social structure, and the causes and implications of traditional behavior in animals.

### *Proximate mechanisms*

Well-studied systems reveal variety in the details of how structure in the relatedness of group members arises, and much current theoretical and empirical work is aimed at explaining this variety. Many animals recognize and behave discriminatingly towards kin (reviewed by Halpin 1991; Hepper 1989), and this is one mechanism by which relatedness patterns in grouping can arise. Diverse cues, including odors in ground squirrels (Mateo 2003) and vocalizations in birds (Sharp *et al.* 2005) have been shown to result in kin recognition. In bottlenose dolphins, signature whistles are known to convey identity information (Janik *et al*. 2006) and to be similar in mother-son pairs (Sayigh *et al.* 1995). Thus, whistles are a potential mechanism for kin recognition in bottlenose dolphins. The extent to which dusky dolphins use cues to recognize kin is unknown.

A "greenbeard effect," whereby a gene (or tightly linked genes) causes a distinct trait, the recognition of that trait in others, and the tendency to behave discriminatingly towards those with the trait, could also promote group structure in (statistical, not genealogical) relatedness (Dawkins 1976). Despite documentation of this phenomenon in nature, such direct recognition between alleles is thought to be uncommon, particularly in macroorganisms (Queller *et al.* 2003). Therefore, the greenbeard effect is unlikely to be a major mechanism by which dusky dolphin groups are structured.

Even without recognition between related individuals or identical genes, proximate mechanisms can create or eliminate the potential for group structure in relatedness. Using computer simulations, Lukas *et al.* (2005) investigated the effects of sex-biased dispersal, group size, and reproductive skew on intragroup relatedness. They concluded that high intragroup average relatedness is only expected for small group sizes consisting of the philopatric sex. The generally low reproductive output of mammals is another proximate mechanism that sets a limit to the number of closely related social partners available (Avilés *et al.* 2004). Other mechanisms that have been shown to be important include habitat fragmentation, which increases the level of within-population-fragment relatedness in the agile antechinus, *Antechinus agilis* (Banks *et al.* 2005), and aggressiveness, which, when experimentally increased in red grouse (*Lagopus lagopus scoticus*) territorial cocks, reduced the clustered spatial arrangement of kin (Mougeot *et al.* 2005).

### ***Kin selection***

A gene's fate, relative to natural selection, is usually tied to the fate of the individual in which it is found; thus, selfish individual behavior readily evolves and persists in simple evolutionary models, whereas altruistic or spiteful behaviors do not (Alcock 2001a; Dawkins 1976). Hamilton (1963; 1964a; 1964b; 1970) recognized that altruistic or spiteful behaviors would be favored by natural selection under the conditions of high or low genetic relatedness of interacting individuals, respectively. His key insights, later labeled "kin selection", were that an individual's genetic representation in the next generation is dependant on the success of the direct (descendant) lineage as well as the indirect (non-descendant) lineage, and that costs of helping a relative are offset proportionately to how closely the interacting individuals are related (Griffin & West 2002). Thus, behavior can be favored by selection if it increases an individual's "inclusive fitness" through its combined effects on the descendent and non-descendant lineages (Alcock 2001a). The idea has successfully explained much otherwise-puzzling behavior. For example, worker bees often die defending a nest of close relatives from intruders (Krause & Ruxton 2002). Some birds have been shown to direct helping behaviors preferentially towards closer relatives (e.g. Emlen & Wrege 1988; Komdeur 1994), as have humans (e.g. Bowles & Posel 2005). Salmon (*Salmo salar*) territorial behavior is kin-biased (Brown & Brown, 1996); gulls (*Larus canus*) that adopt chicks tend to adopt relatives (Bukacinski *et al.* 2000); Siberian jays (*Perisoreus infaustus*) exhibit nepotism in vigilance against predation, alarm calling, and mobbing (Griesser 2003; Griesser & Ekman 2004; Griesser & Ekman 2005). The list could easily continue.

Relatedness among interacting individuals is, no doubt, a key parameter necessary for describing behavior; without it, one cannot know the inclusive fitness implications of a behavior. Nevertheless, the idea of kin-selected behavior has been called a "bandwagon" (Dawkins 1979), implying that, at times, the theory has been invoked without sufficient critical analysis and empirical evidence. Several instances of purported kin-selected behavior did not hold up to scrutiny (e.g. helping behavior in meerkats *Suricata suricatta*: Clutton-Brock *et al.* 2000; fighting behavior in wasps: Griffin & West 2002; West 2001). Detractors of the kin-selection-bandwagon note that many seemingly altruistic behaviors may enhance individual fitness directly (Clutton-

Brock 2002), that competition between relatives may counteract kin selection (Griffiths *et al.* 2003; West *et al.* 2002), and that kin biases in behavior may be the result of processes besides kin selection (Silk 2006).

Progress in understanding non-kin-based mechanisms that favor or stabilize non-selfish behavior has made "the commons" (Hardin 1968) no longer look so bleakly tragic.  Besides kin selection, reciprocity (Queller 1985; Trivers 1971), pseudo-reciprocity (Connor 1986), active repression of internal competition (Boyd & Richardson 1992; Frank 1995), limits to the range of possible cheating mechanisms that can evolve (Velicer 2005), random or egalitarian distribution of benefits (Avilés *et al.*, 2004), and multi-level selection (Goodnight 2005) can all affect the types of animal behaviors that are likely to evolve.

To what extent kin selection, alone or in concert with other mechanisms, drives the evolution of particular behaviors is unknown for many situations.  Authors have shed light on this question by determining the genetic relatedness among interacting individuals, thus confirming the potential for or eliminating the possibility of kin selection (e.g. cardinalfish: Kolm *et al.* 2005; chimpanzees: Vigilant *et al.* 2001; dolphins: Krützen *et al.* 2003; guppies: Russell *et al.* 2004; humpback whales: Valsecchi *et al.* 2002; hyenas: Van Horn *et al.* 2004; wolves: Vucetich *et al.* 2004).

Dolphin societies tend to be highly cooperative (Norris 1994), and the coordinated fish herding observed in some populations of dusky dolphin (Markowitz 2004; Markowitz *et al.* 2004; Würsig *et al.* 1997; Würsig & Würsig, 1980) indicate that dusky dolphins also cooperate routinely.  Nevertheless, the fitness effects of particular dusky dolphin behaviors have not been characterized in detail.  Particularly high or low relatedness among group members would indicate that kin selection may have caused the evolution of altruistic or spiteful behaviors.  Alternately, if relatedness in small groups is close to zero, kin selection will be eliminated as a viable explanation should altruistic or spiteful behaviors that affect all group members equally be documented in this population of dusky dolphins.

### ***Behavioral traditions***

The significance and even the existence of socially learned (i.e. "cultural" or "traditional") behavior in non-humans is a debated topic (e.g. Rendell & Whitehead 2001), and calls for cetacean cultural conservation (e.g. Whitehead *et al.* 2004) highlight the important implications of the debate. Evidence suggests that social learning and culture are important in some of the better-studied cetacean species, especially bottlenose dolphins, killer whales, and humpback whales (Rendell & Whitehead 2001).

Genetic relatedness data are most relevant to the "group contrast model" of behavioral traditions[7] which has been criticized as, at best, a starting point for identifying candidate traditions (Fragaszy & Perry 2003). Whitehead *et al.* (2004) noted that the repeated use by some dusky dolphins of the Marlborough Sounds, New Zealand as winter foraging habitat is a candidate cultural tradition. The genetic data presented here, in a group contrast model context, are relevant to this possibility.

### ***Rationale***

This chapter describes the level and patterns of relatedness in small groups of dusky dolphins and is meant to lay the groundwork for developing and testing hypotheses relevant to the biological issues described above. These data provide a unique and valuable perspective because knowledge of social life in large-group-living delphinids is relatively sparse.

### ***Microsatellites and relatedness***

Pairwise genetic relatedness, *r*, is the probability that a gene is identical by descent in two individuals. It is also a measure of the genetic similarity of two individuals relative to a reference population (Blouin 2003). Values range from zero to one (though some estimators also allow for negative values), and can easily be calculated from pedigrees. In the absence of pedigree information, genetic markers can be used to infer the proportion of genes that are identical by state in a pair of individuals.

---

[7] This model involves identifying two groups that are genetically similar, but behaviorally distinct. If no obvious environmental factors seem to elicit the behavioral difference, then (by process of elimination) the behavior is likely traditional (Fragaszy & Perry 2003) .

A variety of methods for estimating pairwise genetic relatedness from this type of information exist (Blouin 2003).

Microsatellites, short segments of DNA that consist of tandem repeats of short (1-6 base pairs long) nucleotide motifs, are well-suited as molecular markers for relatedness estimation (Queller *et al.* 1993). Microsatellite alleles differ in the number of times the motif is repeated, and in many wild outbred populations, microsatellite genes are highly polymorphic. Microsatellite loci are common in eukaryotic DNA and can be amplified from small amounts of DNA using PCR. The alleles found in individuals can be scored by electophoresis on polyacrylamide gels. Each allele is a particular size, and it travels through the gel at a rate inversely proportional to its size. Using a standard consisting of molecules of known size, alleles can be consistently scored across different gels (Queller *et al.* 1993). The identification of appropriate microsatellite primers is often the most costly and difficult aspect of microsatellite analyses (Queller *et al.* 1993). Primers are typically identified by screening genomic libraries and are often used for closely related species, though it cannot be assumed that the amplification product is the same across species (Queller *et al.* 1993).

### ***Mitochondrial DNA***

Mitochondria are found in the cytoplasm of most eukaryotic cells, and contain multiple copies of a genome (mtDNA) that is commonly examined by molecular ecologists (Beebee & Rowe 2004). Animal mtDNAs are circular double-stranded molecules that are typically 15−17.5 kbp in size. mtDNA is not strictly maternally inherited, but it can usually be analyzed as if it were because of extremely low levels of paternally-inherited mitochondria. Besides uniparental inheritance, other important features that distinguish mtDNA from nuclear DNA are the lack of recombination and relatively high nucleotide substitution rate. These features allow for analysis of genetic variation in maternal lineages both within and between species (Beebee & Rowe 2004).

## Materials and methods

### *Genetic methods*

Total genomic DNA was isolated using a DNeasy kit (Qiagen). DNA was suspended in water, and negative controls were included for all extractions. For some samples, DNA template amount was increased by using a Genomiphi whole-genome amplification kit (GE Healthcare).

Individuals were genotyped for 12 microsatellite loci. Some primers were dusky dolphin-specific (Cassens *et al.* 2005; unpublished primers developed by Harlin-Cognato) and some (Buchanan *et al.* 1996; Shinohara *et al.* 1997) were designed for other dolphin species (Table 3). Microsatellite loci were amplified by multiplexed PCRs carried out at the Nevada Genomics Center (University of Nevada, Reno, Nevada). Annealing temperatures are listed in Table 3. The PCR products and size standards were run on a 3730 automated sequencer (Applied Biosystems). Electropherograms were analyzed using GENEMAPPER (Applied Biosystems), and the resulting allele calls were exported into a Microsoft Excel spreadsheet.

A 472-base pair fragment from the d-loop region of the mtDNA was amplified by PCR following the protocol and primers of Baker *et al.* (1996). PCR products were purified with Qiaquick (Qiagen) spin columns and were sequenced with Big Dye termination chemistry (Applied Biosystems) on a 377 automated sequencer (Applied Biosystems). Sequences were aligned using the program SEQUENCHER (Gene Codes Corporation) and haplotypes were identified using the program DNASP, version 4.10.8 (www.ub.es/dnnasp/).

**Table 3** Summary of primer information.

| Reference | Target species | Locus | Repeat sequence | $T_a$ (°C) | Fragment size (bp) | No. of alleles | $H_E$ |
|---|---|---|---|---|---|---|---|
| Shinohara *et al.* 1997 | *Tursiops truncatus* | D14 | $(AC)_{16}$ | 56 | 120 | 5 | 0.74 |
|  |  | D28 | $(CA)_{24}$ | 57 | 145 | 6 | 0.74 |
| Buchanan *et al.* 1996 | *Delphinapterus leucas* | DlrFBC3 |  | 60 | 141−173* | 15 | 0.86 |
|  |  | DlrFBC11 |  | 56 | 110−144* | 8 | 0.48 |
| Cognato-Harlin, personal communication | *Lagenorhynchus obscurus* | Lo105 |  | 57 |  |  |  |
|  |  | Lo514 |  | 56 |  |  |  |
|  |  | Lo6 |  | 60 |  |  |  |
| Cassens *et al.* 2005 | *Lagenorhynchus obscurus* | Lobs_Di7.1 | $(TG)_{28}$† | 60 | 118−152 | 17 |  |
|  |  | Lobs_Di9 | $(TG)_{16}$ | 56 | 86−112 | 13 |  |
|  |  | Lobs_Di19 | $(CA)_{11}$ | 57 | 86−128 | 18 |  |
|  |  | Lobs_Di21 | $(TG)_{15}$ | 57 | 98−128 | 16 |  |
|  |  | Lobs_Di24 | $(GT)_9(GA)_{10}$ | 60 | 102−130 | 15 |  |

*Buchanan, personal communication. †The structure of the cloned sequence also included unique sequences that intervened among the repeated elements. See Cassens *et al.* (2005) for details.

### *Analytical methods*

Unless otherwise noted, calculations were conducted and graphs were produced using either Microsoft Excel or SPSS version 12.0.1. The program DROPOUT (McKelvey & Schwartz 2005) was used to plot the distribution of genetic differences between samples. Expected heterozygosity ($H_E$) was calculated with the program ML-RELATE (Kalinowski *et al.* 2006), which employs Nei's (1978) unbiased $H_E$ estimate. A web-based (http://wbiomed.curtin.edu.au/genepop) version of GENEPOP (Raymond & Rousset, 1995) was used to test the null hypothesis of random union of gametes (Guo & Thompson 1992; Haldane 1954) and to estimate the value of Fst (Weir & Cockerham 1984). A general excess of homozygote genotypes (in all allele size classes) indicates that null alleles may be affecting the dataset. A deficiency of heterozygote geneotypes with alleles differing by one repeat (in this case, two base pairs) is likely caused by mis-scoring due to stuttering patterns on the electropherograms. Both of these possibilities were examined for each locus using the program MICRO-CHECKER (Van Oosterhout *et al.* 2004). Loci were tested for linkage using the Fisher exact test implemented by GENEPOP (Raymond & Rousset 1995). P-values were considered significant at the $a = 0.05$ level, and, when necessary, were analyzed using the sequential Bonferroni technique to allow for multiple comparisons (Rice 1989).

Maximum likelihood values for relatedness coefficients were calculated using the program ML-RELATE (Kalinowski *et al.* 2006). This method can be biased, but also has a relatively low root mean squared error and can accommodate the presence of null alleles (Kalinowski *et al.* 2006; Milligan 2003).

Using the “Groups: pairwise relationship test” in the program PERM (Duchesne *et al.* 2006), the question of whether groups are structured by relatedness was addressed. This program sums pairwise *r* values within each observed group. The *r* values are then re-arranged 1000 times into “random” groups of the same sizes as those observed, and this process is repeated for 10 iterations. Comparing the observed sum of within-group *r* values to the distribution of created sums produces estimated p-values.

The relationship between relatedness and level of association was also examined. Association data were based on information collected by members of the Marine Mammal Research Program (Texas A&M University) and was summarized by

Markowitz (2004). The program SOCPROG (compiled version 2.3, documentation available at: http://myweb.dal.ca/~hwhitehe/social.htm) was used to calculate the simple ratio index of association (Ginsberg & Young 1992).

For the mtDNA haplotypes, the probability that any two samples, drawn at random from those sampled, would have the same haplotype was calculated using the formula $\sum_i (p_i)^2$, where $p$ is the frequency of the $i^{\text{th}}$ haplotype in the dataset (Ott & Longnecker 2001). This probability was multiplied by the number of within-group pairs to get the expected number of within-group haplotype matches for each type of group. The expected number of matches was compared to the number of matches observed in the dataset. Patterns of mtDNA variation were also examined in light of the photographic sighting record of individuals.

## Results

One of the 12 microsatellite primers, DlrFBC3, showed very little variation and was not considered further. Of the 188 samples examined, 97 samples were genotyped for at least seven of the remaining 11 loci; only these samples were considered in subsequent analyses. Size range, number of alleles, and expected heterozygosity were calculated (Table 4).

**Table 4** Summary of microsatellite alleles observed in this study.

| Locus | No. of samples | Fragment size (bp) | No. of alleles | $H_E$ |
|---|---|---|---|---|
| D14 | 72 | 119−137 | 10 | 0.77 |
| D28 | 66 | 131−165 | 16 | 0.88 |
| DlrFBC3 | 94 | 133−145 | 5 | 0.06 |
| DlrFBC11 | 87 | 99−133 | 9 | 0.81 |
| Lo105 | 85 | 232−250 | 8 | 0.80 |
| Lo514 | 96 | 231−239 | 5 | 0.64 |
| Lo6 | 86 | 145−211 | 22 | 0.92 |
| Lobs_Di7.1 | 83 | 123−153 | 14 | 0.87 |
| Lobs_Di9 | 87 | 86−114 | 12 | 0.87 |
| Lobs_Di19 | 81 | 94−124 | 15 | 0.86 |
| Lobs_Di21 | 86 | 99−119 | 11 | 0.85 |
| Lobs_Di24 | 91 | 106−132 | 12 | 0.83 |

Some individual-locus combinations were repeated in order to assess the accuracy of the genotypes. Between 24 and 38 samples were repeated for each locus. Loci varied in the level of discrepancies between the original and repeated samples (Table 5).

**Table 5** Observed genotyping error rate in a subset of individuals that were genotyped twice.

| Locus | Percent scored differently |
|---|---|
| D14 | 12.5 |
| D28 | 6.5 |
| DlrFBC3 | 6.3 |
| DlrFBC11 | 2.8 |
| Lo105 | 8.6 |
| Lo514 | 7.9 |
| Lo6 | 9.4 |
| Lobs_Di7.1 | 3.2 |
| Lobs_Di9 | 5.7 |
| Lobs_Di19 | 9.1 |
| Lobs_Di21 | 8.1 |
| Lobs_Di24 | 0.0 |

Bell-shaped relatedness patterns are expected in a large outbred population, and this pattern should be reflected in the distribution of the number of loci by which each pair differs (McKelvey & Schwartz 2005). The program DROPOUT was used to plot the number of loci by which each pair differs, but because these data were not collected in a mark-recapture framework, the interpretation of this figure does not follow the interpretations discussed by McKelvey and Schwartz (2005). These data show two patterns that would not be expected from a group of distinct individuals taken from a large outbred population: pairs that differ by very few loci and bi-modality (Figure 5).

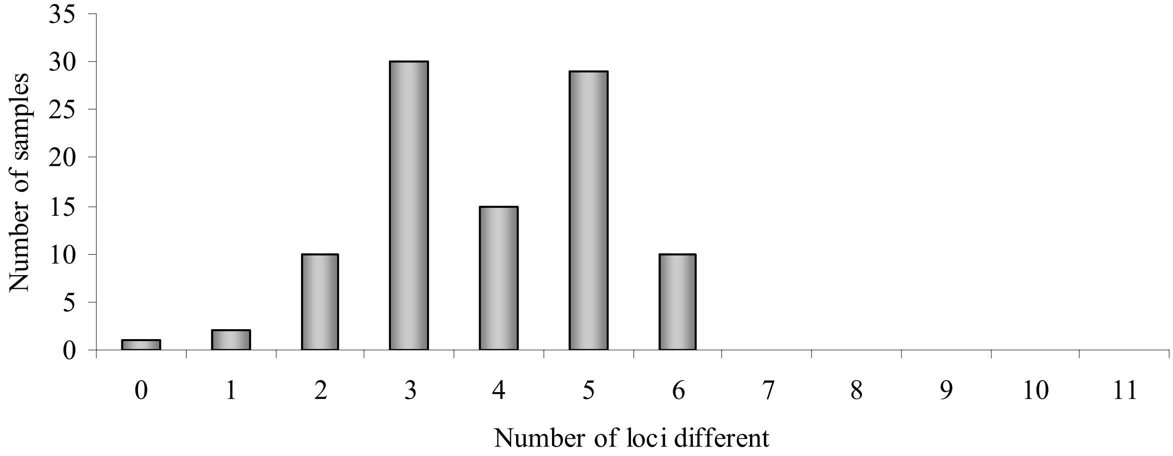

**Figure 5** Distribution of genetic difference between samples.

If lack of completeness in the dataset is causing the observed pattern, one would expect that pairs with a relatively low number of differing loci also have a relatively low number of loci scored (i.e. a high proportion of missing data).

Figure 6 shows that most of the pairs differing by a small number of loci also were scored at relatively few loci, but also indicates the presence of several problematic pairs (that differ by only a few loci in spite of relatively complete genotypes, found in the front corner of Figure 6). All information known about these pairs was examined in an effort to determine whether or not they are re-captures of an individual (Table 6).

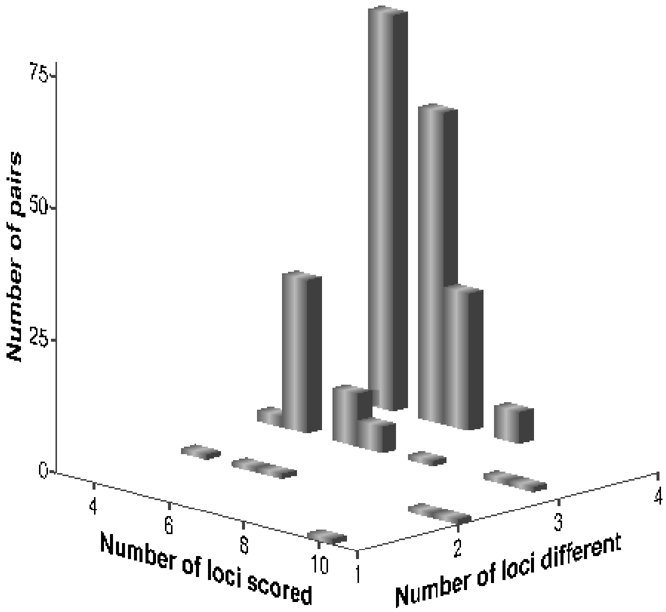

**Figure 6** Relationship between missing data and genetic difference between samples.

**Table 6** Sample pairs that may be re-captures of the same individual.

| Pair | Sample no. | Date collected | Photographic catalog no. | Sex | D-loop haplotype | Conflicting loci | Missing loci |
|---|---|---|---|---|---|---|---|
| 1 | AB0699006 | 3-Jun-99 | | M | GG | 0 | 0 |
| | AB0700026 | 8-Jul-00 | | M | | | |
| 2 | AB0701112 | 14-Jul-01 | 131a | M | M | 1 | 1 |
| | AB0701146 | 20-Jul-01 | | M | | | |
| 3 | AB0700029 | 8-Jul-00 | | M | KK | 2 | 0 |
| | AB0701124 | 15-Jul-01 | | M | | | |
| 4 | AB0700043 | 8-Jul-00 | 067a | M | H | 2 | 1 |
| | AB0700046 | 8-Jul-00 | | M | | | |

Pairs 1 and 2 were treated as re-sights of the same individual in subsequent relatedness analyses. The second member of the pair was eliminated from the dataset while assumptions were being checked. It was less clear whether the patterns observed in pairs 3 and 4 resulted from re-sights or from a combination of closely related individuals and genotyping errors. The second sample from pairs 3 and 4 was eliminated from the relatedness analyses.

Of the 93 unique individuals, 66 were sampled in Admiralty Bay and 27 were sampled in Kaikoura.[8] The Fst value for the two areas was 0.0055. Because of this, and because individuals are known to move between the two areas, samples were pooled while testing for Hardy-Weinberg proportions. After correcting for multiple comparisons, half of the loci showed deviations from Hardy-Weinberg proportions (Table 7). This result is not altogether surprising, considering that the male bias in samples from Admiralty Bay (Chapter II) indicates that these individuals are not representative of the overall breeding population in the area. However, the fact that all of the Hardy-Weinberg deviations were due to an excess of homozygotes indicates that null alleles are a potential concern. Additionally, a few loci showed evidence of mis-scoring due to stuttering (Table 7), and three of the 55 pairs of loci showed evidence (at the $\alpha$=0.05 level, corrected for multiple comparisons) of being linked.

**Table 7** Tests for Hardy-Weinberg proportions and for scoring errors due to stuttering.

| Locus | P-value | S.E. | Significant deviation from HWP? | Homozygote excess? | Mis-scoring due to stuttering? |
|---|---|---|---|---|---|
| D14 | 0.000 | 0.000 | Yes | Yes | Yes |
| D28 | 0.015 | 0.006 | No | | No |
| DlrFBC3 | 1.000 | 0.000 | No | | No |
| DlrFBC11 | 0.202 | 0.016 | No | | No |
| Lo105 | 0.000 | 0.000 | Yes | Yes | Yes |
| Lo514 | 0.005 | 0.001 | Yes | Yes | No |
| Lo6 | 0.000 | 0.000 | Yes | Yes | No |
| Lobs_Di7.1 | 0.000 | 0.000 | Yes | Yes | No |
| Lobs_Di9 | 0.001 | 0.001 | Yes | Yes | No |
| Lobs_Di19 | 0.322 | 0.031 | No | | No |
| Lobs_Di21 | 0.098 | 0.014 | No | | Yes |
| Lobs_Di24 | 0.032 | 0.008 | No | | No |

---

[8] One individual sampled in Kaikoura was also observed in Admiralty Bay.

Checking for Hardy-Weinberg proportions and linkage was repeated with a restricted dataset in an attempt to use a dataset that meets the assumptions necessary for relatedness analyses. In the restricted dataset, 4 loci (D14, Lo105, Lo514, and Lo6) were eliminated based on high error rate, low proportion of individuals scored, highly significant deviation from Hardy-Weinberg proportions, or a combination of these factors. Further, individuals who were not scored for at least 6 of the remaining 7 loci were eliminated, leaving 47 individuals from Admiralty Bay and 17 individuals from Kaikoura. The Fst for the two locations in this dataset was 0.0078, so the samples were again pooled. Two loci (Lobs_Di7.1 and Lobs_Di9) still showed deviation from Hardy-Weinberg proportions in the restricted dataset. None of the loci showed evidence for linkage. The restricted dataset was used in subsequent relatedness analyses.

Maximum-likelihood values for the relatedness coefficient were calculated for every pair in the dataset. Allele frequencies for Lobs_Di7.1 and Lobs_Di9 were adjusted to accommodate for null alleles (Kalinowski *et al.* 2006). This resulted in pairwise *r* values for 2,016 pairs, 51 of which were collected from the same group (46 feeding group pairs, three mating group pairs, one nursery group pair, one adult group pair). The *r* values ranged from 0.00 to 0.80, with a median value of 0.00. The relationship between grouping patterns and relatedness was examined with a permutation test for Admiralty Bay feeding groups. The observed intragroup sum of *r* values was 2.840. The high resulting p-value, p=0.404, indicates that the intragroup sum of *r* values in “random” groups was comparable to the observed value and that grouping is independent of relatedness.

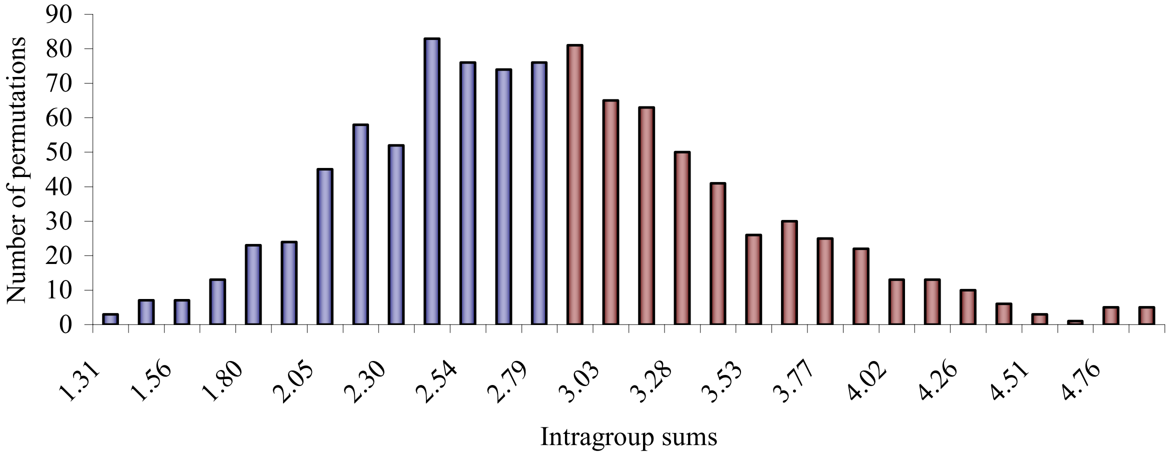

**Figure 7** Results of a pairwise-relationship permutation test. Permutations which produced intragroup sum values lower than the observed value of 2.840 are shown in blue; those which produced higher-than-observed values are shown in red.

Thirteen genotyped samples (in the restricted dataset) are also individually identified by dorsal fin photographs. A sociogram (Figure 8) shows the level of association (simple ratio index) among individuals. Individuals observed photographed in the same group were assumed to be associated, and each distinct group was considered a new "sampling period". The simple ratio index of association was plotted against the coefficient of relatedness for these samples (Figure 9), and the scatter-plot does not show an obvious relationship between the variables. The relationship between relatedness and the photographic record was further examined by plotting the distribution of r values for pairs that have been sighted together at least once separately from the distribution of pairs that have only been sighted apart (Figure 10).

The d-loop region of the mitochondrial DNA was sequenced for 197 individual dusky dolphins in Kaikoura and Admiralty Bay. Seventy-three distinct haplotypes were identified. The expected number of within-group haplotype matches was compared to the number of matches observed in the dataset (Table 8). Additionally, a sociogram of photographed individuals whose haplotypes were identified was produced (Figure 11). The distribution of association indices was plotted separately for pairs with matching and non-matching mtDNA haplotypes (Figure 12).

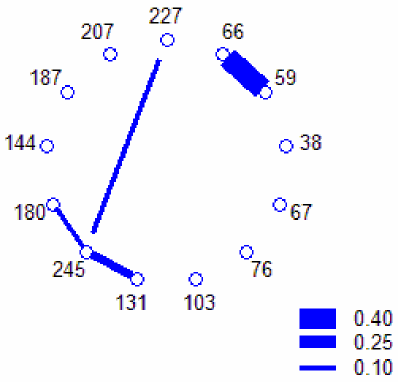

**Figure 8** Sociogram showing the strength of simple ratio association indices among microsatellite-genotyped individuals. Each individual is indicated by a number, which corresponds to the photographic catalog.

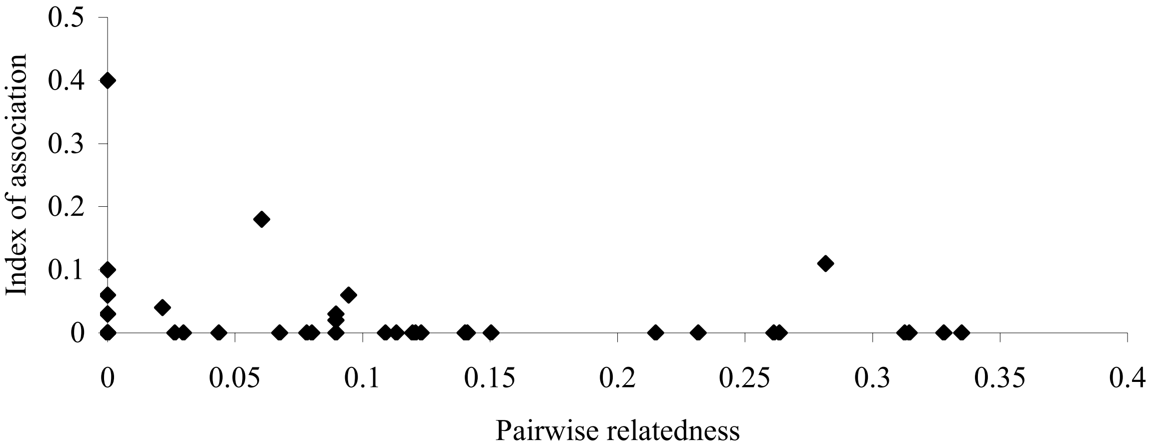

**Figure 9** Scatterplot of pairwise relatedness and association index values. The coefficients of relatedness were estimated by maximum-likelihood methods and associations were estimated by the simple ratio index.

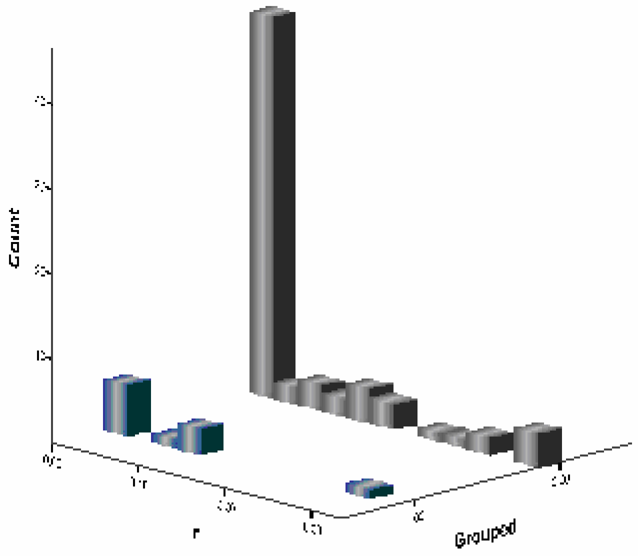

**Figure 10** Distribution of pairwise relatedness values for photographed pairs. Pairs photographed at least once together are shown in blue and those that were photographed apart but not together are shown in gray.

**Table 8** Comparison of the expected and the observed number of within-group mtDNA d-loop haplotype matches.

| Location | Group type | No. of within-group pairs | No. of expected matches | No. of observed matches |
|---|---|---|---|---|
| Kaikoura | Nursery | 4 | 0.15 | 3 |
| | Mating | 34 | 1.24 | 1 |
| | Dyad | 1 | 0.04 | 1 |
| | Adult | 4 | 0.15 | 0 |
| Admiralty Bay | Feeding | 80 | 2.92 | 4 |
| | Adult | 2 | 0.07 | 0 |

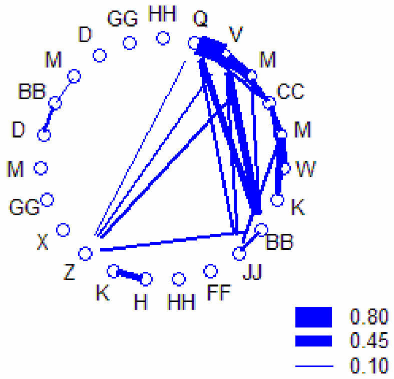

**Figure 11** Sociogram showing the strength of simple ratio association indices among individuals that were characterized by mtDNA haplotype. Letters indicate a distinct mtDNA haplotype.

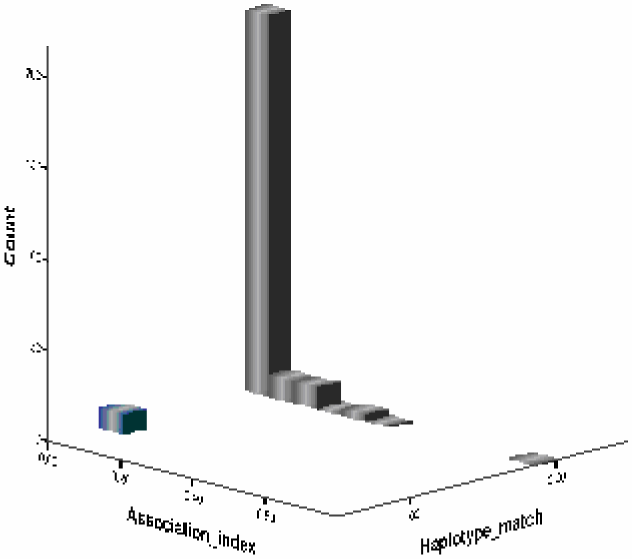

**Figure 12** Distribution of simple ratio association index values for pairs that were characterized by mtDNA d-loop haplotype. Pairs with matching mtDNA haplotypes are shown in blue and those that and those with different mtDNA haplotypes are shown in gray.

## Discussion

It is difficult to evaluate the power that these methods have to discriminate grouping patterns in relatedness. The observed error rate in genotyping (Table 5), the proportion of missing data (Table 4), and the lack of Hardy-Weinberg equilibrium at some loci (Table 7) indicate potential problems. Even for datasets produced under optimal conditions (i.e. high quantities of template DNA and large, optimized primer sets), estimating pairwise relatedness precisely and accurately from codominant markers can be problematic. For example, Toro *et al.* (2002) compared eight pairwise estimators of co-ancestry with known genealogical values (calculated from pedigrees going 20 generations back) for pigs and found that the estimators similarly underestimated the genealogical values, apparently due to lack of information about true allele frequencies in the founder population. At least ten estimators of pairwise relatedness have been published (e.g. Queller & Goodnight 1989; Wang 2002), and most estimators are known to be biased and to have low precision (Lynch & Ritland 1999). The usefulness of relatedness estimators hinges most clearly on the number and polymorphism of the loci examined and the level of precision needed to address the research question. Other factors, including the distribution of alleles in the dataset (Van de Casteele *et al.* 2001) and the presence of genotyping errors can also affect the usefulness of a particular estimator. Recently, analytical methods that are potentially more robust to violations of common assumptions have been proposed (e.g. Fernández & Toro 2006; Kalinowski *et al.* 2006), and more authors explicitly consider the effects that genenotyping errors could have on their analyses (Pompanon *et al.* 2005).

The data presented here indicate that Admiralty Bay feeding groups of dusky dolphins are not likely to be strongly structured by relatedness. Results of a permutation test (p=0.404 for the null hypothesis of no group structure in relatedness) show that relatedness is not a factor by which dusky dolphins segregate into feeding groups, and the number of within-group mtDNA haplotype matches was similar to what was expected by chance within feeding groups. Similarly, no association was found between indices of association (which integrate grouping patterns over time) and relatedness.

Additionally, limited evidence hints at relatedness structure in Kaikoura nursery groups. When comparing the expected to the observed within-group mtDNA haplotype matches (Table 8), only the Kaikoura nursery groups have notably more matches than would be expected if grouping was independent of maternal lineage. The nursery groups that showed matching haplotypes consisted of two adult-adult pairs (one pair of unknown sex and one pair with one adult male) and one adult-juvenile pair (unknown sex). The adult-adult pair of unknown sex was the only one included in the "restricted" microsatellite dataset. This pair also showed a remarkably high *r* value.

The only kin association (i.e. grouping) pattern known to occur in dusky dolphins is that of mother-calf pairs. Dusky dolphin mothers nurse their dependent young and associate closely with them for at least a year. In Kaikoura, they are known to separate into small ("nursery") groups, which often include adult non-mothers, generally found somewhat apart from the main pod (Markowitz 2004) and to preferentially use shallow-water habitats (Weir *et al*. 2005). When young dusky dolphins separate from their mothers, is that the end of kin-based social relationships? This overarching question was the motivation behind this investigation into group-level relatedness, but several more specific questions about the potential nature of kin-based social relationships are also relevant. To what extent do adult offspring and mothers interact? Do dusky dolphins have the ability to identify (directly or indirectly, *via* a familiarity heuristic) other types of relatives, such as maternal half-siblings? Is there reason and opportunity for dusky dolphins to seek out relatives as social partners? Data from this and other studies shed light on these questions and suggest possible avenues of future research.

To what extent do adult offspring and mothers interact? The answer to this question is not known for dusky dolphins. Limited evidence presented here indicates that adult nursery group members may be closely related; this pattern could be explained if adult offspring tended to associate with their mothers. In the bottlenose dolphins of Sarasota Bay, Florida and Monkey Mia, Australia, both males and females seem to exhibit natal philopatry, and thus likely encounter their mother as adults (Connor *et al.* 2000).

Do dusky dolphins have the ability to identify (directly or indirectly, *via* a familiarity heuristic) other types of relatives, such as maternal half-siblings? Again, this is a yet-unanswered question for dusky dolphins. For bottlenose dolphins, signature whistles (which are not produced by dusky dolphins) convey identity information (Janik *et al.* 2006) and are similar in mother-son pairs (Sayigh *et al.* 1995); thus, whistles could be a mechanism that facilitates kin discrimination. Bottlenose dolphin populations in which males form alliances along kinship lines (e.g. Krützen *et al.* 2003) are clearly able to discriminate kin by some mechanism. In Sarasota Bay, there is anecdotal evidence that adults could recognize maternal half-siblings by associating with their mother at opportune times (i.e. just after the birth of a new half-sibling) (Wells 1991a).

Is there reason and opportunity for dusky dolphins to seek out relatives as social partners? Dusky dolphins live in extensive societies compared to some better-studied dolphins, and it is not known whether individuals encounter relatives frequently enough to benefit from grouping preferentially with them. Situations in which individuals cooperate for non-divisible rewards (such as conceptions), situations in which successful cooperation requires low levels of "cheating", and situations in which individuals can help relatives at little individual cost could provide reasons to partner preferentially with relatives. We are only beginning to discover how the various aspects of dusky dolphin life—such as herding fish, avoiding predators, competing for mates, and raising young—fit into this framework and affect social patterning.

# CHAPTER IV

# CONCLUSION

Group membership is an ephemeral property in “fission-fusion” societies, such as that of the dusky dolphin. It is both a result of and an influence on natural selection. Therefore, characterizing group membership—at any moment and though time—and understanding the evolution of grouping patterns are challenging tasks. This study contributes some information relative to the types of individuals that characterize dusky dolphin groups that is needed to meet this challenge.

Both sex and relatedness are known to be important categories that can affect grouping patterns and social relationships. The data presented here indicate that dusky dolphins in Admiralty Bay may group preferentially with same-sex individuals while herding and feeding on small schooling fishes. The data also strongly support a larger-scale separation of the sexes, as the majority of animals identified in Admiralty Bay in the winter were male. The sociobiological perspective suggests important avenues for future investigations into the reasons for this pattern. Sex differences in reproductive strategies and behavioral repertoires likely influence the fitness implications of sexual segregation.

For the most part, these data indicate that groups are not strongly structured by relatedness of group members. An exception is Kaikoura small nursery groups, for which limited evidence indicates that adult group members could be closely related. These patterns leave many questions open to future investigation. Do fish-herding group members behave altruistically and if so, how is that behavior maintained? How and from whom do individuals learn to use Admiralty Bay? Do adult non-mothers provide help in caring for offspring within nursery groups and is kin selection important in maintaining the grouping pattern? Does the evolution of reproductive output, group size, and dispersal patterns limit the possibility for kin relationships to develop within dusky dolphin societies? As these and related questions are addressed, knowledge of dusky dolphin social life will provide an important example of how and why gregarious marine animal societies evolve.

# REFERENCES

Acevedo-Gutiérrez A, Parker N (2000) Surface behavior of bottlenose dolphins is related to spatial arrangement of prey. *Marine Mammal Science*, **16**, 287−289.

Alcock J (2001a) *Animal Behavior: An Evolutionary Approach, Seventh Edition*. Sinauer Associates, Inc., Sunderland, Massachusetts.

Alcock J (2001b) *The Triumph of Sociobiology*. Oxford University Press, Oxford.

Amos W, Schlotterer C, Tautz D (1993) Social structure of pilot whales revealed by analytical DNA profiling. *Science*, **260**, 670−672.

Anderson DJ, Porter ET, Ferree ED (2004) Non-breeding Nazca boobies (*Sula granti*) show social and sexual interest in chicks: behavioral and ecological aspects. *Behaviour*, **141**, 959−977.

Armitage KB, Schwartz OA (2000) Social enhancement of fitness in yellow-bellied marmots. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 12149−12152.

Avilés L, Fletcher JA, Cutter AD (2004) The kin composition of social groups: trading group size for degree of altruism. *The American Naturalist*, **164**, 132−144.

Baird RW (2000) The killer whale: foraging specializations and group hunting. In: *Cetacean Societies: Field Studies of Dolphins and Whales* (eds. Mann J, Connor RC, Tyack PL, Whitehead H), pp. 127−153. University of Chicago Press, Chicago, Illinois.

Baird RW, Dill LM (1995) Occurrence and behavior of transient killer whales—seasonal and pod-specific variability, foraging behavior, and prey handling. *Canadian Journal of Zoology*, **73**, 1300−1311.

Baird RW, McSweeney DJ, Bane C, Barlow J, Salden DR, *et al.* (2006) Killer whales in Hawaiian waters: information on population identity and feeding habits. *Pacific Science*, **60**, 523−530.

Baker CS, Cipriano F, Palumbi SR (1996) Molecular genetic identification of whale and dolphin products from commercial markets in Korea and Japan. *Molecular Ecology*, **5**, 671−685.

Banks JD, Levine KF, Syvanen M, Theis J, Gilson A (1995) DNA tissue gender typing. In: *Standard Operating Procedure of the Wildlife Forensic Laboratory of the California Department of Fish and Game*. Sacramento, California.

Banks SC, Ward SJ, Lindenmayer DB, Finlayson GR, Lawson SJ, *et al.* (2005) The effects of habitat fragmentation on the social kin structure and mating system of the agile antechinus, *Antechinus agilis*. *Molecular Ecology*, **14**, 1789−1801.

Barr K, Slooten E (1998) Effects of tourism on dusky dolphins at Kaikoura. *Proceedings of the International Whaling Commission*, SC/50/WW10, 1−30.

Barber I, Downey LC, Braithwaite VA (1998) Parasitism, oddity and the mechanism of shoal choice. *Journal of Fish Biology*, **53**, 1365−1368.

Beebee T, Rowe G (2004) *An Introduction to Molecular Ecology*. Oxford University Press, Oxford.

Benoit-Bird KJ, Au WWL (2003) Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. *Behavioral Ecology and Sociobiology*, **53**, 364−373.

Benoit-Bird KJ, Würsig B, McFadden CJ (2004) Dusky dolphin (*Lagenorhynchus obscurus*) foraging in two different habitats: active acoustic detection of dolphins and their prey. *Marine Mammal Science*, **20**, 215−231.

Bigg M, Olesiuk P, Ellis G, Ford J, Balcomb K (1990) Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. In: *Individual Recognition of Cetaceans: Use of Photo-identificaiton and Other Techniques to Estimate Population Parameters, Special Issue 12* (eds. Hammond P, Mizroch S, Conovan G), pp. 383−405. International Whaling Commission, Cambridge, Massachusetts.

Birkhead TR, Møller AP (1992) *Sperm Competition and Sexual Selection*. Academic Press, San Diego, California.

Blouin MS (2003) DNA-based methods for pedigree reconstruction and kinship analysis in natural populations. *Trends in Ecology & Evolution*, **18**, 503−511.

Boesch C, Boesch H (1989) Hunting behaviour of wild chimpanzees in the Taï National Park. *American Journal of Physical Anthropology*, **78**, 547–573.

Boinski S (2000) Social manipulation within and between troops mediates primate group movement. In: *On the Move: How and Why Animals Travel in Groups* (eds. Boinski S, Garber PA), pp. 421−469. University of Chicago Press, Chicago, Illinois.

Bon R, Campan R (1996) Unexplained sexual segregation in polygamous ungulates: a defense of an ontogenetic approach. *Behavioural Processes*, **38**, 131–154.

Bon R, Rideau C, Villaret JC, Joachim J (2001) Segregation is not only a matter of sex in Alpine ibex, *Capra ibex ibex*. *Animal Behaviour*, **62**, 495−504.

Bowles S, Posel D (2005) Genetic relatedness predicts South African migrant workers' remittances to their families. *Nature*, **434**, 380−383.

Boyd P, LaRoche J, Gall M, Frew R, McKay RML (1999) Role of iron, light, and silicate in controlling algal biomass in subantarctic waters SE of New Zealand. *Journal of Geophysical Research-Oceans*, **104**, 13395−13408.

Boyd R, Richardson PJ (1992) Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology*, **13**, 171−195.

Brown GE, Brown JA (1996) Does kin-biased territorial behavior increase kin-biased foraging in juvenile salmonids? *Behavioral Ecology*, **7**, 24−29.

Bshary R, Wickler W, Fricke H (2002) Fish cognition: a primate's eye view. *Animal Cognition*, **5**, 1−13.

Buchanan FC, Friesen MK, Littlejohn RP, Clayton JW (1996) Microsatellites from the beluga whale *Delphinapterus leucas*. *Molecular Ecology*, **5**, 571−575.

Bukacinski D, Bukacinska M, Lubjuhn T (2000) Adoption of chicks and the level of relatedness in common gull, *Larus canus*, colonies: DNA fingerprinting analyses. *Animal Behaviour*, **59**, 289−299.

Cassens I, Van Waerebeek K, Best PB, Crespo EA, Reyes J, *et al.* (2003) The phylogeography of dusky dolphins (*Lagenorhynchus obscurus*): a critical examination of network methods and rooting procedures. *Molecular Ecology* **12**, 1781−1792.

Cassens I, Van Waerebeek K, Best PB, Tzika A, Van Helden AL, *et al.* (2005) Evidence for male dispersal along the coasts but no migration in pelagic waters in dusky dolphins (*Lagenorhynchus obscurus*). *Molecular Ecology*, **14**, 107−121.

Cipriano F (1992) *Behavior and occurrence patterns, feeding ecology, and life history of dusky dolphins* (Lagenorhynchus obscurus) *off Kaikoura, New Zealand*, PhD Thesis, University of Arizona, Tucson, Arizona.

Cipriano F, Würsig B, Würsig M (1989) Diurnal variation in dive-times and movements of dusky dolphins feeding on deep scattering layer-associated prey. *American Society of Zoologists*, **29**, A68.

Claridge DE (2005) Age-class segregation of Blainville's beaked whale (*Mesoplodon densirostris*) groups in the Bahamas. *In: Abstracts of the 16th Biennial Conference on the Biology of Marine Mammals,* 12−16 December 2005, San Diego, California. Society for Marine Mammalogy, pp. 59−60.

Clarke GW (1970) Light conditions in the sea in relation to the diurnal vertical migrations of animals. In: *Proceedings of an International Symposium on Biological Sound Scattering in the Ocean* (ed. Farquar GB), pp. 41−50. Department of the Navy, Washington, D.C.

Clutton-Brock T (2002) Behavioral ecology—breeding together: kin selection and mutualism in cooperative vertebrates. *Science*, **296**, 69−72.

Clutton-Brock TH, Brotherton PNM, O'Riain MJ, Griffin AS, Gaynor D, *et al.* (2000) Individual contributions to babysitting in a cooperative mongoose, *Suricata suricatta*. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **267**, 301−305.

Connor R (1996) "Pop" goes the dolphin: a vocalization male bottlenose dolphins produce during consortships. *Behaviour*, **133**, 643−662.

Connor R, Heithaus MR, Barre LM (1999) Super-alliance of bottlenose dolphins. *Nature*, **397**, 571−572.

Connor R, Mann J, Watson-Capps J (2006) A sex-specific affiliative contact behavior in Indian Ocean bottlenose dolphins, *Tursiops* sp. *Ethology*, **112**, 631−638.

Connor R, Smolker R, Richards A (1992a) Dolphin alliances and coalitions. In: *Coalitions and Alliances in Humans and Other Animals* (eds. Harcourt AH, de Waal FBM), pp. 415−443. Oxford University Press, Oxford.

Connor R, Wells RS, Mann J, Read AJ (2000) The bottlenose dolphin: social relationships in a fission-fusion society. In: *Cetacean Societies: Field Studies of Dolphins and Whales* (eds. Mann J, Connor RC, Tyack PL, Whitehead H), pp. 91−126. University of Chicago Press, Chicago, Illinois.

Connor RC (1986) Pseudo-reciprocity: investing in mutualism. *Animal Behaviour*, **34**, 1562−1584.

Connor RC (2000) Group living in whales and dolphins. In: *Cetacean Societies: Field Studies of Dolphins and Whales* (eds. Mann J, Connor RC, Tyack PL, Whitehead H), pp. 199−218. University of Chicago Press, Chicago, Illinois.

Connor RC, Smolker RA, Richards AF (1992b) 2 levels of alliance formation among male bottle-nosed dolphins (*Tursiops* sp). *Proceedings of the National Academy of Sciences of the United States of America*, **89**, 987−990.

Conradt L (1998) Measuring the degree of sexual segregation in group-living animals. *Journal of Animal Ecology*, **67**, 217−226.

Conradt L (1999) Social segregation is not a consequence of habitat segregation in red deer and feral soay sheep. *Animal Behaviour*, **57**, 1151−1157.

Conradt L, Clutton-Brock TH, Guinness FE (2000) Sex differences in weather sensitivity can cause habitat segregation: red deer as an example. *Animal Behaviour*, **59**, 1049–1060.

Conradt L, Roper TJ (2000) Activity synchrony and social cohesion: a fission-fusion model. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **267**, 2213−2218.

Creel S, Creel NM (1995) Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour*, **50**, 1325−1339.

Croft DP, Morrell LJ, Wade AS, Piyapong C, Ioannou CC, *et al.* (2006) Predation risk as a driving force for sexual segregation: a cross-population comparison. *American Naturalist*, **167**, 867−878.

Darwin C (1981) *The Descent of Man, and Selection in Relation to Sex*. Princeton University Press, Princeton, New Jersey. (Originally published in 1871, Appleton, New York.)

Darwin C (1999) *The Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life*. Bantam Books, New York. (Originally published in 1859, Murray, London.)

Dawkins R (1976) *The Selfish Gene*. Oxford University Press, Oxford.

Dawkins R (1979) Twelve misunderstandings of kin selection. *Z Tirpsychol*, **51**, 184−200.

Dawkins R (1982) *The Extended Phenotype*. Oxford University Press, Oxford.

Defran RH, Weller DW (1999) Occurrence, distribution, site fidelity, and school size of bottlenose dolphins (*Tursiops truncatus*) off San Diego, California. *Marine Mammal Science*, **15**, 366−380.

Defran RH, Weller DW, Kelly DL, Espinosa MA (1999) Range characteristics of Pacific coast bottlenose dolphins (*Tursiops truncatus*) in the Southern California Bight. *Marine Mammal Science*, **15**, 381−393.

DeYoung RW, Honeycutt RL (2005) The molecular toolbox: genetic techniques in wildlife ecology and management. *Journal of Wildlife Management*, **69**, 1362−1384.

Duchesne P, Étienne C, Bernatchez L (2006) PERM: a computer program to detect structuring factors in social units. *Molecular Ecology Notes*, doi: 10.1111/j.1471-8286.2006.01414.x.

Duffield DA, Wells RS (1991) The combined application of chromosome protein and molecular data for the investigation of social unit structure and dynamics in *Tursiops truncatus*. In: *Genetic Ecology of Whales and Dolphins: Incorporating the Proceedings of the Workshop on the Genetic Analysis of Cetacean Populations, Special Issue 13* (ed. Hoelzel AR), pp. 155−170. International Whaling Commission, Cambridge, Massachusetts.

Dugatkin LA (2000) *The Imitation Factor: Evolution Beyond the Gene*. The Free Press, New York.

Emlen ST, Wrege PH (1988) The role of kinship in helping decisions among white-fronted bee-eaters. *Behavioral Ecology and Sociobiology*, **23**, 305−315.

Encarnacao JA, Kierdorf U, Holweg D, Jasnoch U, Wolters V (2005) Sex-related differences in roost-site selection by Daubenton's bats, *Myotis daubentonii*, during the nursery period. *Mammal Review*, **35**, 285−294.

Fernández J, Toro MA (2006) A new method to estimate relatedness from molecular markers. *Molecular Ecology*, **15**, 1657−1667.

Fisher RA (1930) *The Genetical Theory of Natural Selection*. Claredon Press, Oxford.

Fragaszy DM, Perry S (2003) Towards a biology of traditions. In: *The Biology of Traditions: Models and Evidence* (eds. Fragaszy DM, Perry S), pp. 1−32. Cambridge University Press, Cambridge.

Frank SA (1995) Mutual policing and the repression of competition in the evolution of cooperative groups. *Nature*, **377**, 520−522.

Gaskin DE (1968) Distribution of Delphinidae (Cetacea) in relation to sea surface termperatures off eastern and southern New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **2**, 527–534.

Gibson RM, Pires D, Delaney KS, Wayne RK (2005) Microsatellite DNA analysis shows that greater sage grouse leks are not kin groups. *Molecular Ecology*, **14**, 4453−4459.

Ginsberg JR, Young TP (1992) Measuring association between individuals or groups in behavioural studies. *Animal Behaviour*, **44**, 377−379.

Gonzalez-Solis J, Croxall JP, Wood AG (2000) Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation. *Oikos*, **90**, 390−398.

Goodall J (1990) *Through a Window: My 30 Years with the Chimpanzees of Gombe*. Houghton Mifflin Company, Boston, Massachusettes.

Goodnight (2005) Multilevel selection: the evolution of cooperation in non-kin groups. *Population Ecology*, **47**, 3−12

Grant BR, Grant PR (1996) Cultural inheritance of song and its role in the evolution of Darwin's finches. *Evolution*, **50**, 2471−2487.

Griesser M (2003) Nepotistic vigilance behavior in Siberian jay parents. *Behavioral Ecology*, **14**, 246−250.

Griesser M, Ekman A (2004) Nepotistic alarm calling in the Siberian jay, *Perisoreus infaustus*. *Animal Behaviour*, **67**, 933−939.

Griesser M, Ekman J (2005) Nepotistic mobbing behaviour in the Siberian jay, *Perisoreus infaustus*. *Animal Behaviour*, **69**, 345−352.

Griffin AS, West SA (2002) Kin selection: fact and fiction. *Trends in Ecology & Evolution*, **17**, 15−21.

Griffiths SW, Armstrong JD, Metcalfe NB (2003) The cost of aggregation: juvenile salmon avoid sharing winter refuges with siblings. *Behavioral Ecology*, **14**, 602−606.

Guo SW, Thompson EA (1992) Performing the exact test of Hardy-Weinberg proportion for multiple alleles. *Biometrics*, **48**, 361−372.

Gurnell J, Wauters LA, Preatoni D, Tosi G (2001) Spacing behaviour, kinship, and population dynamics of grey squirrels in a newly colonized broadleaf woodland in Italy. *Canadian Journal of Zoology*, **79**, 1533−1543.

Haldane JBS (1954) An exact test for randomness of mating. *Journal of Genetics*, **52**, 631−635.

Halpin ZT (1991) Kin recognition cues of vertebrates. In: *Kin Recognition* (ed. Hepper PG), pp. 220−258. Cambridge University Press, Cambridge.

Hamilton WD (1963) The evolution of altruistic behavior. *The American Naturalist*, **97**, 354−356.

Hamilton WD (1964a) The genetical evolution of social behavior I. *Journal of Theoretical Biology*, **7**, 1−16.

Hamilton WD (1964b) The genetical evolution of social behavior II. *Journal of Theoretical Biology*, **7**, 17−52.

Hamilton WD (1970) Selfish and spiteful behaviour in an evolutionary model. *Nature*, **228**, 1218−1220.

Harcourt AH (1992) Coalitions and alliances: are primates more complex than non-primates. In: *Coalitions and Alliances in Humans and Other Animals* (eds. Harcourt AH, de Waal FBM), pp. 445−471. Oxford University Press, Oxford.

Harcourt AH, de Waal FBM (1992) *Coalitions and Alliances in Humans and Other Animals*. Oxford University Press, Oxford.

Hardin G (1968) Tragedy of commons. *Science*, **162**, 1243−1248.

Harlin AD (2004) *Molecular systematics and phylogeography of* Lagenorhynchus obscurus *derived from nuclear and mitochondrial loci*, PhD Thesis, Texas A&M University.

Harlin AD, Markowitz T, Baker CS, Würsig B, Honeycutt RL (2003) Genetic structure, diversity, and historical demography of New Zealand's dusky dolphin (*Lagenorhynchus obscurus*). *Journal of Mammalogy*, **84**, 702−717.

Harlin AD, Würsig B, Baker CS, Markowitz TM (1999) Skin swabbing for genetic analysis: application to dusky dolphins (*Lagenorhynchus obscurus*). *Marine Mammal Science*, **15**, 409−425.

Helfman GS, Schultz ET (1984) Social transmission of behavioural traditions in a coral reef fish. *Animal Behaviour*, **32**, 379–384.

Hepper PG (1989) Recognizing kin = recognizing genetic similarity. *Behavioral and Brain Sciences*, **12**, 530−530.

Hiatt RW, Brock VE (1948) On the herding of prey and the schooling of the black skipjack, *Euthynnus yaito* Kishinouye. *Pacific Science*, **2**, 297–298.

Hobson ES (1968) Predatory behavior of some shore fishes in the Gulf of California. *U.S. Fish and Wildlife Service Research Report*, **73**, 1–92.

Hoelzel AR (1993) Foraging behavior and social group dynamics in Puget Sound killer whales. *Animal Behaviour*, **45**, 581−591.

Hughes C (1998) Integrating molecular techniques with field methods in studies of social behavior: a revolution results. *Ecology*, **79**, 383−399.

Janik VM, Sayigh LS, Wells RS (2006) Signature whistle shape conveys identity information to bottlenose dolphins. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 8293−8297.

Jefferson T, Leatherwood S, Webber M (1994) Species identification sheet: *Lagenorhynchus obscurus*. In: *FAO Species Identification Guide. Marine Mammals of the World* (eds. Carpenter K, Sommer C, Bogusch A, Agnalt A-L), pp. 142−143. FAO, Rome.

Jurasz CM, Jurasz VP (1979) Feeding modes of the humpback whale, *Megaptera novaeangliae*, in the southeast Alaska. *Scientific Report of the Whales Research Institute of Tokyo*, **31**, 69−83.

Kalinowski ST, Wagner AP, Taper ML (2006) ML-RELATE: a computer program for maximum likelihood estimation of relatedness and relationship. *Molecular Ecology Notes*, **6**, 576−579.

Kaminski G, Brandt S, Baubet E, Baudoin C (2005) Life-history patterns in female wild boars (*Sus scrofa*): mother-daughter postweaning associations. *Canadian Journal of Zoology*, **83**, 474−480.

Karczmarski L, Würsig B, Gailey G, Larson KW, Vanderlip C (2005) Spinner dolphins in a remote Hawaiian atoll: social grouping and population structure. *Behavioral Ecology*, **16**, 675−685.

Katona SK, Kraus S (1999) Efforts to conserve the North Atlantic right whale. In: *Conservation and Management of Marine Mammals* (eds. Twiss JR, Reeves RR), pp. 311–331. Smithsonian Institution Press, Washington, D.C.

Kerth G, Mayer F, Konig B (2000) Mitochondrial DNA (mtDNA) reveals that female Bechstein's bats live in closed societies. *Molecular Ecology*, **9**, 793−800.

Kolm N, Hoffman EA, Olsson J, Berglund A, AG Jones (2005) Group stability and homing behavior but no kin group structures in a coral reef fish. *Behavioral Ecology*, **16**, 521−527.

Komdeur J (1994) The effect of kinship on helping in the cooperative breeding Seychelles warbler (*Acrocephalus sechellensis*). *Proceedings of the Royal Society of London Series B-Biological Sciences*, **256**, 47−52.

Krause J, Ruxton GD (2002) *Living in Groups*. Oxford University Press, Oxford.

Krützen M, Mann J, Heithaus MR, Connor RC, Bejder L, *et al.* (2005) Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 8939−8943.

Krützen M, Sherwin WB, Connor RC, *et al.* (2003) Contrasting relatedness patterns in bottlenose dolphins (*Tursiops* sp.) with different alliance strategies. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 497−502.

Kuker KJ, Thomson JA, Tscherter U (2005) Novel surface feeding tactics of minke whales, *Balaenoptera acutorostrata*, in the Saguenay-St.Lawrence National Marine Park. *The Canadian Field Naturalist*, **119**, 214−218.

Laidre KL, Heide-Jorgensen MP, Dietz R, Hobbs RC, Jorgensen OA (2003) Deep-diving by narwhals *Monodon monoceros*: differences in foraging behavior between wintering areas? *Marine Ecology-Progress Series*, **261**, 269−281.

Laland KN, Williams K (1998) Social transmission of maladaptive information in the guppy. *Behavioral Ecology*, **9**, 493−499.

Leatherwood S, Reeves RR (1983) *The Sierra Club Handbook of Whales and Dolphins*. Sierra Club Books, San Francisco, California.

Legault F, Strayer FF (1991) Genesis of gender based segregation and behavioral-differences among preschool-children. *Behaviour*, **119**, 285–301.

Lewis KB, Barnes PL (1999) Kaikoura Canyon, New Zealand: active conduit from near-shore sediment zones to trench-axis channel. *Marine Geology*, **162**, 39−69.

Lukas D, Reynolds V, Boesch C, Vigilant L (2005) To what extent does living in a group mean living with kin? *Molecular Ecology*, **14**, 2181−2196.

Lusseau D, Schneider K, Boisseau OJ, Haase P, Slooten E, *et al.* (2003) The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations—can geographic isolation explain this unique trait? *Behavioral Ecology and Sociobiology*, **54**, 396−405.

Lynch M, Ritland K (1999) Estimation of pairwise relatedness with molecular markers. *Genetics*, **152**, 1753−1766.

Lyrholm T, Gyllensten U (1998) Global matrilineal population structure in sperm whales as indicated by mitochondrial DNA sequences. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **265**, 1679−1684.

MacFarlane AM, Coulson G (2005) Synchrony and timing of breeding influences sexual segregation in western grey and red kangaroos (*Macropus fuliginosus* and *Macropus rufus*). *Journal of Zoology*, **267**, 419−429.

Main MB, Weckerly FW, Bleich VC (1996) Sexual segregation in ungulates: new directions for research. *Journal of Mammalogy*, **77**, 449−461.

Manly FJ (1997) *Randomization, Bootstrap, and Monte Carlo Methods in Biology, Second Edition*. Chapman & Hall, London.

Mann, J (2002) Parental behavior. In: *Encyclopedia of Marine Mammals* (eds. Perrin WF, Würsig B, Thewissen JGM), pp. 876−882. Academic Press, San Diego, California.

Mann J, Smuts BB (1998) Natal attraction: allomaternal care and mother-infant separations in wild bottlenose dolphins. *Animal Behaviour*, **55**, 1097−1113.

Markowitz T (2004) *Social organization of the New Zealand dusky dolphin*, PhD Thesis, Texas A&M University.

Markowitz T, Würsig B (2004) Distribution, abundance, and group structure of dusky dolphins inhabiting Admiralty Bay New Zealand during winter 2004, with comparisons to previous years. *A Report to the Marlborough District Council and the New Zealand Department of Conservation.*

Markowitz TM, Harlin AD, Würsig B, McFadden CJ (2004) Dusky dolphin foraging habitat: overlap with aquaculture in New Zealand. *Aquatic Conservation-Marine and Freshwater Ecosystems*, **14**, 133−149.

Marsh H, Kasuya T (1984) Changes in the ovaries of the short-finned pilot whale, *Globicephala macrorhynchus*, with age and reproductive activity. In: *Reproduction in Whales, Dolphins, and Porpoises: Proceedings of the Conference, Cetacean Reproduction, Estimating Parameters for Stock Assessment and Management, Special Issue 6* (eds. Perrin WF, Brownell Jr. RL, deMaster DP), pp. 311−335. International Whaling Commission, Cambridge, Massachusetts.

Martin AR, da Silva VME (2004) River dolphins and flooded forest: seasonal habitat use and sexual segregation of botos (*Inia geoffrensis*) in an extreme cetacean environment. *Journal of Zoology*, **263**, 295−305.

Mateo JM (2003) Kin recognition in ground squirrels and other rodents. *Journal of Mammalogy*, **84**, 1163−1181.

Maynard Smith J (1982) *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.

Maynard Smith J, Price GR (1973) The logic of animal conflict. *Nature*, **246**, 15−18.

McFadden CJ (2003) *Behavioral flexibility of feeding dusky dolphins* (Lagenorhynchus obscurus) *in Admiralty Bay, New Zealand*, MS Thesis, Texas A&M University.

McKelvey KS, Schwartz MK (2005) DROPOUT: a program to identify problem loci and samples for noninvasive genetic samples in a capture-mark-recapture framework. *Molecular Ecology Notes*, **5**, 716−718.

McKinnon L, Gilchrist HG, Scribner KT (2006) Genetic evidence for kin-based female social structure in common eiders (*Somateria mollissima*). *Behavioral Ecology*, **17**, 614−621.

Michod RE (1999) *Darwinian Dynamics*. Princeton University Press, Princeton, New Jersey.

Milligan BG (2003) Maximum-likelihood estimation of relatedness. *Genetics*, **163**, 1153−1167.

Möller LM, Beheregaray LB, Harcourt RG, Krützen M (2001) Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Proceedings of the Royal Society B-Biological Sciences*, **268**, 1941−1947.

Mougeot F, Piertney SB, Leckie F, Evans S, Moss R, *et al.* (2005) Experimentally increased aggressiveness reduces population kin structure and subsequent recruitment in red grouse *Lagopus lagopus scoticus*. *Journal of Animal Ecology*, **74**, 488−497.

Nei M (1978) Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics*, **89**, 583−590.

Norris KS (1994) Comparative view of cetacean social ecology, culture, and evolution. In: *The Hawaiian Spinner Dolphin* (eds. Norris KS, Würsig B, Wells RS, Würsig M), pp. 301−344. University of California Press, Berkeley, California.

Norris KS, Dohl TP (1980) Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. *Fishery Bulletin*, **77**, 821−849.

Norris KS, Würsig B, Wells RS, Würsig M (1994) *The Hawaiian spinner dolphin*. University of California Press, Berkeley, California.

Nowak MA (1990) An evolutionarily stable strategy may be inaccessible. *Journal of Theoretical Biology*, **142**, 237−241.

O'Connor D, Shine R (2003) Lizards in 'nuclear families': a novel reptilian social system in *Egernia saxatilis* (Scincidae). *Molecular Ecology*, **12**, 743−752.

Östman JSO (1994) *Social organization and social behavior of Hawai'ian spinner dolphins* (Stenella longirostris), PhD Thesis, University of California, Santa Cruz.

Ott RL, Longnecker M (2001) *An Introduction to Statistical Methods and Data Analysis, Fifth Edition*. Duxbury, Pacific Grove, California.

Pandolfi SS, Van Schaik CP, Pusey AE (2003) Sex differences in termite fishing among Gombe chimpanzees. In: *Animal Social Complexity* (eds. de Waal FBM, Tyack PL), pp. 414−418. Harvard University Press, Cambridge, Massachusetts.

Parrish JK (1999) Using behavior and ecology to exploit schooling fishes. *Environmental Biology of Fishes*, **55**, 157−181.

Parsons KM, Durban JW, Claridge DE, Balcomb KC, Noble LR, *et al.* (2003) Kinship as a basis for alliance formation between male bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. *Animal Behaviour*, **66**, 185−194.

Perrin WF, Mesnick SL (2003) Sexual ecology of the spinner dolphin, *Stenella longirostris*: geographic variation in mating system. *Marine Mammal Science*, **19**, 462−483.

Pompanon F, Bonin A, Bellemain E, Taberlet P (2005) Genotyping errors: causes, consequences and solutions. *Nature Reviews Genetics*, **6**, 847−859.

Pryor, K (2001) Cultural transmission of behavior in animals: how a modern training technology uses spontaneous social imitation in cetaceans and facilitates social imitation in horses and dogs. *Behavioral and Brain Sciences*, **24**, 352.

Pryor K, Shallenberger IK (1991) Social structure in spotted dolphins (*Stenella attenuata*) in the tuna purse seine fishery in the Eastern Tropical Pacific. In: *Dolphin Societies: Discoveries and Puzzles* (eds. Pryor K, Norris KS), pp. 161−196. University of California Press, Berkeley, California.

Queller DC (1985) Kinship, reciprocity and synergism in the evolution of social-behavior. *Nature*, **318**, 366−367.

Queller DC, Goodnight KF (1989) Estimating relatedness using genetic-markers. *Evolution*, **43**, 258−275.

Queller DC, Ponte E, Bozzaro S, Strassmann JE (2003) Single-gene greenbeard effects in the social amoeba *Dictyostelium discoideum*. *Science*, **299**, 105−106.

Queller DC, Strassmann JE, Hughes CR (1993) Microsatellites and kinship. *Trends in Ecology & Evolution*, **8**, 285−288.

Ranta E, Rita H, Lindstrom K (1993) Competition versus cooperation—Success of individuals foraging alone and in groups. *American Naturalist*, **142**, 42−58.

Raymond M, Rousset F (1995) GENEPOP (version 1.2) —Population-genetics software for exact tests and ecumenicism. *Journal of Heredity*, **86**, 248−249.

Rendell L, Whitehead H (2001) Culture in whales and dolphins. *Behavioral and Brain Sciences*, **24**, 309−382.

Renfree MB, Shaw G (2000) Diapause. *Annual Review of Physiology*, **62**, 353−375.

Rice WR (1989) Analyzing tables of statistical tests. *Evolution*, **43**, 223−225.

Rosel PE (2003) PCR-based sex determination in Odontocete cetaceans. *Conservation Genetics*, **4**, 647−649.

Ruckstuhl KE (1998) Foraging behaviour and sexual segregation in bighorn sheep. *Animal Behaviour*, **56**, 99−106.

Russell ST, Kelley JL, Graves JA, Magurran AE (2004) Kin structure and shoal composition dynamics in the guppy, *Poecilia reticulata*. *Oikos*, **106**, 520−526.

Sayigh LS, Tyack PL, Wells RS, Scott MD, Irvine AB (1995) Sex difference in signature whistle production of free-ranging bottle-nosed dolphins, *Tursiops truncatus*. *Behavioral Ecology and Sociobiology*, **36**, 171−177.

Schaller GB (1972) *The Serengeti Lion*. University of Chicago Press, Chicago, Illinois.

Schlupp I, Marler C, Ryan M (1994) Males benefit by mating with heterospecific females. *Science*, **263**, 373−374.

Schmitt RJ, Strand SW (1982) Cooperative foraging by yellow-tail, *Seriola lalandei* (Carangidae), on 2 species of fish prey. *Copeia*, **3**, 715−717.

Shane SH, Wells RS, Würsig B (1986) Ecology, behavior and social-organization of the bottle-nosed-dolphin—a review. *Marine Mammal Science*, **2**, 34−63.

Sharp SP, McGowan A, Wood MJ, Hatchwell BJ (2005) Learned kin recognition cues in a social bird. *Nature*, **434**, 1127−1130.

Shinohara M, DomingoRoura X, Takenaka O (1997) Microsatellites in the bottlenose dolphin, *Tursiops truncatus*. *Molecular Ecology*, **6**, 695−696.

Silk JB (1999) Why are infants so attractive to others? The form and function of infant handling in bonnet macaques. *Animal Behaviour*, **57**, 1021−1032.

Silk JB (2006) Practicing Hamilton's rule: kin selection in primate groups. In: *Cooperation in Primates and Humans: Mechanisms and Evolution* (eds. Kappeler PM, van Schaik CP), pp. 25−46. Springer, Berlin, Germany.

Similä T, Ugarte F (1993) Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Canadian Journal of Zoology*, **71**, 1494−1499.

Smolker R, Richards A, Connor R, Mann J, Berggren P (1997) Sponge carrying by dolphins (Delphinidae, *Tursiops* sp.): a foraging specialization involving tool use? *Ethology*, **103**, 454−465.

Smolker RA, Richards AF, Connor RC, Pepper JW (1992) Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour*, **123**, 38−69.

Smultea MA (1994) Segregation by humpback whale (*Megaptera novaeangliae*) cows with a calf in coastal habitat near the island of Hawaii. *Canadian Journal of Zoology*, **72**, 805−811.

Sober, E (2006) *Conceptual Issues in Evolutionary Biology, Third Edition*. The MIT Press, Cambridge, Massachusetts.

Tinbergen N (1953) *Social Behaviour in Animals with Special Reference to Vertebrates.* Methuen, London.

Toro MA, Barragán C, Óvilo C, Rodriganez J, Rodriguez C, *et al.* (2002) Estimation of co-ancestry in Iberian pigs using molecular markers. *Conservation Genetics*, **3**, 309–320.

Toro MA, Fernández A, García-Cortés LA, Rodrigáñez J, Silió L (2006) Sex ratio variation in Iberian pigs. *Genetics*, **173**, 911–917.

Trivers RL (1971) Evolution of reciprocal altruism. *Quarterly Review of Biology*, **46**, 35−57.

Trivers RL (1985) *Social Evolution*. Benjamin Cummings, Menlo Park, California.

Trivers RL (2002) *Natural Selection and Social Theory: Selected Papers of Robert Trivers*. Oxford University Press, Oxford.

Valsecchi E, Hale P, Corkeron P, Amos W (2002) Social structure in migrating humpback whales (*Megaptera novaeangliae*). *Molecular Ecology*, **11**, 507−518.

Van de Casteele T, Galbusera P, Matthysen E (2001) A comparison of microsatellite-based pairwise relatedness estimators. *Molecular Ecology*, **10**, 1539−1549.

Van Horn RC, Engh AL, Scribner KT, Funk SM, Holekamp KE (2004) Behavioural structuring of relatedness in the spotted hyena (*Crocuta crocuta*) suggests direct fitness benefits of clan-level cooperation. *Molecular Ecology*, **13**, 449−458.

Van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004) MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes*, **4**, 535−538.

Van Schaik CP, Pandit SA, Vogel ER (2006) Towards a general model for male-male coalitions in primate groups. In: *Cooperaion in Primates and Humans: Mechanisms and Evolution* (eds. Kappeler PM, van Schaik CP), pp. 151−171. Springer, Berlin, Germany.

Van Waerebeek K, Read AJ (1994) Reproduction of dusky dolphins, *Lagenorhynchus obscurus*, from coastal Peru. *Journal of Mammalogy*, **75**, 1054−1062.

Van Waerebeek K, van Bree PJH, Best PB (1995) On the identity of *Prodelphinus petersii* (Lütken 1889) and records of dusky dolphin, *Lagenorhynchus obscurus* (Gray 1828), from the southern Indian and Atlantic Oceans. *South African Journal of Marine Science*, **16**, 25−35.

Velicer GJ (2005) Evolution of cooperation: does selfishness restraint lie within? *Current Biology*, **15**, R173−R175.

Vigilant L, Hofreiter M, Siedel H, Boesch C (2001) Paternity and relatedness in wild chimpanzee communities. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 12890−12895.

Vucetich JA, Peterson RO, Waite TA (2004) Raven scavenging favours group foraging in wolves. *Animal Behaviour*, **67**, 1117−1126.

Wang JL (2002) An estimator for pairwise relatedness using molecular markers. *Genetics*, **160**, 1203−1215.

Ward AJW, Axford S, Krause J (2003) Cross-species familiarity in shoaling fishes. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 1157−1161.

Warner RR (1988) Traditionality of mating site preferences in a coral reef fish. *Nature*, **335**, 719–721.

Warner RR (1990) Resource assessment versus traditionality in mating site determination. *American Naturalist*, **135,** 205–217.

Webb BF (1973) Cetaceans sighted off the west coast of the South Island, New Zealand, summer 1970. *New Zealand Journal of Marine and Freshwater Research*, **7**, 179−182.

Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population-structure. *Evolution*, **38**, 1358−1370.

Weir JS, Duprey NM, Würsig B (2005) Distribution and behavior of dusky dolphin "nursery" groups off Kaikoura, NZ. *In: Abstracts of the 16th Biennial Conference on the Biology of Marine Mammals,* 12−16 December 2005, San Diego, California. Society for Marine Mammalogy, pp. 300−301.

Wells RS (1991a) Brining up baby. *Natural History*, **8**, 56−62.

Wells RS (1991b) The role of long-term study in understanding the social structure of a bottlenose dolphin community. In: *Dolphin Societies: Discoveries and Puzzles* (eds. Pryor K, Norris KS), pp. 199−225. University of California Press, Berkeley, California.

Wells RS, Scott MD, Irvine AB (1987) The social structure of free-ranging bottlenose dolphins. In: *Current Mammalogy* (ed. Genoways H), pp. 247−305. Plenum Press, New York.

West SA (2001) Testing Hamilton's rule with competition between relatives. *Nature*, **409**, 510–513.

West SA, Pen I, Griffin AS (2002) Conflict and cooperation—cooperation and competition between relatives. *Science*, **296**, 72−75.

Whitehead H (1996) Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behavioral Ecology and Sociobiology*, **38**, 237−244.

Whitehead H (1998) Cultural selection and genetic diversity in matrilineal whales. *Science*, **282**, 1708−1711.

Whitehead H (2005a) Genetic diversity in the matrilineal whales: models of cultural hitchhiking and group-specific non-heritable demographic variation. *Marine Mammal Science*, **21**, 58−79.

Whitehead H (2005b) Climate, learning, and the evolution of cultural capacity on land and sea. *In: Abstracts of the 16th Biennial Conference on the Biology of Marine Mammals,* 12−16 December 2005, San Diego, California. Society for Marine Mammalogy, p. 303.

Whitehead H, Rendell L, Osborne RW, Würsig B (2004) Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. *Biological Conservation*, **120**, 427−437.

Whitehead H, Weilgart L (2000) The sperm whale: social females and roving males. In: *Cetacean Societies: Field Studies of Dolphins and Whales* (eds. Mann J, Connor RC, Tyack PL, Whitehead H), pp. 154−172. University of Chicago Press, Chicago, Illinois.

Williams TM (1999) The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. *Philosophical Transactions of the Royal Society of London*, **354**, 193−201.

Wilson B (1995) *The ecology of bottlenose dolphins in the Moray Firth, Scotland: a population at the northern extreme of the species' range*, PhD Thesis, University of Aberdeen.

Wilson EO (1998) *Conscilience: The Unity of Knowledge*. Alfred A. Knopf, Inc., New York.

Wilson EO (2000) *Sociobiology: The New Synthesis, 25th Anniversary Edition*. Belknap Press of Harvard University Press, Cambridge, Massachusetts.

Wolf JBW, Kauermann G, Trillmich F (2005) Males in the shade: habitat use and sexual segregation in the Galapagos sea lion (*Zalophus californianus wollebaeki*). *Behavioral Ecology and Sociobiology*, **59**, 293−302.

Wrangham R (1982) Mutualism, kinship, and social evolution. In: *Current Problems in Sociobiology* (ed. Group KCS). Cambridge University Press, Cambridge.

Würsig B, Cipriano F, Slooten E, R. Constantine, K. Barr, *et al.* (1997) Dusky dolphins (*Lagenorhynchus obscurus*) of New Zealand: status of present knowledge. *Reports of the International Whaling Commission*, **47**, 715−722.

Würsig B, Cipriano F, Würsig M (1991) Dolphin movement patterns: information from radio and theodolite tracking studies. In: *Dolphin Societies: Discoveries and Puzzles* (eds. Pryor K, Norris KS), pp. 79−112. University of California Press, Berkeley, California.

Würsig B, Jefferson T (1990) Methods of photo-identification for small cetaceans. *Reports of the International Whaling Commission*, **12**, 43−52.

Würsig B, Wells RS, Norris KS (1994) Food and feeding. In: *The Hawaiian Spinner Dolphin* (eds. Norris KS, Würsig B, Wells RS, Würsig M), pp. 216−231. University of California Press, Berkley, California.

Würsig B, Würsig M (1977) The photographic determination of group size, composition and stability of coastal porpoises (*Tursiops truncatus*). *Science*, **198**, 755−756.

Würsig B, Würsig M (1980) Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the South Atlantic. *Fishery Bulletin*, **77**, 871−890.

Würsig B, Würsig M, Cipriano F (1989) Dolphins in different worlds. *Oceanus*, **32**, 71−75.

# VITA

Name: Deborah Ellen Shelton

Address: Marine Mammal Research Program
Texas A&M University, Galveston
5007 Avenue U
Galveston, TX 77551

Email address: deborah.shelton@gmail.com

Education: M.S., Wildlife and Fisheries Sciences, Texas A&M University, 2006
B.S., Biology, Wake Forest University, 2003