FISSION-FUSION SOCIALITY IN DUSKY DOLPHINS (*Lagenorhynchus obscurus*), WITH COMPARISONS TO OTHER DOLPHINS AND GREAT APES

A Dissertation

by

HEIDI CHRISTINE PEARSON

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

DOCTOR OF PHILOSOPHY

August 2008

Major Subject: Wildlife and Fisheries Sciences

FISSION-FUSION SOCIALITY IN DUSKY DOLPHINS (*Lagenorhynchus obscurus*), WITH COMPARISONS TO OTHER DOLPHINS AND GREAT APES

A Dissertation

by

HEIDI CHRISTINE PEARSON

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

DOCTOR OF PHILOSOPHY

Approved by:

Chair of Committee,	Bernd Würsig
Committee Members,	Randall Davis
	Sharon Gursky
	Jane Packard
Head of Department,	Thomas Lacher

August 2008

Major Subject: Wildlife and Fisheries Sciences

ABSTRACT

Fission-fusion Sociality in Dusky Dolphins (*Lagenorhynchus obscurus*), with
Comparisons to Other Dolphins and Great Apes. (August 2008)
Heidi Christine Pearson, B.S., Duke University
Chair of Advisory Committee: Dr. Bernd Würsig

I examined fission-fusion sociality in dusky dolphins (*Lagenorhynchus obscurus*), and investigated aspects of social convergence between dolphins and great apes. I used boat-based group focal follows and photo-identification to collect data in Admiralty Bay, New Zealand during 2005-2006. I used generalized estimating equations to examine relationships between party (group) size, rate of party fission-fusion, activity, and location; and relationships between leaping frequency and behavior. Using photo-identification images from 2001-2006, I analyzed the strength and temporal patterning of associations, short- and long-term association patterns, preferred/avoided associations, and behaviorally-specific preferred associations. To analyze social convergence between dolphins and great apes, I compared female bottlenose dolphin (*Tursiops* spp.) and chimpanzee (*Pan troglodytes*) social strategies through literature review.

I conducted 171 group focal follows, totaling 157 observation hours. Mean party size was 7.0±6.0 individuals. Party size changed every 5.4±7.6 min on average. The most frequent activity was resting (37%), followed by traveling (29%), foraging (18%), and socializing (15%). Foraging was positively related to party size and rate of fission-fusion. Near mussel farms, foraging increased, traveling decreased, and rate of party fusion increased. “Clean” leaps were the most frequent leap type (84%) and were positively related to party size and foraging. Noisy and coordinated leaps were positively related to party size; noisy leaps were negatively related to foraging.

Associations during 2001-2006 (*N* = 228 individuals) were nonrandom for 125 days; associations within one field season were nonrandom for 60 days. Individuals formed preferred/avoided associations during most years. The strongest associations occurred during foraging and socializing; the weakest associations occurred during traveling. Individuals formed preferred associations during foraging, resting, and socializing.

Review of female bottlenose dolphin and chimpanzee sociality revealed that: 1) females form weaker bonds and are less social than males, 2) females associate mostly with other females, 3) mothers are often alone with their offspring, 4) mothers (*vs*. non-mothers) and non-cycling (*vs*. cycling) females associate less with males, and 5) non-cycling (*vs*. cycling) females occur in smaller parties. Female dolphins may be more social than female chimpanzees due to decreased scramble competition, increased predation risk, and decreased cost of transport for dolphins *vs.* chimpanzees.

For my family
And in loving memory of my Grandma Beau

ACKNOWLEDGEMENTS

Scientific research is not a solo effort, and I have many people to thank who have helped me achieve this goal. First, I am grateful to my committee for their advice and wisdom as the focus of my dissertation research evolved. I thank Bernd Würsig for his endless support and encouragement, inspiration, enthusiasm, and humor. I am grateful for the guidance he provided, while still letting me find my own way. I thank Randy Davis for first taking me on as a graduate student, for his guidance during my sea otter research, and for seeing me through my dissertation research. I thank Jane Packard for sharing her wealth of knowledge in ethology and behavioral ecology, and for guiding me through both my sea otter and dusky dolphin research. I thank Sharon Gursky for sharing her primatological knowledge and helping me to bridge the fields of cetology and primatology.

I thank all of the interns who assisted in fin matching: Heidi Amin , Elizabeth Foster, Emily Gillespie, Nikki Hughes, Heather Majors, Sarah Piwetz, Kimberly Smelker, Kerri Smith, Amanda Wilson, and all the other interns who came before my time. This was an enormous undertaking which would not have been possible without their assistance.

Thanks to Chris Pearson, Robin Vaughn, Sierra Deutsch, Lauren Wilson, and all of the Earthwatch volunteers for field assistance. I am grateful to Tim Markowitz and Jody Weir for showing me the ropes with Punua Aihe. I also thank Tim Markowitz, Jody Weir, and Cynthia McFadden for providing fin images from the years prior to the commencement of this study, and Gwénaël Beauplet for coordinating a portion of the image matching.

I am indebted to Danny and Lyn Boulton; Ross and Vera McDonald; and Brian Lloyd, Laura Boren, Paul Fisher, and Nadine Newton from the New Zealand Department of Conservation (DOC) for logistical support and friendship in French Pass. I am

especially grateful to the DOC crew for sharing their home with us during the final weeks of my Admiralty Bay field season.

I thank Janet Mann, Anne Pusey, Jana Watson-Capps, and Carson Murray for advice and many helpful discussions regarding dolphin-chimpanzee comparisons, and Jill Pruetz for the opportunity to visit the Fongoli chimpanzees in Senegal. For statistical assistance, I am indebted to Mahbubur Rahman for helping me with GEE analyses, Shannon Gowans for advice on SOCPROG, and Kristen Lennox for help with my initial analyses in SPSS. For help navigating through the Texas A&M University (TAMU) and Texas A&M University at Galveston (TAMUG) systems, I am grateful to Stacie Arms, Jennifer Baker, and David Wentling.

Funding for this research came from multiple sources, including the Earthwatch Institute, National Geographic Society, New Zealand DOC, the Marlborough District Council, Erma Lee and Luke Mooney, Department of Marine Biology at TAMUG, Office of Research and Graduate Studies at TAMUG, Department of Wildlife and Fisheries Sciences at TAMU, the Tom Slick Graduate Student Fellowship from TAMU, and generous support from the Würsigs.

I thank Susy Flores and Lori Cabrera for their friendship and for taking good care of my Girls while I was in the field. I am also grateful to my current and former labmates Adrian Dahood, Robin Vaughn, Sierra Deutsch, Mridula Srinivasan, Jody Weir, Nick Duprey, Deborah Shelton, Paula Moreno, Gwénaël Beauplet, and Leszek Karczcmarski for their support, friendship, and discussions in the lab and the field. Thanks also to my colleagues at The University of Texas Medical Branch (UTMB) for their support, and especially to Carmen Radecki Breitkopf for her friendship, statistical knowledge, encouragement, and pep talks. She has been a mentor and role model to me throughout my graduate career, and I owe much of my scientific development to her.

Finally, I am eternally grateful to my family for their love, support, and encouragement – my Mom, Dad, sister, Auntie Barbara, and Grandpa Chris. I am especially grateful to my parents for that first trip to Africa when I was 15 years old that sparked my lifelong passion for understanding animal behavior and conservation. And

finally, to Chris, thanks for your patience, humor, wondrous photographic skills and advice, and for taking all of those fin shots for me. Thanks for enduring the hot Galveston summers, for putting up with my long absences in the field, and my long "absences" in front of my Gateway. I could not have done this without your encouragement, love, and support.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER I

INTRODUCTION

Overview of fission-fusion sociality

Fission-fusion sociality is a highly-flexible yet complex form of social structure whereby members within a community frequently join and split from parties (groups) (e.g., Würsig 1978; Wrangham and Smuts 1980; Smolker et al. 1992; Chapman et al. 1993). Individual-based fission-fusion sociality, whereby party size and composition change as a result of individual movements (van Schaik 1999), is present in several delphinid and primate species: bottlenose dolphins (*Tursiops* spp.; e.g., Smolker et al. 1992); dusky dolphins (*Lagenorhynchus obscurus*; e.g., Würsig and Würsig 1980), spinner dolphins (*Stenella longirostris*; e.g., Karczmarski et al. 2005), common dolphins (*Delphinus delphis*; e.g., Bruno et al. 2004), spider monkeys (*Ateles geoffroyi*; e.g., Symington 1990), chimpanzees (*Pan troglodytes*; e.g., Lehmann et al. 2007*)*, bonobos (*P. paniscus*; e.g., Chapman et al. 1993), and orangutans (*Pongo pygmaeus*, van Schaik 1999). This form of sociality may have evolved in response to patchy and ephemeral food sources (e.g, fruit and fish), where intragroup competition may be reduced if individuals join and split from parties according to resource availability (e.g., Würsig 1978; Wells et al. 1987), and perhaps as related to social and predator pressures as well (e.g., van Schaik and van Hooff 1983).

The size and composition of parties may change on a daily or hourly basis (Connor et al. 2000b; Bearzi et al. 2005), according to socioecological changes. For example, large party size may serve to increase predator protection or mating interactions, but when food is patchily distributed in space and time, large parties may be disadvantageous by increasing feeding competition. Within these rapidly changing parties, however, individuals maintain preferential associations.

This dissertation follows the style of Behavioral Ecology and Sociobiology.

The variability in party size inherent to fission-fusion societies offers a natural experiment in which to examine the factors influencing grouping patterns (Anderson et al. 2002). Social, ecological, demographic, and life history factors may influence fission-fusion social dynamics. Specific factors include: food density and distribution, predator pressure, community size, presence and number of estrous females, cooperative hunting, intragroup competition and aggression, infant socialization, and social pressures to "meet" and interact with all individuals in the community (e.g., Goodall 1986; Doran 1997; van Schaik 1999; Boesch and Boesch-Acherman 2000; Lehmann and Boesch 2004). Understanding how parties fission and fusion and in what context (e.g., during which activities, with whom, and for how long) will provide greater insight into the evolution of this form of social organization.

Morphological and environmental factors may differentially affect fission-fusion sociality in marine and terrestrial species. Due to their fusiform body shape and low cost of transport (Williams et al. 1992), dolphins require less energy than primates to move though their environment. As a result, fission-fusion dynamics may be more “fluid” in marine systems; party composition may change more rapidly, and dolphins may have a wider social network since they may encounter dispersed conspecifics at a lower energetic cost. Additionally, there may be a higher degree of spatio-temporal variability in the marine than terrestrial environment, making individual learning more costly in the marine environment (Steele 1985; Whitehead 1998; Rendell and Whitehead 2001; Whitehead 2007). Thus, social learning or culture is likely to be an efficient conduit of information transfer in cetaceans (Whitehead 1998; Rendell and Whitehead 2001).

Social convergence between delphinids and pongids

In addition to fission-fusion sociality, delphinids (dolphins) and pongids (great apes) share other aspects of social convergence such as: male alliances, tool use, cooperative hunting, multi-mate mating systems, alloparental care, aggressive mating consortships, and culture (e.g., Smolker et al. 1992; Connor et al. 1998; Connor et al. 2000b; Marino 2002; Whitehead et al. 2004; Bearzi and Stanford 2008). The similarities between delphinids and pongids are striking because the two taxonomic families inhabit vastly different environments, and their last common ancestor was *c.a.* 95 million years ago (Bromham et al. 1999).

Large brains and complex cognition

Delphinids and pongids are the two most highly encephalized mammalian groups (i.e., those with the largest relative brain sizes) (e.g., Marino 1996, 1998). Although "ecological" and "social" problems are inter-related and may not be neatly separated, two main hypotheses have been put forth to explain the adaptive value of large brains. The "ecological intelligence" hypothesis posits that large brains evolved to solve complex ecological problems, such as forming a "mental map" to locate patchy food resources (Clutton-Brock and Harvey 1980). The "social intelligence" or "social brain" hypothesis posits that large brains evolved to solve complex social problems, such as "keeping track" of changing group properties, social hierarchies, and networks of relationships (e.g., Jolly 1966; Humphrey 1976; Dunbar and Shultz 2007). Most current studies are in favor of the social brain hypothesis (e.g., Dunbar and Shultz 2007). Although ecological unpredictability (e.g., the need to forage on patchy prey resources) may have been the initial impetus for large brain evolution, the need to solve ecological problems and keep track of relationships within a changing social environment likely fueled the increasing spiral of complex cognition (after Dunbar 2003).

Dusky dolphins as a model species

Dusky dolphins have one of the largest known encephalization quotients (EQ = brain weight/(0.12 * body weight$^{0.67}$)); Jerison 1973) of any mammal (Marino et al. 2004). The dusky dolphin EQ (4.7) is larger than all non-human primates, and lies between that of a chimpanzee (EQ = 2.3) and that of a modern human (*Homo sapiens*, EQ = 7.6) (Jerison 1973; Marino et al. 2004) (Fig. 1). In addition to having a large brain, dusky dolphins exhibit other indicators of complex cognition (as outlined by Simmonds 2006) such as: 1) a slow life history, with a long lifespan, long period of offspring dependence, and long juvenile period (Cipriano 1992; van Waerebeek and Read 1994); 2) evidence of culture (Whitehead et al. 2004; chapter IV, this volume); 3)

Fig. 1. Representative primate and cetacean species, in order of increasing encephalization quotient (EQ). Clockwise from top left: mountain gorilla (*Gorilla gorilla beringei*, EQ = 1.6 for *G. g.*), chacma baboon (*Papio ursinus*, EQ = 1.8), western chimpanzee (*Pan troglodytes verus*, EQ = 2.3 for *P. t.*), bottlenose dolphin (*Tursiops* spp., EQ = 4.0), common dolphin (*Delphinus delphis*, EQ = 4.3), and dusky dolphin (*Lagenorhynchus obscurus*, EQ = 4.7). Primate EQ's are from Jerison 1973; delphinid EQ's are from Marino et al. 2004. All photos except mountain gorilla and chimpanzee courtesy of Chris Pearson.

exploitation of patchy prey resources (Würsig and Würsig 1980; chapter II, this volume); 4) closely coordinated foraging and social behaviors (Würsig and Würsig 1980; Markowitz 2004; Vaughn et al. 2007; chapters II-IV, this volume); and 5) formation of long-term associations with preferred companions (chapter IV, this volume).

Three study sites

Dusky dolphins are a semi-pelagic species (i.e., inhabiting coastal zones and shallow shelves and slopes of the continental shelf; after Würsig et al. 2007), occurring only in the southern hemisphere and primarily off the coasts of southwest Africa (Namibia, South Africa), South America (Peru, Chile, Argentina), and New Zealand (Würsig and Würsig 1980; Würsig et al. 1989; Würsig et al. 1997; Cassens et al. 2005). In New Zealand, dusky dolphins are distributed as far east as Chatham Island, as far south as Stewart Island, and as far north as Hawke Bay (Gaskin 1968; Würsig et al. 1997; Reeves et al. 2002). The primary concentration of dusky dolphins in New Zealand occurs off the Kaikoura Peninsula, where upwelling from the subtropical convergence zone supports an abundant food supply for dusky dolphins in this region (Gaskin 1968). Dusky dolphins are also seasonally abundant in Admiralty Bay, 275 km north of Kaikoura at the tip of the South Island. Dusky dolphins are present in Admiralty Bay primarily during the winter, when small schooling fish such as pilchard (*Sardinops pilchardus*) are present (Markowitz et al. 2004).

Dusky dolphin behavior has primarily been studied in Golfo San José, Argentina (Würsig and Würsig 1980); Kaikoura, New Zealand (Benoit-Bird et al. 2004; Markowitz 2004); and Admiralty Bay, New Zealand (Benoit-Bird et al. 2004; Markowitz et al. 2004; Vaughn et al. 2007; this volume). While each population demonstrates fission-fusion sociality, the patterns of party fission and fusion vary according to socioecological pressures. In particular, differences in prey availability and predation risk have differentially impacted social strategies in each area.

Golfo San José, Argentina

In Golfo San José, Argentina, dusky dolphins typically occur <5 km from shore at depths of <200 m. During the day, dusky dolphins spread out in search of patchily-distributed southern anchovy (*Engraulis anchoita*) by forming widely spaced groups of 6-15 individuals. Up to 300 individuals may cooperate to herd fish into prey balls, and there is evidence for "temporary restraint" as individuals "take turns" feeding on and herding prey balls. At the conclusion of a feeding bout, a high degree of socio-sexual behavior occurs. It is likely that social bonds are reinforced during this time, which may facilitate cooperative foraging strategies. After feeding and socializing, individuals split into smaller parties once again. In short, dusky dolphin parties in Argentina aggregate primarily to feed and socialize; when not engaged in these activities, individuals form small parties and may rest nearshore to avoid killer whale (*Orcinus orca*) and shark predation (Würsig and Würsig 1980; Würsig 1986; Würsig et al. 1989).

Kaikoura, New Zealand

In the deep waters (≤2000 m) off Kaikoura, dusky dolphins form large parties of 200-1000 individuals, likely for predator protection (Würsig et al. 1997) (Fig. 2).

Fig. 2. A portion of a large dusky dolphin party off Kaikoura, New Zealand. Photo courtesy of Chris Pearson.

Large parties are composed of several loosely connected subgroups (i.e., mother-calf nurseries, mating adult, non-mating adults) (Würsig et al. 1989; Würsig et al. 1997; Markowitz 2004). There is a continual low level of socio-sexual activity within large parties. During the night, dusky dolphins forage on lantern fish (family Mycyophidae) and squid (*Nototodarus* sp. and *Todaroides* sp.) within the deep-scattering layer (DSL). Foraging subgroup size ranges from 1 to 5 individuals and individuals may cooperatively forage as prey becomes less evenly distributed (Benoit-Bird et al. 2004). However, in contrast to cooperative fish-herding behavior in Golfo San José, cooperative foraging in Kaikoura is less intense and likely serves as a means of information sharing to detect prey (Würsig et al. 1989; Benoit-Bird et al. 2004).

Admiralty Bay, New Zealand

During the austral winter, a subset of the dusky dolphin population in Kaikoura migrates to Admiralty Bay. The fact that some of the same individuals annually travel between these two areas may be evidence for a cultural tradition (Whitehead et al. 2004; Chapter IV, this volume). Unlike the pelagic waters off Kaikoura where killer whales and large sharks pose a predatory threat (Constantine 1998; Weir 2007), dusky dolphins in the relatively shallow, enclosed waters of Admiralty Bay have few predators during the winter and early spring (McFadden 2003; D. Boulton, French Pass Sea Safaris, personal communication; C. Duffy, Marine Science Unit, New Zealand Department of Conservation, personal communication).

Dusky dolphins in Admiralty Bay behave more similarly to dusky dolphins in Golfo San José than in Kaikoura. In Admiralty Bay, dusky dolphins cooperatively herd small schooling fishes such as New Zealand pilchard (*Sardinops neopilchardus*), yellow-eyed mullet (*Aldrichetta forsteri*), and sprat (*Sprattus antipodum*) into prey balls (Fig. 3) (Markowitz et al. 2004; Vaughn et al. 2007). Overall, the pattern of group fission and fusion in Admiralty Bay appears to be more “muted” than in Golfo San José because party size does not oscillate as dramatically between large feeding and socio-sexual groups, and small traveling and resting parties (Markowitz 2004; Chapter II, this volume).

Fig. 3. Dusky dolphin foraging strategies in Admiralty Bay, New Zealand. Top: Dusky dolphins coordinate surface behaviors during foraging. Dusky dolphins often feed in conjunction with seabirds; the splash in the background indicates that an Australasian gannet (*Morus serrator*) has just taken a plunge dive down towards a school of fish. Bottom: Coordinated dusky dolphin foraging involves herding small schooling fishes such as pilchard (*Sardinops neopilchardus*) into prey balls; dusky dolphins may use the surface of the water as a barrier against which to herd prey balls.

Admiralty Bay is a "natural laboratory" in which to test hypotheses about fission-fusion sociality. From a logistical perspective, this relatively shallow, enclosed bay containing small dusky dolphin parties (mean party size = 7; Chapter II, this volume) permits a detailed examination of dusky dolphin behavior. From a theoretical perspective, by comparing social organization in Admiralty Bay with other dusky dolphin sites, and (more broadly) with great apes, potential factors leading to the evolution of fission-fusion sociality may be identified.

Research objectives

The purpose of this research is to examine the evolution of fission-fusion sociality in cognitively complex species such as dusky dolphins, bottlenose dolphins, and chimpanzees. In short, I ask, "How are these species using their large brains to navigate through their complex socioecological environments?" I focus on dusky dolphins as a model species in which to explore potential reasons for the evolution of fission-fusion sociality, and incorporate aspects of dusky dolphin behavior into a comparative framework with other delphinids, and pongids. Additionally, I provide a detailed comparison between delphinids and pongids by presenting a comparative literature review between bottlenose dolphins and chimpanzees, two of the best studied delphinids and pongids, respectively.

My specific research objectives were to:

1) examine the relationships between party size, behavior, and location for dusky dolphins in Admiralty Bay
2) examine patterns of association, within and between years, for dusky dolphins in Admiralty Bay;
3) compare social strategies between female bottlenose dolphins and chimpanzees.

Overview of chapters

Fission-fusion sociality may be analyzed according to behavioral, grouping, and association patterns. Chapters II and III examine behavioral and grouping patterns, Chapter IV examines behavioral and association patterns, while Chapter V examines behavioral, grouping, and association patterns.

Chapter II examines how dusky dolphins join and split from parties according to the shifting balance of costs and benefits associated with grouping. Specifically, this chapter provides an analysis of how coordinated foraging strategies, predation risk, and mussel farming affect grouping patterns.

Chapter III uses the social facilitation and prey capture hypotheses to examine the context and function of leaping behavior in dusky dolphins. Specifically, this chapter examines the influence of party size and behavior on the frequency of four leap types.

Chapter IV examines short- and long-term association patterns of dusky dolphins by analyzing social “fluidity” (strength and temporal patterning of associations) and preferred associations. In addition (to my knowledge), this is the first study to test for the presence of behaviorally-specific preferred associations in dusky dolphins, and one of few cetacean studies to analyze this.

Chapter V provides a detailed examination of social convergence between dolphins and great apes by providing a comparative literature review of female social strategies in bottlenose dolphins and chimpanzees. This chapter focuses on understanding females, as female social strategies may drive the social and mating systems of a species as a whole.

Importance of research

This research has both theoretical and practical importance. First, compared to better-known coastal species such as bottlenose dolphins, less is known about fission-fusion sociality in semi-pelagic species such as dusky dolphins. Patterns of fission-fusion sociality may differ between the coastal and semi-pelagic species, due to varying intensities in ecological pressures (e.g., prey availability and predation risk). By increasing our understanding of dusky dolphin fission-fusion sociality, insight into the evolution of this type of social system in delphinids may be obtained.

Second, New Zealand dusky dolphins are of interest because a subset of the population migrates annually between Kaikoura and Admiralty Bay. As a result, some individuals dramatically switch their foraging and social patterns, from foraging nocturnally in large parties off Kaikoura to foraging diurnally in smaller, coordinated parties in Admiralty Bay. By examining patterns of fission-fusion sociality in Admiralty Bay, we will increase our understanding of this potential cultural unit (see Whitehead et al. 2004).

Third, a detailed comparison of social strategies in female bottlenose dolphins and chimpanzees will advance our knowledge of social convergence between delphinids and pongids. While other studies have compared dolphins and great apes with respect to cognition (Marino 1996, 1998, 2002), sympatric associations (Bearzi and Stanford 2007), and culture (Rendell and Whitehead 2001; Whitehead et al. 2004), to my knowledge no review has focused explicitly on female social strategies.

Finally, although dusky dolphins are not threatened or endangered, the International Union for the Conservation of Nature (IUCN) has listed the dusky dolphin as a species for which more data are needed to properly assess its conservation status (IUCN 2007). Thus, results of this study fill a gap in our knowledge of dusky dolphin sociality by examining behavior in Admiralty Bay, an area threatened by an increase in mussel farming. Since dusky dolphins do not use areas within mussel farms (Markowitz et al. 2004; H. Pearson, unpublished data), increasing the number of farms could decrease the amount of habitat available for dusky dolphins, and change or limit their ranging and behavioral patterns. Furthermore, if mussel farming continues to expand in Admiralty Bay, the subset of the dusky dolphin population that forages in Kaikoura during the summer and in Admiralty Bay during the winter could be detrimentally affected (Markowitz et al. 2004; Whitehead et al. 2004). Although many wildlife conservation efforts are focused on the maintenance of genetic diversity, the maintenance of cultural diversity may be equally important for long-term species survival (Whitehead et al. 2004). By examining the relationship (if any) between dusky dolphins and mussel farms, effective conservation management strategies may be implemented.

CHAPTER II

INFLUENCES ON DUSKY DOLPHIN (*Lagenorhynchus obscurus*) FISSION-FUSION SOCIALITY IN ADMIRALTY BAY, NEW ZEALAND

Introduction

Social structure may be influenced by opposing forces. Variables such as group size, group cohesion, and time devoted to vigilance, resting, or aggression may either enhance or diminish fitness by differentially impacting factors such as foraging efficiency and predation risk (Janson 1998 and references therein). Therefore, social structure may be viewed as a multivariate optimization to various pressures, and does not result from one ultimate cause (Caraco 1979). For example, guppies (*Poecilia reticulata*) that form schools as an anti-predator behavior are weaker competitors for food, demonstrating a compromise between predator protection and resource defense (Margurran and Seghers 1991). As yellow-eyed junco (*Junco phaeonotus*) flock size increases, each member may devote less time to vigilance and more time to feeding, but intra-group aggression increases (Caraco 1979; Caraco et al. 1980).

Within fission-fusion societies, opposing pressures (e.g., predation risk, food availability, mating opportunities, demographics) may change as individuals join and split from groups or parties (e.g., Würsig 1978; Lehmann et al 2007). Party size and composition are not stable and may change on a daily or hourly basis (e.g., Connor et al. 2000b; Bearzi et al. 2005). Optimality models would predict that an individual would join a party when the benefits outweigh the costs, and leave a party when the costs of grouping outweigh the benefits (Krebs and Davies 1993). The party fluidity inherent to fission-fusion societies thus offers a natural experiment to examine the factors influencing grouping patterns (Anderson et al. 2002). Furthermore, by comparing patterns of fission-fusion sociality between distantly related taxa (e.g., cetaceans and primates), “phylogenetic complication” (after Chapman et al. 1995) is minimized and alternative models for the evolution of fission-fusion sociality may be evaluated.

Influences on fission-fusion sociality may vary both between and within species. For black spider monkeys (*Ateles paniscus chamek*) in southeastern Peru, intraparty feeding competition is the most important determinant of fission-fusion sociality, as evidenced by a linear relationship between feeding party and patch size (Symington 1988). However, for chimpanzees (*Pan troglodytes*) in the Kalinzu Forest, Uganda, increased party size is associated with presence of estrous females, whereas fruit abundance and distribution has no effect (Hashimoto et al. 2001). Bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Australia form smaller parties while foraging to reduce competition, and form larger parties while resting and in shallow waters so as to reduce shark predation risk (Heithaus and Dill 2002). In contrast, Hawaiian spinner dolphins (*Stenella longirostris*) increase prey-finding abilities by forming large parties when traveling offshore to meet the nocturnally-rising deep scattering layer (DSL). During the day, they form small parties to "fit" within small nearshore bays, and reduce predation risk by resting over light-colored sand (Norris and Dohl 1980a; Würsig et al. 1989; Würsig et al. 1994).

Intraspecies variation in fission-fusion dynamics may reflect habitat-specific costs and benefits of grouping (Lehmann et al. 2007). For example, at Bossou, Guinea, chimpanzees form smaller parties for feeding and larger parties when in dangerous situations such as crossing roads (Sakura 1994). Conversely, due to the dense, low-visibility environment in Taï National Park, Côte d'Ivoire, as predation risk increases, chimpanzees decrease party size in order to minimize the party's noise level (Boesch 1991).

Dusky dolphins also exhibit habitat-specific fission-fusion strategies, making it an appropriate species in which to examine the evolution of this type of sociality. Dusky dolphin foraging and social behaviors have been studied primarily in Golfo San José, Argentina (Würsig and Würsig 1980); off Kaikoura, New Zealand (Benoit-Bird et al. 2004; Markowitz 2004); and in Admiralty Bay, Marlborough Sounds, New Zealand (Benoit-Bird et al. 2004; Markowitz et al. 2004; McFadden 2003). Differences in prey availability and predation risk between these three areas influence fission-fusion strategies.

In Golfo San José, dusky dolphins cooperatively forage during the day on southern anchovy (*Engraulis anchoita*). Parties of ≤ 300 individuals may form to feed; after feeding, dusky dolphins engage in intense bouts of socio-sexual behavior. When resting, parties may enter shallow nearshore waters to avoid killer whale (*Orcinus orca*) and shark predation (Würsig and Würsig 1980; Würsig et al. 1989). In contrast, dusky dolphins off Kaikoura primarily forage nocturnally and individually on the DSL (Benoit-Bird et al 2004). Dusky dolphins may avoid predation by forming large parties of ≤ 1000 individuals, and resting in nearshore waters during the day (Cipriano 1992; Würsig et al. 1997; Würsig et al. 2007).

During the winter and early spring, some dusky dolphins travel 275 km north of Kaikoura to Admiralty Bay, where they exhibit fission-fusion strategies that appear to be more similar to that found in Golfo San José than off Kaikoura. In Admiralty Bay, dusky dolphins exhibit coordinated herding of small schooling fishes such as New Zealand pilchard (*Sardinops neopilchardus*), yellow-eyed mullet (*Aldrichetta forsteri*), and sprat (*Sprattus antipodum*) into prey balls during the day (Markowitz et al. 2004, Vaughn et al. 2007). Some of the same individuals return to Admiralty Bay each winter with preferred foraging companions, which may indicate culture (Markowitz et al. 2004, Whitehead et al. 2004).

Potential dusky dolphin shark predators in Admiralty Bay include broadnose sevengill sharks (*Notorynchus cepedianus*), great white sharks, (*Carcharodon carcharias*), and blue sharks (*Prionace glauca*). However, these species most commonly occur inshore during the summer (C. Duffy, Marine Science Unit, New Zealand Department of Conservation, personal communication). Additionally, although killer whales occur periodically in Admiralty Bay throughout the year, they are rare during the winter and early spring (D. Boulton, French Pass Sea Safaris, personal communication). Thus, there is likely to be little predation risk for dusky dolphins in Admiralty Bay during the winter and early spring.

Despite reduced predation risk in Admiralty Bay, nearshore mussel farms pose a potential threat to dusky dolphins (Markowitz et al. 2004). Green-lipped mussel (*Perna canaliculus*) farming is a major industry in New Zealand, and is rapidly expanding in the Marlborough Sounds (Lloyd 2003). Since much expansion of mussel farming is proposed in Admiralty Bay, there is an urgent need to assess its potential impact on dusky dolphins.

Dusky dolphins rarely use areas within farms (Markowitz et al. 2004; H. Pearson, unpublished data). Therefore, mussel farms may affect dusky dolphins by limiting available habitat (Würsig and Gailey 2002). It is important to monitor the impact of mussel farms on dusky dolphins in Admiralty Bay, because if negative effects occur, the subset (and potentially the cultural unit) of the dusky dolphin population that feeds in Kaikoura during the summer and in Admiralty Bay during the winter may be detrimentally affected (Markowitz et al. 2004; Whitehead et al. 2004). Additionally, in light of the rapid expansion of marine farming worldwide (FAO 2007) more data are needed to quantify the behavioral effects of mussel farming on dolphins in order to facilitate effective conservation management strategies.

The present study describes grouping and behavioral patterns for dusky dolphins in Admiralty Bay, New Zealand. Specifically, I describe how coordinated foraging strategies, predation risk, and mussel farming affect fission-fusion dynamics of dusky dolphins. The following null hypotheses were tested: 1) coordinated foraging strategies do not affect party size and rate of fission-fusion (percent change in party size from one interval to the next), 2) predation risk does not affect party size and behavioral state, and 3) mussel farms do not affect party size, behavioral state, and rate of fission-fusion. Null and alternative hypotheses are presented in Table 1. Alternative hypotheses are based on results from dusky dolphin studies by Würsig, Markowitz, and colleagues (e.g., Würsig and Würsig 1980; Würsig and Gailey 2002; Markowitz et al. 2004) and personal observations obtained during a preliminary study in Admiralty Bay during August 2004.

Table 1. Null (H_0) and alternative (H_a) hypotheses regarding influences on fission-fusion sociality for dusky dolphins in Admiralty Bay.

H_0. Coordinated foraging strategies do not affect party size and rate of fission-fusion.
  - H_a. Party size is positively related to foraging as more individuals converge to herd prey.
  - H_a. Rates of party fusion are positively related to foraging as individuals join parties during coordinated herding of prey.

H_0. Predation risk does not affect party size and behavioral state.
  - H_a. Due to low predation risk, party size is either negatively or not related to resting.
  - H_a. Due to low predation risk, resting does not occur less often in the middle of the Bay relative to nearshore areas.

H_0. Mussel farms do not affect party size, behavioral state, and rate of fission-fusion.
  - H_a. Party size is negatively related to mussel farms (relative to nearshore comparison areas) as parties become fragmented when circumventing the farms.
  - H_a. Rate of party fission is positively related to mussel farms as parties become fragmented.
  - H_a. Traveling is positively related to mussel farms as individuals move around the farms; foraging, resting, and socializing are negatively related to mussel farms.

Methods

Study site and surveys

Dusky dolphins were observed in Admiralty Bay (40° 56' S, 173° 53' E), at the northern tip of New Zealand's South Island (Fig. 4). Admiralty Bay opens up to the French Pass in the southwest and the Cook Strait in the northeast. French Pass is a narrow waterway connecting Tasman Bay with the Cook Strait, where colliding currents and tidal changes create turbulent waters. These hydrographic processes may enhance primary productivity and attract aggregations of schooling fish that are fed on by dusky dolphins and seabirds (Baker 1972). Admiralty Bay has an area of 117 km^2, maximum depth of 105 m, and has a benthos primarily composed of mud substrate (McFadden 2003). At the time of this study, there were 53 mussel farms in Admiralty Bay, covering a total area of 1.20 km^2.

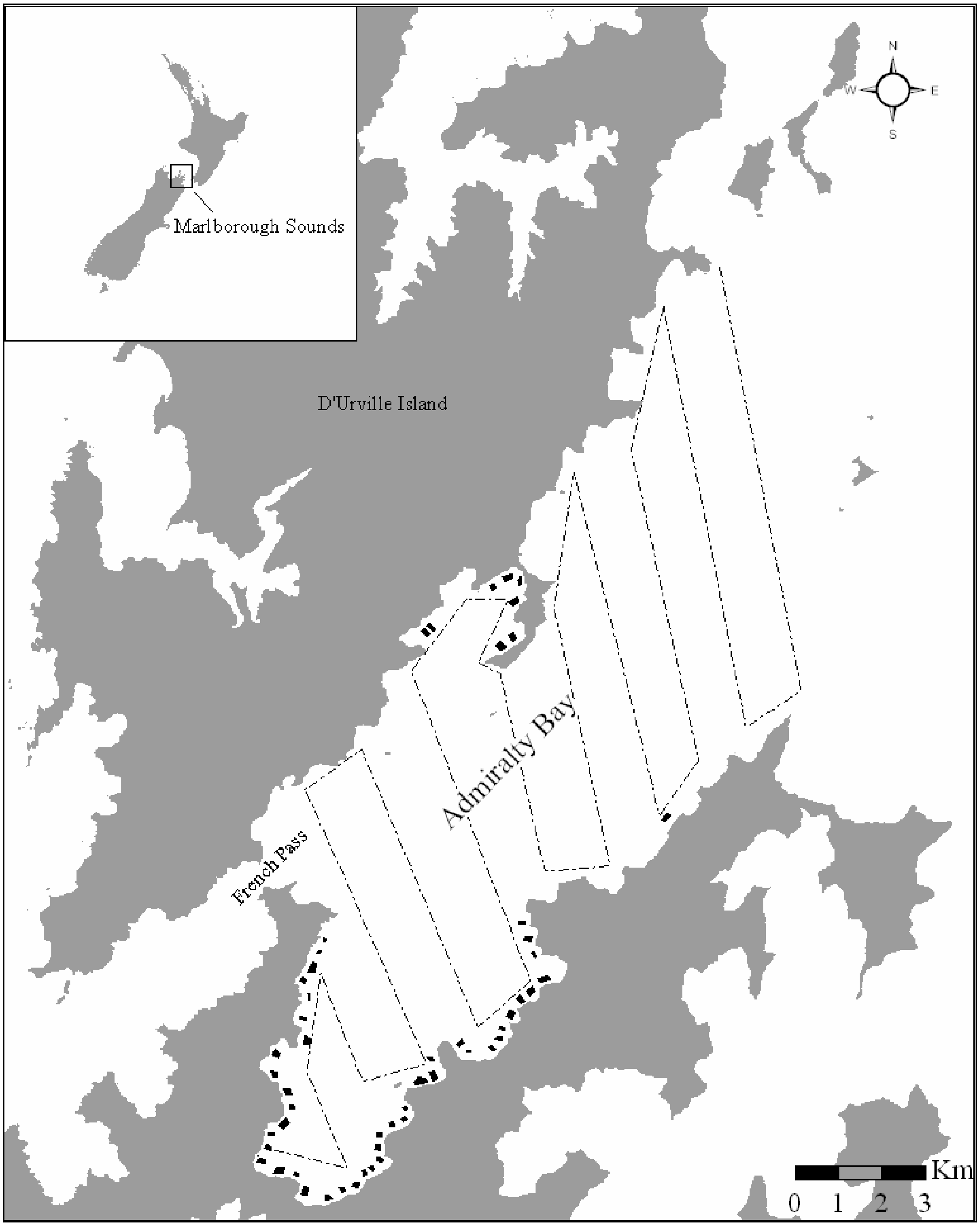

Fig. 4. Map of dusky dolphin study area in Admiralty Bay, New Zealand. Survey transect lines followed during 2005-2006 are shown by dotted lines, and mussel farm locations are shown by black polygons. The inset shows location of the study area in relation to the rest of New Zealand.

Systematic surveys were conducted to locate dusky dolphin parties using a 5.5 m rigid-hull, semi-inflatable skiff. The research team and I conducted surveys at speeds of 10-13 knots and in sea conditions of Beaufort 0-3 with no to light rain. Transect lines were followed according to a pre-determined route programmed into a Garmin 76 global positioning system (GPS) (Fig. 4). To avoid sampling the same areas at the same time of day, survey start positions were varied each day. An attempt was made to start surveying each day at the approximate location where the previous day's survey ended, weather permitting. Dolphins were also located opportunistically while driving to the survey start position.

Two to six observers were positioned on the boat to permit a 360° scan of the water. When dolphins were spotted, a GPS location was taken on the transect line before approaching the party. I use the term "party" instead of "group" to reflect the fluid nature of dolphin aggregations within fission-fusion societies (after Smolker et al. 1992). At the conclusion of behavioral observations, an attempt was made to resume surveying at the transect location where we left off, weather permitting. As one measure of predation risk, data regarding presence and location of killer whales were also recorded.

Focal observations

Behavioral observations were conducted using a focal group sampling technique (Lehner 1996). Parties were defined using a combination of the 10-m chain rule (an individual is part of a party if it is within 10 m of any another individual; Smolker et al. 1992), and coordinated activity (Mann 2000), *viz*. parties with members ≤ 10 m apart may be engaged in different activities, but parties with members spaced > 10 m apart must be engaged in the same activity to be considered in the same party. Additionally, any two individuals could be separated by no more than 100 m to be considered in the same party. During a focal follow, we matched the party's speed and followed the party in a parallel direction. If a party fissioned (i.e., separated) during the focal follow, an attempt was made to alternate between following the larger party and the smaller party (e.g., during fission #1, the smaller party was followed; during fission #2 the larger party was followed; during fission #3 the smaller party was followed, etc.; after Mann 1999).

For each focal follow, time of day (morning [0800-1100 h], mid-day[1100-1400 h], afternoon [1400-1700 h]) and season (winter [May-Aug], spring [Sep-Oct]) were recorded. Instantaneous samples (Lehner 1996) were taken at 2 min intervals to record party size, behavioral state, and GPS location of the research boat. To estimate party size, I used the maximum number of individuals surfacing at any given time or sequentially in different locations; opportunistically, party size was also estimated by counting the number of animals as the party swam under the research boat. To determine behavioral state, the party was systematically scanned and each individual was recorded as foraging, resting, socializing, traveling, or other/unknown (Table 2). Thus, for each sampling interval, the proportion of individuals engaged in each behavioral state was calculated.

Table 2. Ethogram for dusky dolphins in Admiralty Bay.

Behavioral state	**Description**
Forage	Searching for or consuming prey, as indicated by long, deep dives followed by loud forceful exhalations (“chuffs”), and directionless movement; may include coordinated “burst swims” (rapid bursts of speed), “clean” noiseless headfirst re-entry leaps, coordinated clean leaps, and tail slaps
Rest	Slow directionless movement at speeds of < 3 knots close to the surface with low activity level; often includes slow surfacings and floating near the surface
Social	Interacting with each other or inanimate objects; usually directionless movement and may include body and pectoral fin rubbing, rolling, belly-up swimming, spyhops (projection of the head above water), splashing at the surface, chasing, leaping, mating, and playing with seaweed
Travel	Steady movement in one direction at speeds of ≥ 3 knots

Mussel farms

Locations of all mussel farms in Admiralty Bay were determined using a GPS. The points were plotted on a map using Geographical Information System software (ArcGIS 9.0, Environmental Systems Research Institute), and a single polygon was created to represent each farm (Fig. 4). GPS locations from each focal follow were also plotted, and each point was categorized into one of three locations: ≤ 500 m from a mussel farm (near farm), ≤ 500 m from shore (nearshore), or > 500 m from a mussel farm or shore (mid-bay). If a point was ≤ 500 m from both a farm and shore, it was categorized as the location to which it was closest. Since all mussel farms were positioned along shore, areas without mussel farms (i.e., nearshore areas) were used as comparison areas to "near farm" areas to determine the influence of mussel farms on party size, rate of fission-fusion, and behavior.

Statistical analyses

To test if parties were observed equally in each behavioral state, a Hotelling's t-squared (T^2) test was run using SPSS software (SPSS 15.0, SPSS Inc., Chicago, IL). To meet the assumptions of this test, focal follows with ≥ 20 observation intervals were used. The mean proportion of time each activity was observed was then analyzed.

The generalized estimating equation procedure (GEE) (SPSS 15.0, SPSS Inc., Chicago, IL) was used to model the effects of: 1) behavioral state and location on party size (Model 1), 2) location on each behavioral state (Models 2a-d), and 3) location and behavioral state on rate of fission-fusion (Models 3a-b). GEE allows analysis of repeated measurements and correlated observations. Furthermore, GEE assumes that cases within subjects are dependent and cases between subjects are independent. GEE was appropriate for this study because it allowed me to use each 2-min observation point within each focal follow; each 2-min interval within a focal follow represented one "case", whereas each focal follow represented one "subject". A first-order autoregressive working correlation matrix was specified for all GEE models because variables recorded at adjacent intervals were likely to be correlated. The party size variable was log-transformed so as to approximate a normal distribution.

Party size, behavioral states, and rate of fission-fusion were entered as continuous variables. Location was entered as a categorical variable, with "nearshore" as the reference group. Time of day and season were entered as categorical variables, with morning and winter, respectively, as the reference groups. If a focal follow spanned two time periods, the follow was coded as the time period during which the majority of the follow occurred. To examine the rate of fission-fusion, separate GEE models were run for positive ("fusion") and negative ("fission") changes in party size. Season and time of day were included in the GEE models for party size and behavior. All sampling intervals for which party size and location were recorded were included in the final dataset for analysis.

The two-tailed significance level for the Hotelling's T^2 test and Model 1 were set at $p < 0.05$. To reduce the risk of committing a Type I error when running separate GEE models for each of the 4 behavioral states (Models 2a-d) and rate of party fission and fusion (Models 3a-b), the two-tailed significance levels for these models were set at $\alpha/4$ or $p < 0.0125$ and $\alpha/2$ or $p < 0.025$, respectively. Means are presented ± standard deviations (SD).

Results

The research team and I searched for dusky dolphins over the course of 76 days, between 0700 and 1700 h New Zealand Standard Time (Table 3). During this period, 107 h were spent on survey, and 169 h were spent conducting 169 focal follows. Killer whales were observed on one occasion in Admiralty Bay. On August 30, 2006, a pod of 6 killer whales was present. No dusky dolphins were observed that day.

General grouping and behavioral patterns

Mean party size was 7.0 ± 6.0 individuals (range 1-50, $N = 4{,}632$ 2-min intervals; Fig. 5). Party size changed on 25.8% of 2-min intervals, and the mean change in party size between consecutive intervals was 19.6 ± 59.4% (range 0-900%, $N = 4{,}323$ 2-min intervals). Party size changed, on average, every 2.7 ± 3.8 intervals, or 5.4 ± 7.6 min (range 1-54 intervals or 2-108 min); therefore, mean party duration was 5.2 min.

Table 3. Summary of research effort in Admiralty Bay from 2005 to 2006.

Month	Data collection days	Survey hours	No. focal follows	Focal follow hours
May [a]	5	12	7	7
June [a]	15	21	40	38
July [a]	12	13	26	28
August [b]	27	32	56	63
September [a]	12	20	31	26
October [a]	5	9	9	7
TOTAL	76	107	169	169

[a] 2006 only

[b] 2005 and 2006

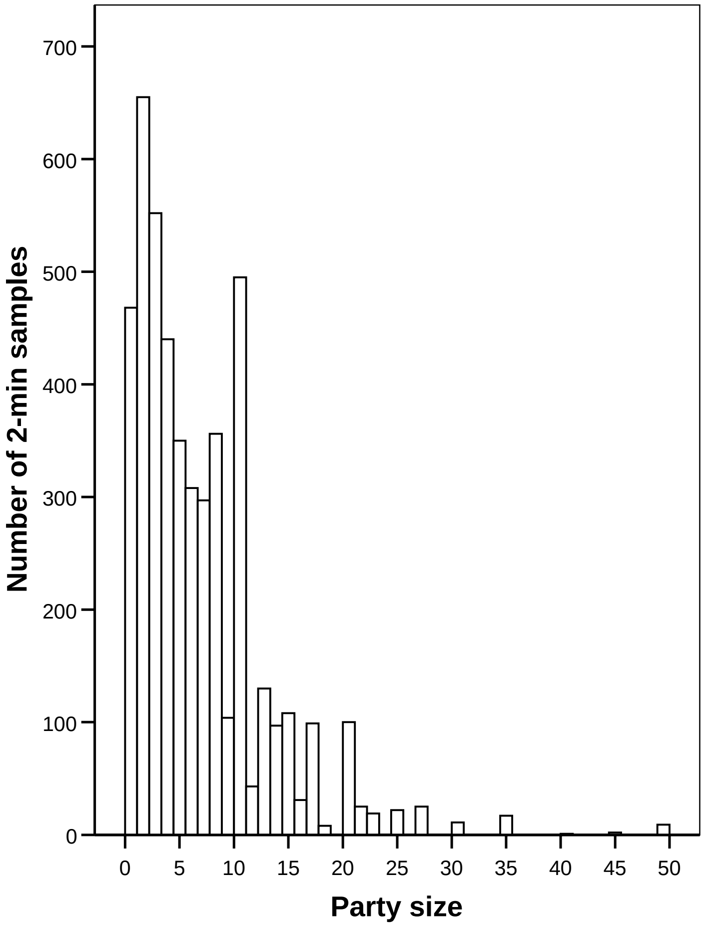

Fig. 5. Frequency distribution of dusky dolphin party sizes in Admiralty Bay ($N = 4{,}632$ 2-min sampling intervals).

Dusky dolphins were not observed equally in each behavioral state ($T^2 = 63.05$, $F [3, 116] = 20.66$, $p < 0.001$). On average, individuals in parties were observed foraging on 18 ± 18.2% of sampling intervals, resting on 36 ± 20.3% of sampling intervals, socializing on 15 ± 17.5% of sampling intervals, and traveling on 29 ± 18.0% of sampling intervals (Fig. 6). Individuals in parties were observed foraging and socializing less than expected by chance, and resting and traveling more than expected by chance.

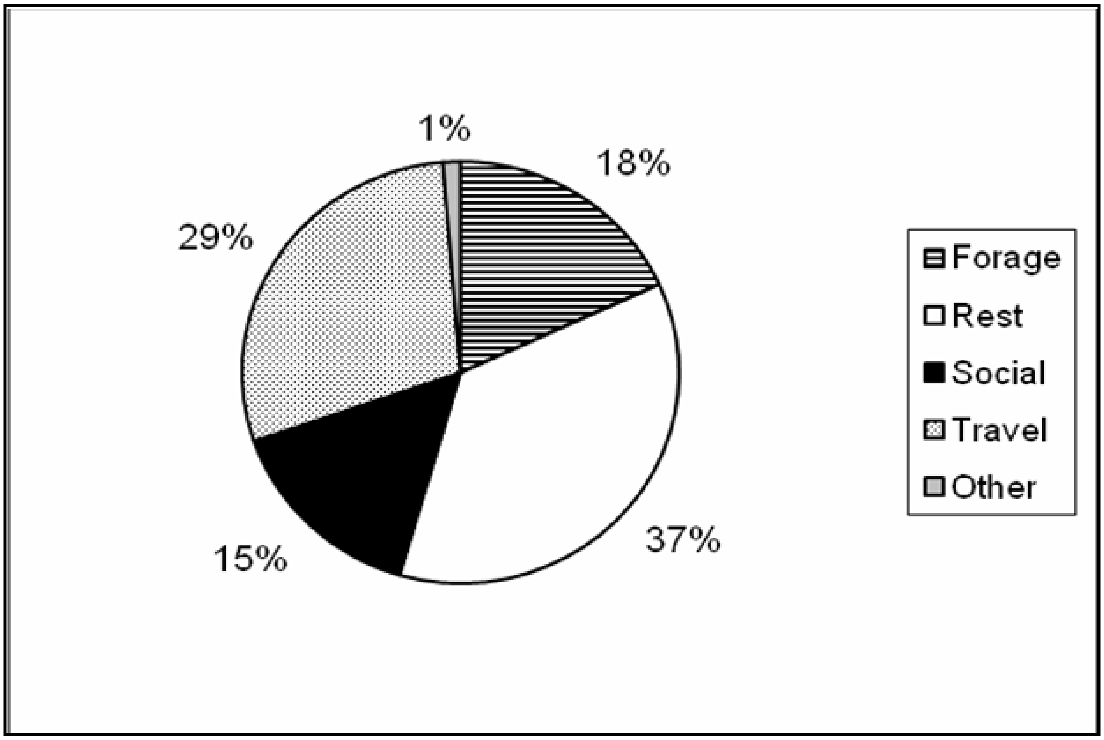

Fig. 6. Activity budget for dusky dolphin parties in Admiralty Bay. Percentages represent the proportion of individuals observed in each behavior during 4,632 2-min sampling intervals.

GEE models

Coordinated foraging strategies exerted a positive influence on fission-fusion dynamics. Foraging was positively related to party size (Table 4) and rates of party fission and fusion (Table 5).

Table 4. Generalized estimating equations model showing the effect of behavioral state and location on party size while controlling for season and time of day ($N = 4{,}632$ 2-min sampling intervals collected during 169 focal follows). Significant variables are in bold type.

Variable	***B*** [a]	**Standard error *B***	***P*-value**
Intercept	1.984	0.088	0.000
Forage	**0.147**	**0.039**	**0.000**
Rest	-0.038	0.034	0.265
Social	**-0.123**	**0.040**	**0.002**
Travel	-0.058	0.038	0.124
Mussel farm	-0.027	0.054	0.617
Mid-bay	-0.029	0.041	0.486
Nearshore	— [b]	—	—
Mid-day	0.069	0.116	0.550
Afternoon	-0.243	0.150	0.105
Morning	—	—	—
Spring	-0.131	0.110	0.230
Winter	—	—	—

[a] Parameter estimate

[b] Reference category

Table 5. Generalized estimating equations models showing the effect of behavioral state and location on rates of party fission (*N* = 4,320 2-min sampling intervals collected during 169 focal follows) and fusion (*N* = 3,765 2-min sampling intervals collected during 169 focal follows). Significant variables are in bold type.

Model	Variable	*B* [a]	Standard error *B*	*P*-value
Negative change in party size ("fission")	Intercept	0.156	0.523	0.003
	Forage	**0.157**	**0.058**	**0.006**
	Rest	-0.018	0.044	0.683
	Social	0.017	0.054	0.749
	Travel	0.003	0.048	0.956
	Mussel farm	0.071	0.033	0.030
	Mid-bay	0.001	0.035	0.981
	Nearshore	— [b]	—	—
Positive change in party size ("fusion")	Intercept	0.119	0.061	0.053
	Forage	**0.177**	**0.070**	**0.011**
	Rest	-0.044	0.058	0.448
	Social	-0.007	0.067	0.914
	Travel	-0.004	0.061	0.950
	Mussel farm	**0.078**	**0.033**	**0.017** [c]
	Mid-bay	0.013	0.032	0.691
	Nearshore	—	—	—

[a] Parameter estimate

[b] Reference category

[c] Bonferroni-adjusted pairwise comparisons revealed no significant differences in rate of party fusion between mussel farm, mid-bay, and nearshore locations

To assess the influence of predation risk, the effects of resting behavior on party size, and location (mid-bay *vs*. nearshore areas) on resting behavior, were examined. Resting had no effect on party size (Table 4), and resting did not occur less often in mid-bay areas relative to nearshore areas (Table 6).

To assess the influence of mussel farms on dusky dolphin fission-fusion dynamics, the effect of location (mussel farms *vs*. nearshore areas) on party size, rates of party fission and fusion, and behavior were examined. Party size did not decrease near mussel farms (Table 4). However, rate of party fusion increased near mussel farms (Table 5). Additionally, near mussel farms, foraging increased while traveling decreased (Table 6).

Table 6. Generalized estimating equations models showing the effect of location on each behavioral state while controlling for season and time of day (N = 4,632 2-min sampling intervals collected during 169 focal follows). Significant variables are in bold type.

Model	**Variable**	***B*** [a]	**Standard error *B***	***P*-value**
Forage	Intercept	0.197	0.036	0.000
	Mussel farm	**0.085**	**0.033**	**0.011** [b]
	Mid-bay	-0.018	0.031	0.557
	Nearshore	— [c]	—	—
	Mid-day	0.001	0.039	0.990
	Afternoon	0.023	0.041	0.582
	Morning	—	—	—
	Spring	-0.042	0.036	0.243
	Winter	—	—	—
Rest	Intercept	0.302	0.037	0.000
	Mussel farm	0.021	0.041	0.616
	Mid-bay	0.033	0.034	0.334
	Nearshore	—	—	—
	Mid-day	-0.022	0.040	0.575
	Afternoon	0.058	0.034	0.085
	Morning	—	—	—
	Spring	0.100	0.051	0.051
	Winter	—	—	—
Social	Intercept	0.161	0.031	0.000
	Mussel farm	-0.020	0.024	0.391
	Mid-bay	-0.010	0.022	0.647
	Mid-day	-0.005	0.036	0.886
	Afternoon	-0.017	0.029	0.550
	Morning	—	—	—
	Spring	0.038	0.040	0.341
	Winter	—	—	—
Travel	Intercept	0.389	0.052	0.000
	Mussel farm	**-0.128**	**0.050**	**0.009** [d]
	Mid-bay	0.055	0.053	0.295
	Nearshore	—	—	—
	Mid-day	-0.033	0.016	0.040
	Afternoon	-0.029	0.016	0.070
	Morning	—	—	—
	Spring	**-0.217**	**0.026**	**0.000** [e]
	Winter	—	—	—

[a] Parameter estimate

[b] Bonferroni-adjusted pairwise comparisons revealed that a greater proportion of individuals were observed foraging near mussel farms than mid-bay (p = 0.001) or nearshore (p = 0.034).

[c] Reference category for location variable

[d] Bonferroni-adjusted pairwise comparisons revealed that a smaller proportion of individuals were observed traveling near mussel farms than mid-bay (p = 0.000) or nearshore (p = 0.028).

[e] Bonferroni-adjusted pairwise comparisons revealed that a greater proportion of individuals were observed traveling during winter than during spring (p = 0.000).

Discussion

This study reveals several important results regarding the influence of coordinated foraging strategies, predation risk, and mussel farming on dusky dolphin fission-fusion sociality. While the data supported all of my alternative hypotheses regarding the influence of coordinated foraging strategies and predation risk, none of my alternative hypotheses regarding mussel farms were supported. Additionally, this study has applications to conservation management strategies, research methods, and evolutionary socioecology.

Coordinated foraging strategies

Foraging was positively related to dusky dolphin party size and rates of fission and fusion, supporting the first two alternative hypotheses presented in Table 1. These results indicate that coordinated foraging strategies shape dusky dolphin grouping patterns in Admiralty Bay. As observed in Golfo San José (Würsig and Würsig 1980), coordinated foraging is facilitated by larger party size. These foraging parties are also fluid in nature, as new individuals join while others leave, possibly after becoming satiated.

Fission-fusion dynamics in Admiralty Bay are not as dramatic as in Golfo San José. Although parties converge to herd prey balls in both areas, maximum party size in Admiralty Bay was 50 individuals, which is much smaller than the maximum size of 300 in Golfo San José (Würsig and Würsig 1980). This may in part be a function of bay structure, as Admiralty Bay is a smaller, more enclosed environment than Golfo San José and therefore may not be able to support such large parties. Additionally, as Admiralty Bay is occupied outside of the peak breeding season and it is estimated that 85% of the population is male (Shelton 2006), the large post-feeding socio-sexual aggregations that occur in Golfo San José are not observed.

Predation risk

Killer whales were observed on 1/72 research days in Admiralty Bay during the winter and early spring. Dusky dolphins thus may respond to minimal killer whale predation risk by not increasing resting party size, and not decreasing time spent resting mid-bay or increasing time spent resting in nearshore areas (supporting the third and fourth alternative hypotheses presented in Table 1). Dusky dolphins that migrate annually between Kaikoura and Admiralty Bay are exposed to dramatically different levels of predation risk, which may result in much larger group formation in Kaikoura than Admiralty Bay. Overall, rich foraging grounds and minimal predation risk may be among the evolutionary pressures responsible for this annual wintertime migration to Admiralty Bay.

In the absence of predation pressure, availability of prey and estrous females are likely to influence sociality. For dusky dolphins inhabiting the relatively predator-free waters of Admiralty Bay outside the peak breeding season, prey availability may be a primary influence on sociality. As in Admiralty Bay, there is little predation risk for bottlenose dolphins inhabiting the Amvrakikos Gulf of northwest Greece. In this region, bottlenose dolphins exhibit a wide range of party sizes (from single individuals to large "supergroups" of 150 individuals) and grouping patterns are likely a response to prey type and availability (G. Bearzi, personal communication; Bearzi et al. 2007). Similarly, there is little predation risk for the chimpanzees of Gombe National Park, Tanzania, and grouping patterns are primarily influenced by food availability and the distribution of estrous females (Goodall 1986).

Mussel farms

Results regarding the influence of mussel farms on dusky dolphin fission-fusion dynamics were unexpected. Specifically, none of the alternative hypotheses regarding mussel farms were supported. Contrary to my prediction, party size was not negatively related to mussel farms. Additionally, party fission and fusion rates, foraging, and traveling displayed opposite relationships with mussel farms than predicted. Foraging showed a positive instead of negative relationship with mussel farms, while traveling showed a negative instead of positive relationship with mussel farms. Additionally, mussel farms were associated with an increased rate of party fusion but had no effect on rate of party fission.

Dusky dolphins appeared to be using areas near, but not in, mussel farms for foraging. This is similar to other studies which have reported dolphins to avoid using areas inside marine farms (Markowitz et al. 2004; Watson-Capps and Mann 2005; Ribeiro et al. 2007). Mussel farm buoys may act as fish aggregating devices (FADs) by providing structures which may be used as fish habitat (e.g., Morrisey et al. 2006). Therefore, my observation of increased foraging near mussel farms may be due to higher prey densities associated with mussel farms. Other studies have also reported dolphins to be attracted to the presumably prey-rich waters near fish (Bearzi et al. 2004; Díaz López et al. 2005; Díaz López 2006; Díaz López and Shirai 2007) and mussel (Ribeiro et al. 2007) farms. However, I rarely observed dusky dolphins foraging inside mussel farms (H. Pearson, unpublished data), indicating that even if prey do occur at high densities inside farms, the complex array of mussel lines and buoys may hinder coordinated foraging strategies.

More data regarding dusky dolphin prey abundance and distribution are needed to determine if mussel farms act as FADs in Admiralty Bay. One study in the Marlborough Sounds, New Zealand, found an overall low abundance and diversity of fishes in mussel farms. Out of the 18 species mentioned as being potential colonizers of mussel farms, only five species were observed (4 of these were demersal species), and they occurred in low abundance. Pilchard and yellow-eyed mullet, which are dusky dolphin prey species, were not present in mussel farms (Morrisey et al. 2006).

Implications for research methods

When studying species with fission-fusion systems, there are difficulties in defining parties, party size, and behavior, especially in three-dimensional environments (e.g., oceans, forests) where it is oftentimes difficult to view all party members simultaneously (Chapman et al. 1993). To effectively compare studies, researchers must clearly state their definition of a "group". Additionally, party duration has implications for determining party size. Mean party duration in the present study was 5 min. Other studies have stated that party size and composition change frequently (e.g., Connor et al. 2000b), but few studies provide exact figures for party duration (but see Bearzi et al.

2005). Knowledge of party duration is particularly important when conducting surveys of parties (as opposed to focal follows) – if change in party size is rapid, researchers must quickly make assessments of size and activity before individuals join or leave a party.

To define party behavior, I recorded the number of party members engaged in each activity, thus allowing for more than one activity state to be present at one time. I believe that by not "forcing" all party members to be engaged in the same activity state, a more precise estimate of behavior was obtained, as opposed to recording predominant group activity (after Mann 1999). In general, when comparing results between studies, one must be cognizant of how party activity and size are determined, as differences may be attributed to varying definitions and may not necessarily reflect "real" differences (after Chapman et al 1993).

Evolutionary socioecology

Intra-group competition for resources, coupled with complex cognition, may have been selective agents for the evolution of the type of fission-fusion sociality present in dolphins, chimpanzees, spider monkeys, elephants, and hyenas (Lehmann et al. 2007). In primates, scramble competition and travel costs may limit group size, and Lehmann et al. (2007) demonstrated how it would be impossible for chimpanzees (*Pan* sp.) to survive anywhere in Africa if they did not have a fission-fusion social system. The ability of community members to reduce travel costs by splitting into small parties during foraging ultimately permits a larger, viable community size which is important for reproduction and territory defense (Lehmann et al. 2007).

In contrast to chimpanzees, dolphins have a low cost of locomotion (Williams et al. 1992) and thus travel costs are unlikely to limit group size. However, the cost of locomotion may still influence fission-fusion strategies in dolphins. Instead of acting as a negative influence on sociality, the cost of locomotion may act as a positive influence on dolphin sociality by permitting a large social network. A large number of associates may be important in the development of cooperative or coordinated foraging strategies (e.g., Würsig and Würsig 1980; Gazda et al. 2005), and alliance-based mating strategies (e.g., Connor et al. 2001). Larger party sizes are also advantageous for predator protection (e.g., Norris and Dohl 1980b; Connor 2000). However, smaller groups may be advantageous when prey items occur singly and cooperative or coordinated foraging is inefficient (e.g., Heithaus and Dill 2002; Mann and Sargeant 2003; Gowans et al 2008). Future studies are warranted which will test the relative importance of factors which may have contributed to fission-fusion sociality in delphinids.

Conclusion

This study has theoretical and practical implications. By continuing to examine fission-fusion sociality within a variety of populations and species, further insight may be gained regarding the relative importance of factors which have shaped the evolution of fission-fusion sociality. I described fission-fusion sociality by examining the ecological influences of coordinated foraging and predation risk, and the anthropogenic effects of mussel farms. However, other factors, such as the effect of estrous females on grouping patterns, should be further explored. Some chimpanzee studies have found the presence of estrous females to exert a stronger force on fission-fusion grouping patterns than food availability or predation risk (Goodall 1986; Hashimoto et al. 2001; Anderson et al. 2002). Studies which explore this relationship in delphinids are also warranted.

From a practical perspective, this study has shown that mussel farms affect behavioral and grouping patterns for dusky dolphins in Admiralty Bay. While dusky dolphins may use areas near mussel farms for foraging, they rarely use areas inside mussel farms. In light of the rapidly expanding marine farming industry worldwide, future studies should continue to monitor dolphin populations which co-occur with marine farms in order to identify possible long-term and “top-down” effects. As some systems may show latent and/or delayed effects, longitudinal studies are warranted.

CHAPTER III

LEAPING BEHAVIOR OF DUSKY DOLPHINS (*Lagenorhynchus obscurus*) IN ADMIRALTY BAY, NEW ZEALAND

Introduction

For leaping to have evolved as a form of energy expenditure in dolphins, it must confer some adaptive benefit to the actor. In captivity, the mean power input required for a dolphin to leap 3m high was 4.0 W kg^{-1}. While this was higher than that required for a dolphin swimming at "preferred" speeds of 1.7 m s^{-1} (approximate mean power input = 2.3 W kg^{-1}), it is similar to that required for a dolphin swimming at "fast" speeds of 3 m s^{-1} (approximate mean power input = 3.7 W kg^{-1}; Yazdi et al. 1999). However, leaping repeatedly in one bout, as exhibited by spinner (*Stenella longirostris*) and dusky (*Lagenorhynchus obscurus*) dolphins, may be more energetically expensive than rapid swimming.

Some types of leaping may conserve energy. When swimming faster than a "crossover" speed, dolphins may perform a series of parabolic forward-moving leaps which are more energetically efficient than swimming that same distance (Au and Weihs 1980; Blake 1983). Similarly, "salmon leaping" (a stiff-bodied and slightly arched leap ending in a side slap) by spinner dolphins is generally seen in fast-moving schools with the proposed function of energy conservation (Norris et al. 1994). Leaping may also remove ectoparasites (Norris et al. 1994; Würsig 2002), and the spinning leaps of spinner dolphins may create enough force to dislodge a remora (order Perciformes, family Echeneididae; Fish et al. 2006; Weihs et al. 2007). However, not all dolphin leaps occur during high-speed travel, not all dolphins which leap have remoras attached (Norris et al. 1994), and there is no evidence that other "acrobatic" dolphins such as dusky dolphins leap for ectoparasite removal. Therefore, leaping must have other functions.

Proposed socioecological functions of leaping include coordination of activity and movement patterns, and reinforcement of social bonds (social facilitation hypothesis, Norris and Dohl 1980a; Norris et al. 1994); and/or facilitation of coordinated herding of prey towards the surface (prey capture hypothesis). The two hypotheses are not mutually exclusive, and dusky dolphin leaping may be used for social facilitation and prey capture (Würsig and Würsig 1980). Acevedo-Gutiérrez (1999) did not find support for the social facilitation hypothesis to explain bottlenose dolphin (*Tursiops truncatus*) hunting behavior and found only weak evidence for the prey capture hypothesis. Slooten (1994) found aerial behaviors to be strongly associated with sexual and aggressive behaviors in Hector's dolphins (*Cephalorhynchus hectori*).

Norris et al. (1994) concluded that leaping may function in more than one context of a society. Others have concluded that different aerial events play different roles, and that specific aerial events should be treated independently and not lumped into one category of aerial behavior (Würsig and Würsig 1980; Lusseau 2006). Thus, in order to understand the causal mechanisms underlying aerial behavior, it is important to examine the overall context in which it occurs and the types of aerial events performed. Furthermore, while the types of leaps contained within a species' behavioral repertoire may be consistent across populations and habitats, the context and function of leaping may vary. Dusky dolphins, which are aerially active across a variety of habitats, provide a natural experiment in which to examine possible selective pressures responsible for the evolution of leaping.

In Golfo San José, Argentina, Würsig and Würsig (1980) described three functions of dusky dolphin leaping associated with daytime foraging. Clean, headfirst, re-entry leaps occur during cooperative herding of fish and allow an individual to quickly catch a breath while at the same time facilitating diving. Noisy leaps occur before and during foraging and may be used to herd fish and as a visual and/or auditory signal to others to join in feeding. Acrobatic leaps occur post-feeding and may be an expression of a high state of alertness as individuals reaffirm socio-sexual bonds

(Würsig and Würsig 1980). Reinforcement of social bonds through leaping may facilitate more effective cooperative foraging strategies (Würsig et al. 1989).

The prevalence and function of leaping differs for dusky dolphins living in large (< 1,000 individuals) groups in deep-water areas off Kaikoura, New Zealand. Noisy leaps are the most common leap type during the day, with the presumptive function of visual and auditory signaling so as to aid in coordinated group movement (e.g., heading, cohesion). Clean leaps are less prevalent off Kaikoura but are present in small mating groups to facilitate socio-sexual interactions (Markowitz 2004). Dusky dolphins off Kaikoura forage almost entirely at night on the deep scattering layer and there is evidence of leaping associated with foraging. In short, leaping behavior off Kaikoura is best explained by the social facilitation hypothesis (Markowitz 2004), while leaping behavior in Golfo San José may be explained by both the social facilitation and prey capture hypotheses (Würsig and Würsig 1980).

I examined dusky dolphin leaping behavior in Admiralty Bay, New Zealand, an area 275 km north of Kaikoura. Dusky dolphins occur in Admiralty Bay during the winter and early spring when their prey (e.g., pilchard, *Sardinops neopilchardus*) are present. During the day, dusky dolphins herd fish into prey balls in a coordinated manner (Vaughn et al. 2007). Some dusky dolphins annually travel between summer mating grounds in Kaikoura and winter foraging grounds in Admiralty Bay (Markowitz et al. 2004).

The physical habitat and social structure differ between Admiralty Bay, Golfo San José, and Kaikoura. Admiralty Bay is smaller in area, group size is smaller, and fission-fusion social dynamics are different (Chapter II, this volume). Thus, by examining dusky dolphin leaping behavior in Admiralty Bay as compared to Kaikoura and Golfo San José, I am able to assess the possible function of leaping.

I use the social facilitation and prey capture hypotheses as testable frameworks in which to explore the proximate context and ultimate function of leaping behavior. Specifically, I collected data on how dusky dolphins leap (i.e., frequency of four types of leaps) and what may cause them to leap (i.e., data on group size and behavior). If the function of leaping is primarily related to the social facilitation hypothesis, I predict the frequency of clean, coordinated, and acrobatic leaps will be positively related to socializing behavior, while the frequency of noisy leaps will be positively related to traveling behavior and party size (Table 7). If the function of leaping is primarily related to the prey capture hypothesis, I predict the frequency of clean and noisy leaping will be positively related to foraging behavior, the frequency of coordinated leaping will be positively related to foraging behavior and party size, and the frequency of acrobatic leaping will be low in general.

Methods

Boat-based surveys

Admiralty Bay (40°56'S, 173°53'E) is located at the northern tip of New Zealand's South Island (Fig. 4). A 5.5 m rigid-hull, semi-inflatable skiff was used to locate dusky dolphin parties, and 2-6 observers were positioned on the skiff to permit a 360° scan of the horizon. I use the term "party" instead of "group" to reflect the fluid nature of dolphin aggregations within fission-fusion societies (after Smolker et al. 1992). Systematic surveys were conducted at speeds of 10-13 knots and in sea conditions of Beaufort 0-3 with no to light rain. We followed transect lines on a pre-determined route programmed into a Garmin 76 global positioning system (GPS) (Fig. 4). Survey start positions were varied each day to avoid sampling the same areas at the same time of day. An attempt was made to start surveying each day at the approximate location where the previous day's survey ended, weather permitting. Dolphins were also located opportunistically while driving to the survey start position. When a party was spotted, a GPS location was taken on the transect line before approaching the party. At the conclusion of behavioral observations, an attempt was made to resume surveying at the transect location where we left off, weather permitting.

Focal observations

Behavioral observations were conducted using a focal group sampling technique (Lehner 1996). Parties were defined using a combination of the 10-m chain rule (an individual is in a party if it is ≤ 10 m of any another individual; Smolker et al.

Table 7. Predictions regarding dusky dolphin leaping behavior in terms of the social facilitation and prey capture hypotheses (see text for descriptions of hypotheses).

Hypothesis	**Leap type**	**Prediction**
1. Social facilitation	Clean	1a. Positively related to socializing: clean leaping will enable an individual to quickly catch a breath during socio-sexual interactions
	Noisy	1b. Positively related to traveling: noisy leaps will facilitate increased cohesion and coordinated movement when traveling
		1c. Positively related to party size: larger parties will require more noisy leaping in order to maintain cohesion and coordinated movement
	Coordinated	1d. Positively related to socializing: individuals will reinforce social bonds by leaping in unison
	Acrobatic	1e. Positively related to socializing: acrobatic leaping may be an expression of a high state of alertness as individuals reaffirm socio-sexual bonds
2. Prey capture	Clean	2a. Positively related to foraging: clean leaping will enable individuals to quickly catch a breath before returning to depth to forage
	Noisy	2b. Positively related to foraging: noisy leaps will function in herding prey or in signaling other individuals to join in foraging
	Coordinated	2c. Positively related to foraging: leaping in unison will enable individuals to coordinate movements so as to more effectively herd and contain prey
		2d. Positively related to party size: larger parties will necessitate more coordination between individuals in order to herd and contain prey
	Acrobatic	2e. Frequency will be low in general: acrobatic leaps have no expected function during foraging

1992) and coordinated activity (Mann 2000). Therefore, parties with members ≤ 10 m apart may be engaged in different activities, but individuals > 10 m apart must be engaged in the same activity to be considered in the same party. Additionally, any two individuals had to be ≤ 100 m apart to be considered in the same party. During a focal follow, we matched the party's speed and followed it in a parallel direction. If a party fissioned (i.e., separated) during the focal follow, an attempt was made to alternate between following the larger party and the smaller party (e.g., during fission #1, we followed the smaller party; during fission #2 we followed the larger party; during fission #3 we followed the smaller party, etc., after Mann 1999).

Leap frequency was recorded during 2-min intervals using all-occurrence sampling (Lehner 1996). After Würsig and Würsig (1980) and Markowitz (2004), leaps were classified into biologically meaningful categories: "clean", noiseless, headfirst re-entry leaps; noisy leaps; and acrobatic leaps (Fig. 7, Table 2). Additionally, I added a category for coordinated leaps which took precedence over all other leap types (e.g., if two individuals displayed clean leaps at the same time, it was recorded as coordinated instead of clean). Noisy leaps were often performed as a repeated series of leaps by the same individual; such cases were recorded as one noisy leap occurrence.

Party size, activity state, GPS location of the research boat, and time of day were recorded using instantaneous point sampling (Lehner 1996) at each 2-min interval. To estimate party size, I counted the maximum number of individuals surfacing at any given time or sequentially in different locations, or by counting the number of individuals as the party swam under our boat. To determine activity state, the party was systematically scanned and each individual was recorded as foraging, resting, socializing, traveling, or other/unknown (Table 2). For each sampling interval, I calculated the proportion of individuals in each activity state.

Analysis plan

Analyses were conducted using the generalized estimating equation procedure (GEE) (SPSS 15.0, SPSS Inc., Chicago, IL). GEE allows analysis of repeated measurements and correlated observations, and assumes that cases within subjects are dependent and cases between subjects are independent. GEE permitted the use of each 2-min observation point within each focal follow; each 2-min interval within a focal follow represented one "case", whereas each focal follow represented one "subject".

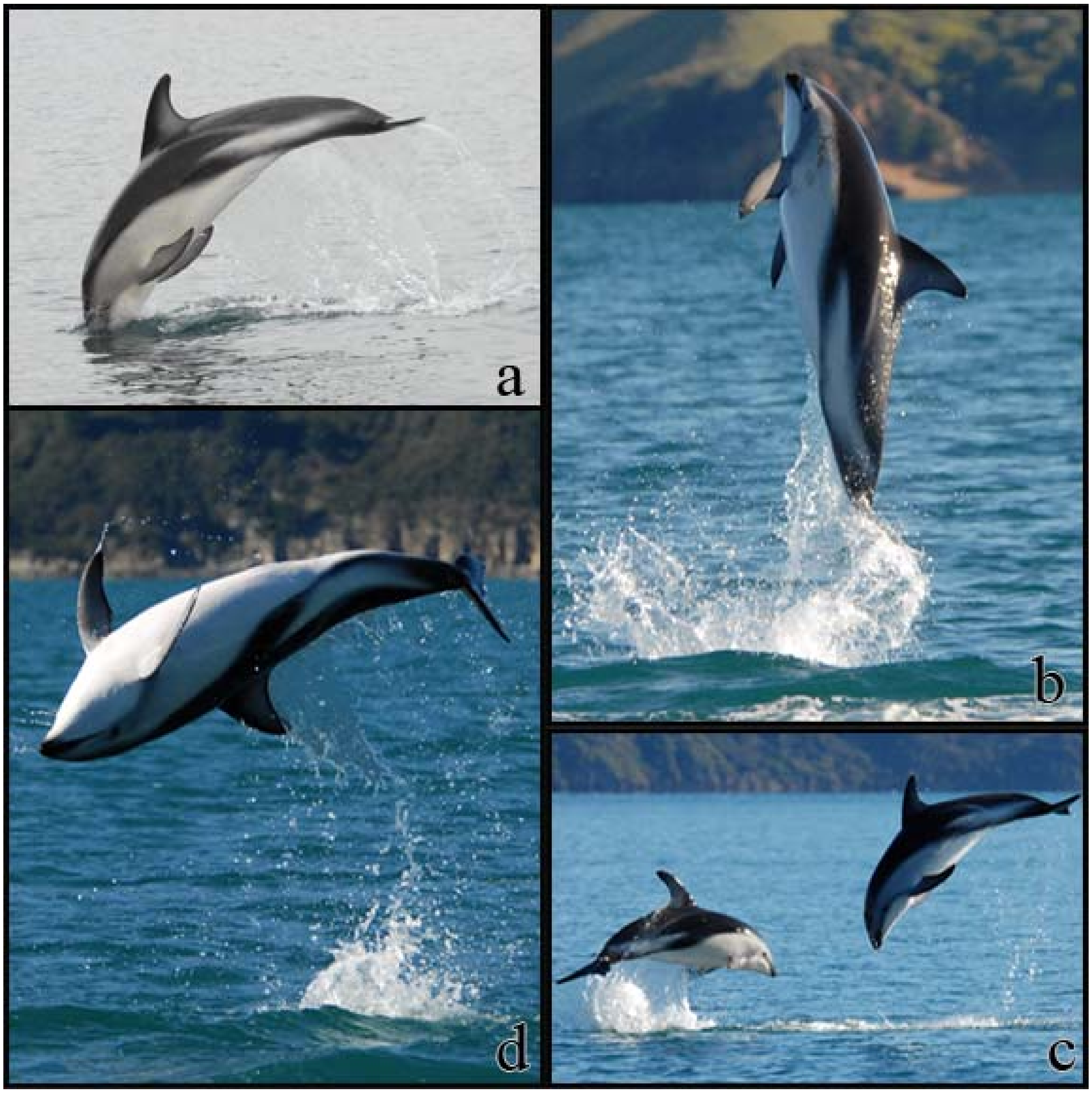

Fig. 7. Leap types recorded for dusky dolphins in Admiralty Bay: a) clean, b) noisy, c) coordinated, and d) acrobatic. All photos except clean leap courtesy of Chris Pearson.

GEE was used to model the effects of party size and behavioral state on the frequency of clean, noisy, and coordinated leaps. A GEE model for acrobatic leaps was not run due to the low frequency ($n = 46$) of this leap type. Time of day and season were included in the models as control variables. A first-order autoregressive working correlation matrix was specified for all GEE models since variables recorded at adjacent intervals were likely to be correlated. All sampling intervals where party size was recorded were included in the final dataset for GEE analyses.

Number of leaps within each 2-min sampling interval, party size, and behavioral states were entered into the GEE models as continuous variables. Number of leaps was log-transformed to approximate a normal distribution. Time of day (morning [0800-1100 h], mid-day [1100-1400 h], afternoon [1400-1700 h]) and season (winter [May-August], spring [September-October]) were entered as categorical variables with morning and winter, respectively, as reference groups. To protect against committing a Type I error when running separate models for each of the three leap types, the two-tailed alpha level was set at 0.05/3, or $p < 0.017$. Means are presented ± SD.

Results

I searched for dusky dolphins for 107 h over 76 d, from 5 August to 24 August 2005 and from 22 May to 8 October 2006. Surveys were conducted between 0700 h and 1700 h New Zealand Standard Time, and 171 focal follows were conducted totaling 157 h of observation time. Mean party size was 7.0 ± 6.0 individuals (range 1-50, $N = 4{,}702$ 2-min intervals). Individuals in parties were observed foraging on 19 ± 37.3% of sampling intervals, resting on 36 ± 45.1% of sampling intervals, socializing on 14 ± 32.8% of sampling intervals, and traveling on 30 ± 44.0% of sampling intervals.

Nineteen percent ($n = 896$) of sampling intervals contained ≥ 1 of the four leap types. For sampling intervals in which leaping behavior was present, leaps occurred at a rate of 0.61± 0.75 leaps/individual (range 0.03-6.60, $n = 896$). Clean leaps were the most frequent type, comprising 84% ($n = 3404$) of all leaping occurrences, followed by coordinated leaps (11%, $n = 448$), noisy leaps (4%, $n = 140$), and acrobatic leaps (1%, $n = 46$; Fig. 8).

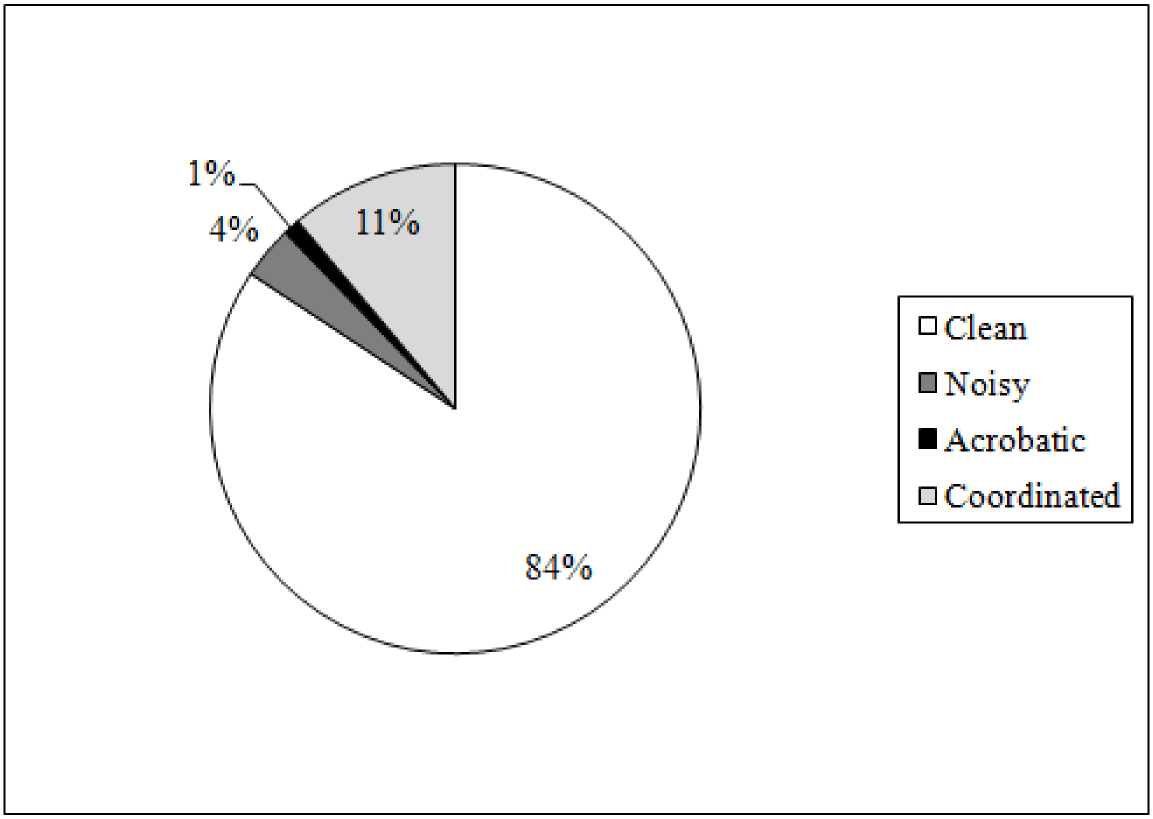

Fig. 8. Proportion of each leap type observed for dusky dolphins (*N* = 4,038 leaps observed over 4,702 2-min samples).

The frequency of clean leaping was positively related to party size and the proportion of individuals foraging within a party (Table 8). The frequency of noisy leaping was positively related to party size, and negatively related to the proportion of individuals foraging within a party. The frequency of coordinated leaps was positively related to party size. Time of day and season were not significant in any model.

Discussion

Of the predictions that could be tested with my dataset, 1 of 5 predictions (prediction 1c) was met for the social facilitation hypothesis, while 3 of 5 predictions (2a, 2d, 2e) were met for the prey capture hypothesis (Table 7). The function of leaping in Admiralty Bay appears to primarily be related to increasing foraging efficiency, but it is apparent that leaping functions in more than one aspect of dusky dolphin society.

Table 8. Generalized estimating equations models showing the effect of behavior and party size on frequency of dusky dolphin leap type while controlling for season and time of day (*N* = 4,702 2-min samples). Significant variables are in bold type.

Model[a]	**Variable**	***B***[b]	**Standard error *B***	***P*-value**
Clean leap	Intercept	-3.106	0.603	0.000
	Party size	**0.064**	**0.006**	**0.000**
	Forage	**3.142**	**0.575**	**0.000**
	Rest	1.164	0.593	0.050
	Social	1.049	0.573	0.067
	Travel	0.767	0.528	0.146
	Afternoon	0.118	0.243	0.627
	Mid-day	0.324	0.289	0.262
	Morning	—[c]	—	—
	Spring	-0.037	0.279	0.896
	Winter	—	—	—
Noisy leap	Intercept	-3.148	0.581	0.000
	Party size	**0.065**	**0.017**	**0.000**
	Forage	**-1.587**	**0.599**	**0.008**
	Rest	-1.131	0.530	0.033
	Social	-0.589	0.571	0.303
	Travel	-0.851	0.585	0.146
	Afternoon	-0.204	0.485	0.674
	Mid-day	-0.012	0.297	0.968
	Morning	—	—	—
	Spring	0.611	0.277	0.028
	Winter	—	—	—
Coordinated leap	Intercept	-26.588	25.192	0.291
	Party size	**0.076**	**0.011**	**0.000**
	Forage	23.804	24.432	0.330
	Rest	21.485	24.520	0.381
	Social	21.884	24.646	0.375
	Travel	20.935	24.511	0.393
	Afternoon	0.057	0.521	0.913
	Mid-day	0.826	0.511	0.106
	Morning	—	—	—
	Spring	-0.657	0.431	0.128
	Winter	—	—	—

[a] A GEE model for acrobatic leaps was not run due to low occurrence of this leap type.
[b] Parameter estimate
[c] Reference category

Inter-site variation in leap frequency and context

Dusky dolphins exhibit the same repertoire of leaps in Admiralty Bay, Golfo San José, and Kaikoura. However, the frequency of each leap type varies between the three areas. While the acrobatic leap is the least frequent leap type in each area, the most frequent type in Admiralty Bay was the clean leap, as compared to the noisy leap in Golfo San José and Kaikoura (Würsig and Würsig 1980; Markowitz 2004).

The behavioral context of leaping also varies between the three dusky dolphin sites. In Admiralty Bay and Golfo San José (Würsig and Würsig 1980), clean leaping primarily occurs in the context of foraging, while in Kaikoura, clean leaping primarily occurs during mating and socializing (Markowitz 2004). However, the likely physiological function of clean leaping, which is to enable an individual to quickly catch a breath before returning to depth (Würsig and Würsig 1980), is the same in all three areas.

Coordinated leaping

Unexpectedly, coordinated leaping was not related to foraging, indicating that coordinated foraging behaviors may be occurring below the surface instead of aerially. Underwater video of foraging behavior in Admiralty Bay reveals that dusky dolphins may coordinate behavior below the surface through rapid swimming in a circular formation around prey balls (pers. obsv. of video obtained by R. Vaughn).

Coordinated, clean, and noisy leaping were positively related to party size, indicating that leaping in general may be a byproduct of intense activity levels in large parties. Alternatively, this may be attributed to the increased probability that ≥ 1 individual in a party will leap if more dolphins are present. A positive relationship between party size and leap frequency was also reported for Atlantic white-sided dolphins (*L. acutus*; Weinrich et al. 2001).

The function of noisy leaping

In contrast to Golfo San José and Kaikoura, the frequency of noisy leaping was low in Admiralty Bay and occurred during neither coordinated foraging (as in Golfo San José) nor coordinated travel (as in Kaikoura). The low noisy leap frequency in

Admiralty Bay may be related to predation pressure. Omni-directional sound generated from percussive leaping likely does not travel as far as more directional sound generated through vocalizations (Finneran et al. 2000; Lusseau 2006). Therefore, in areas such as Kaikoura where predation risk is high (Würsig et al. 1997), leaping may be used as a form of rapid and efficient communication to avoid long-range detection by predators such as killer whales (*Orcinus orca*; Lusseau 2006). In Admiralty Bay, there may be less pressure for dusky dolphins to engage in noisy leaping as a conduit for short-range communication because killer whales are rare during the winter and early spring (Chapter II, this volume).

Noisy leaping may be used to convey the actor's internal energy state to other group members, or as a form of male display. The majority (85%) of individuals in Admiralty Bay are male (Shelton 2006), and preliminary evidence suggest that many noisy leapers are male (H. Pearson, unpublished data). Thus, males may use noisy leaping as a display of fitness in that a "better" male may be able to perform more repetitions of noisy leaps within a single leaping bout. Physical stamina may be an important contributor to dusky dolphin reproductive success during "mating of the quickest" strategies which often involve high-speed chases (Markowitz 2004). Male dusky dolphin displays may thus be akin to male displays present in some ungulates, such as red deer stags (*Cervus elaphus*) which assess each others' competitive abilities through roaring and parallel walking displays (Clutton-Brock and Albon 1979).

Percussive non-vocal communication in terrestrial mammals

Some cetacean leap types may be a form of percussive non-vocal communication, and noisy leaping may be similar to drumming behavior in terrestrial mammals. Drumming may occur in a variety of contexts including territorial advertisement and defense, agonistic interactions, mating, dominance relationships, and predator alarm (Randall 2001). The substrate for terrestrial drumming may be the earth (i.e., seismic drumming) or an object in the environment (e.g., buttress drumming). Sound generated from seismic drumming may propagate through the air or the earth, just as sound generated from noisy leaping may propagate through the air or the water.

Rodents may use seismic drumming for conspecific communication by striking the ground with the head, front incisors, or feet (reviewed in Randall 2001). Banner-tailed kangaroo rats (*Dipodomys spectabilis*) foot drum, where individually-distinct signals may act as a signature to advertise the drummer's age, sex, and reproductive potential (Randall 1989).

Chimpanzees (*Pan troglodytes*) drum on tree buttresses with their hands and/or feet to create loud, low-frequency sounds which reverberate through the forest (Arcadi et al. 2004; Goodall 1986). This may have several functions, including conveying the drummer's location, advertising territory boundaries, coordinating party activity, directing party travel speed and direction, and display (Boesch and Boesch-Acherman 2000; Goodall 1986). Both buttress drumming and noisy leaping may function in maintaining group cohesion within the three-dimensional forest and ocean environments.

Conclusions

The context of dusky dolphin leaping in Admiralty Bay primarily supports the prey capture hypothesis. Dusky dolphins may increase foraging efficiency by clean leaping, which enables them to quickly catch a breath before returning to depth to forage. Noisy leaps may act as a form of male display; however, more data are needed. Additionally, more data are needed to quantify variation in sound produced via vocalizations, different types of leaps, and leaping in various contexts (e.g., foraging, socializing, fright-response). Although the leaping repertoire of dusky dolphins appears to be consistent between study sites, the frequency, context, and proximate consequences of leaping appear to vary according to habitat type, grouping and behavioral patterns, and perhaps predation pressure. As studies continue to examine the specific behavioral contexts in which leaping occurs, we will increase our understanding of the selective pressures responsible for the evolution of these impressive and energetic behaviors.

CHAPTER IV

ASSOCIATION PATTERNS OF DUSKY DOLPHIN (*Lagenorhynchus obscurus*) IN ADMIRALTY BAY, NEW ZEALAND

Introduction

Fission-fusion societies are characterized by flexibility in size and composition of groups within a community (Chapman et al. 1993). While some groups may remain stable over a period of days or months (e.g., African elephants, *Loxodonta africana*; Wittemyer et al. 2005), other groups may change in composition over a period of minutes (e.g., bottlenose dolphins, *Tursiops* spp.; Connor et al. 2000b). A crucial component of fission-fusion societies is how individuals relate to one another within a changing social environment. Hinde's (1976) conceptual framework depicts the hierarchical connection between interactions, relationships, and social structure. Relationships are defined by the kind, quality, and temporal patterning of interactions between individuals. In turn, social structure is defined by the kind, quality, and patterning of relationships. Using this framework, the fundamental components of a society may be understood. When analyzing social structure under circumstances in which interactions between individuals are difficult to observe, records of associations (i.e., the presence of dyads occurring under circumstances in which interactions are known to occur) may be substituted for interactions (Whitehead 1997; Whitehead and Dufault 1999).

Certain ungulate, carnivore, primate, and cetacean species exhibit fission-fusion sociality, and these species may be divided into one of two categories (Fig. 9). The first category consists of species in which fission-fusion occurs as a result of subgroups joining and splitting from groups (e.g., African buffalo, *Syncerus caffer*, Cross et al. 2005; Grevy's zebra, *Equus grevyi*, Sundaresan et al. 2007; hamadryas baboons, *Papio hamadryas*, Kummer 1968). The second category consists of species in which fission-fusion occurs as a result of individuals joining and splitting from groups (e.g., hyenas, *Crocuta crocuta*, Szykman et al. 2001; African elephants, Couzin 2006; lions, *Panthera leo*, Packer et al. 1990; spider monkeys, *Ateles geoffroyi,* Chapman et al. 1993; chimpanzees, *Pan troglodytes*, Goodall 1986; bonobos, *P. paniscus,* Chapman et al. 1993; orangutans, *Pongo pygmaeus*, van Schaik 1999; bottlenose dolphins, Connor et al.

Fig. 9. Examples of species which exhibit “complex” fission-fusion sociality, whereby individuals join and split from parties. Species names (clockwise from top left): bottlenose dolphin (*Tursiops* spp.), common dolphin (*Delphinus delphis*), dusky dolphin (*Lagenorhynchus obscurus*), African elephant (*Loxodonta africana*), western chimpanzee (*Pan troglodytes verus*), lion (*Panthera leo*), spotted hyena (*Crocuta crocuta*). All photos except dusky dolphin and chimpanzee courtesy of Chris Pearson.

2000b; common dolphins, *Delphinus delphis*, Bruno et al. 2004). For species in the latter category, an individual's ability to recognize and differentiate between conspecifics and maintain preferential stable relationships within a changing environment may be related to aspects of cognition (Lehmann et al. 2007). In fact, complex social strategies and high cognition may have evolved in a positive feedback loop: complex social strategies necessitate high cognition, while high cognition enables complex social strategies (Humphrey 1976).

In the marine environment, our understanding of fission-fusion social structure in delphinids has been advanced by numerous studies of coastal species (e.g., bottlenose dolphins, Wells et al. 1987, Quintana-Rizzo and Wells 2001, Lusseau et al. 2003, Gero et al. 2005, Möller et al. 2006; Hector's dolphins, *Cephalorhynchus hectori,* Slooten 1994, Bejder et al. 1998; Indo-Pacific humpback dolphins, *Sousa chinensis,* Karczmarski 1999, Jefferson 2000). However, there have been fewer studies of "semi-pelagic" species (inhabiting coastal zones and shallow shelves and slopes of the continental shelf; after Würsig et al. 2007). The intensity of ecological factors such as competition for resources and predation pressure may differ between semi-pelagic and coastal habitats, and these differences may in turn influence a species' social structure. Therefore, in order to more fully account for the variability inherent to delphinid fission-fusion sociality, it is important to expand our knowledge of the social structure of semi-pelagic species.

In this study, I examine the social structure of dusky dolphins, a semi-pelagic species which primarily occurs off the coasts of New Zealand, southwestern Africa (Namibia and South Africa), and South America (Peru, Chile, and Argentina) in cool, temperate waters < 2000 m deep. In New Zealand, the largest concentration of dusky dolphins occurs off Kaikoura (estimated total population size > 12,000 individuals), where they form large groups of ≤ 1,000 individuals and feed nocturnally on the deep scattering layer (DSL) (summarized in Würsig et al. 2007). During the winter, a subset of this population migrates to Admiralty Bay, a shallow enclosed bay in the Marlborough Sounds region of the South Island. Dusky dolphins in Admiralty Bay form smaller groups than in Kaikoura and forage during the day on small schooling fish (Markowitz 2004). Estimated population size during any given week during the winter in Admiralty Bay is 220 individuals, and an estimated 1,000 individuals used Admiralty Bay during the winters of 1998-2002 (Markowitz et al. 2004).

By examining the social structure of a species which alternates between a semi-pelagic and coastal existence, insight into the ecological pressures on fission-fusion sociality may be obtained. In this study, I describe the social structure of dusky dolphins in Admiralty Bay by examining three main aspects: 1) social "fluidity", 2) preferred/avoided associations, and 3) behaviorally-specific preferred/avoided associations.

First, I examine the fluidity of this society by examining the strength and temporal stability of associations. Indicators of a highly fluid society include many weak and few strong associations (Bruno et al. 2004) and short-lived associations. Second, as a fundamental component of social structure is that individuals associate in a non-random manner (Whitehead and Dufault 1999), I test the following null hypotheses: 1) individuals do not have preferred/avoided short-term associates, and 2) individuals do not have preferred/avoided long-term associates. Third, I test for the presence of behaviorally-specific preferred/avoided associations, as reported for bottlenose dolphins (Gero et al. 2005). As there is evidence for coordinated or cooperative foraging in Admiralty Bay (Vaughn et al. 2007), I predict the presence of strong association indices (AI) and preferred associations during foraging. Additionally, as social bonding is a fundamental part of many delphinid societies and may enhance dusky dolphin foraging strategies (e.g., through "social facilitation", Norris and Dohl 1980a; Würsig et al. 1989; Norris et al. 1994), I also predict the presence of strong AI's and preferred associations during socializing.

When examining association patterns, it is important to consider the influence of spatio-temporal variability. Therefore, I examine spatial variability by providing a descriptive comparison of association patterns between Admiralty Bay and Kaikoura, and temporal variability by comparing annual *vs.* pooled (across all years) association patterns (after Rogers et al. 2004).

Methods

Study site

Dusky dolphins were observed in Admiralty Bay (40° 56' S, 173° 53' E) from 1998 to 2006 (Fig. 4). Admiralty Bay is located at the northern tip of New Zealand's South Island, opening to the French Pass in the southwest and the Cook Strait in the northeast. French Pass is a narrow waterway connecting Tasman Bay with the Cook Strait, where colliding currents and tidal changes create turbulent waters. These hydrographic processes may enhance primary productivity and attract aggregations of schooling fish that are fed on by dusky dolphins and seabirds (Baker 1972). Admiralty Bay has an area of 117 km^2, maximum depth of 105 m, and has a benthos primarily composed of mud substrate (McFadden 2003).

Survey method

Data were collected from 1998 to 2006, during the austral winter and early spring (mid May to early Oct). Additional data were obtained during 2 d in Nov-Dec 2002, 1 d in Nov 2003, and 7 d in Oct-Nov 2005. These data are included in descriptions of the number of individuals sighted during 1998-2006, and resighting rates between years, but are excluded from association analyses (see below).

Dusky dolphins were located by trained observers using 4–6 m vessels with 25–85 hp outboard motors traveling at speeds of 9-13 knots. Non-systematic exploratory surveys were conducted during May 1998, June 1999, and Jul 2000 (Markowitz 2004). Data from 1998 to 2000 are not included in association analyses (see below) but are used in descriptive statistics of research effort and resighting rate.

From 2001 to 2006 (Jul-Sept 2001, Jun-Aug 2002, Jul-Aug 2003, Jul-Aug 2004, May-Aug 2005, May-Oct 2006), systematic surveys were conducted by following pre-determined transect lines which were programmed into a Garmin global positioning system (model 12X or 76). Some dusky dolphin groups were also located opportunistically (e.g., when driving to the survey start position).

Group follows

Focal group follows (Whitehead 2004) were used to collect association and behavioral data. As individuals in Admiralty Bay join and split from groups on average every 5.4 min (Chapter II, this volume), group follows (as opposed to surveys or individual follows) were appropriate because associations within groups changed faster than groups were found and surveyed (Whitehead 2004).

Dusky dolphin associations were defined using the “gambit of the group”, which assumes that animals which are clustered are interacting with one another (Whitehead and Dufault 1999). Therefore, association was defined by membership in the same group. Additionally, because membership in dusky dolphin groups changes rapidly, individuals were considered associated if they were part of the same cluster of groups which merged during the time span of the group focal follow (after Slooten et al. 1993).

From May 1998 to Jul 2005, groups were defined using the 10-m chain rule (an individual is part of a group if it is within 10 m of any another individual; Smolker et al. 1992). From Aug 2005 to Oct 2006, groups were defined using a combination of the 10-m chain rule and coordinated activity (Mann 2000); *viz*. groups with members ≤ 10 m apart may be engaged in different activities, but groups with members spaced > 10 m apart must be engaged in the same activity to be considered in the same group. Additionally, any two individuals could be separated by no more than 100 m to be considered in the same group.

During a group follow, we matched the group’s speed and followed the group in a parallel direction. If a group fissioned (i.e., separated) during the group follow, an attempt was made to alternate between following the larger group and the smaller group (e.g., during fission #1, the smaller group was followed; during fission #2 the larger group was followed; during fission #3 the smaller group was followed, etc.; after Mann 1999). Group size, behavioral state, GPS location of the research vessel, and time of day were recorded at 2-min intervals using instantaneous point sampling (Lehner 1996). During 2006 (the year for which behavioral analyses were conducted, see below), behavioral state was determined by systematically scanning the group and the behavior (foraging, resting, socializing, traveling, other/unknown) for each individual was recorded (Table 2). Thus, for each sampling interval, the proportion of individuals engaged in each behavioral state was calculated.

Photo-identification

Photo-identification was used to determine group membership, a technique used widely in cetacean studies since the late 1970's (Würsig and Würsig 1977; Würsig and Jefferson 1990) and successfully applied to dusky dolphins (Markowitz et al. 2003). Photographs were taken throughout the duration of each group focal follow in an attempt to photograph each individual in the group (Fig. 10). During 1998-1999, slide film was used to obtain photographs of dolphin dorsal fins with a Nikon N90 camera with 80-200 mm and 100-300 mm lenses. The slides were later digitized for analysis. During 2000-2006, digital images were obtained using Nikon cameras (D1, D1H, D200) with 80-200mm, 100-300 mm, and 80-400 mm lenses.

Fig. 10. A distinctive dusky dolphin dorsal fin. Individuals are recognized by the pattern of nicks and notches on the trailing edge of the dorsal fin.

From each group encounter, the best image(s) for each individual was selected and entered into a digital catalogue. In general, only photos in sharp focus with the entire dorsal fin exposed and at a parallel angle to the camera were used (after Slooten et al. 1992; Markowitz et al. 2003). However, for individuals with highly distinctive markings, lower quality photos were used (after Gilkinson et al. 2007). In a few cases, highly distinctive individuals were positively identified within a group but a photograph was not obtained; these individuals are included in the dataset.

Images from each individual were matched using the Finscan v. 1.5.4 Computer Assisted Dolphin Photo-Identification System (Hillman et al. 2003). Finscan creates string- and curve-based algorithms to describe the distinctive pattern of nicks and notches along the trailing edge of a dorsal fin (Araabi et al. 2000; Hillman et al. 2003). Based on these algorithms, Finscan provides the user with the most likely matches for an individual dolphin, in order of similarity. However, it is ultimately the user's decision to determine which fins are matches. In this study, additional body markings (rake marks, scars, disfigurements) and distinctive dorsal fin shape were used as secondary characteristics to aid in positive identifications of individuals. All final matching decisions were made by trained observers.

The mark rate, or the percentage of individuals with distinctive markings, was obtained by one of two methods. During 1998-2004, mark rate was obtained by taking photographs of all dolphins at random and obtaining the ratio of photographs with marked *vs*. unmarked individuals (Markowitz et al. 2004). During 2005-2006, mark rate was obtained by taking photographs of all individuals when knowledge of group size was 100% certain (e.g., when it was possible to count all individuals as they swam under the research vessel); the ratio of photographs with marked *vs*. unmarked individuals was then obtained. To obtain more precise mark rates, the mark rate procedure was repeated several times each season. Mark rate was 75% from 1998 to 2004 (Markowitz and Würsig 2004) and 81% in 2006.

Data analysis

Sampling period and selection criteria

Except for analyses of preferred/avoided associations (see below), the sampling period was set to 1 d since associations between but not within days were assumed to be random. For analyses of preferred/avoided associations, the sampling period was set to 8 d (see explanation in "Preferred/avoided associates" below).

Choosing selection criteria for analyses of social structure is a balance between proper representation (maximum number of individuals) and reliability (maximum number of sightings per individual) of the data. Lower sighting frequencies may be appropriate for broad-scale questions regarding overall community structure, while higher sighting frequencies may be more appropriate for detailed questions regarding long-term associations or interactions (Chilvers and Corkeron 2002). In the present study, I chose a mid-point between the two options. As general patterns of community structure in Admiralty Bay have already been examined by Markowitz (2004), the present study aims to provide a more in-depth analysis of fission-fusion sociality and thus uses more stringent selection criteria. However, as there are many transient individuals in Admiralty Bay, I did not want selection criteria so stringent that an unrepresentative sample would be produced.

I used the frequency distribution of re-sighting rates during 2001-2006 to choose selection criteria for the pooled and annual analyses. Individuals sighted ≥ 5 times were included in the pooled analyses (Fig. 11). Unless stated otherwise, individuals sighted ≥ 3 times were included in the annual analyses (Fig. 12). All individuals included in the annual analyses were included in the pooled analyses, but not all individuals in the pooled analyses met selection criteria for the annual analyses. If an individual was photographed in > 1 group/day, only the first sighting of the day was used.

Association index

All association analyses were conducted in the compiled version of SOCPROG 2.3 (available for free download at http://whitelab.biology.dal.ca/index.html). The association index (AI) refers to the proportion of time two individuals spend together,

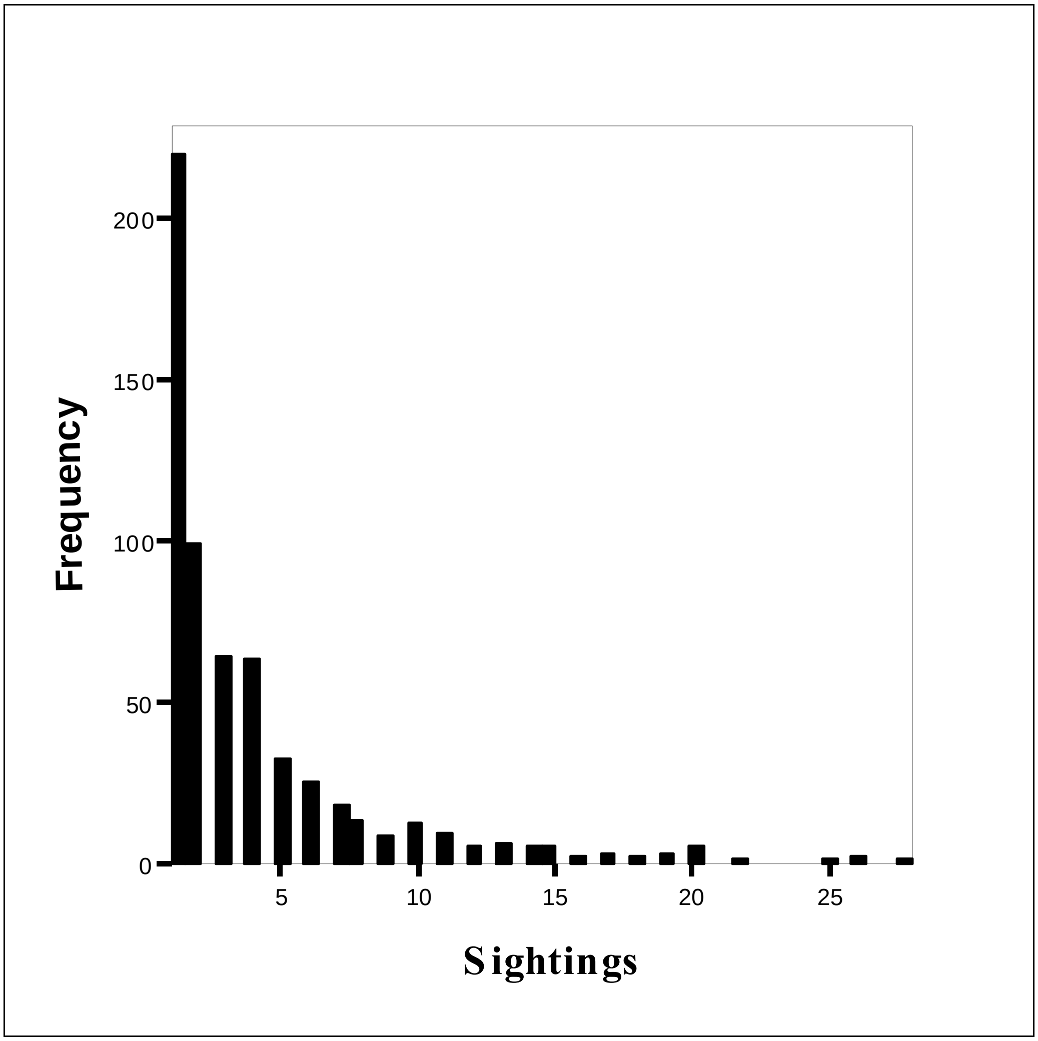

Fig. 11. Frequency distribution of the number of times a dusky dolphin was sighted in Admiralty Bay during 2001-2006.

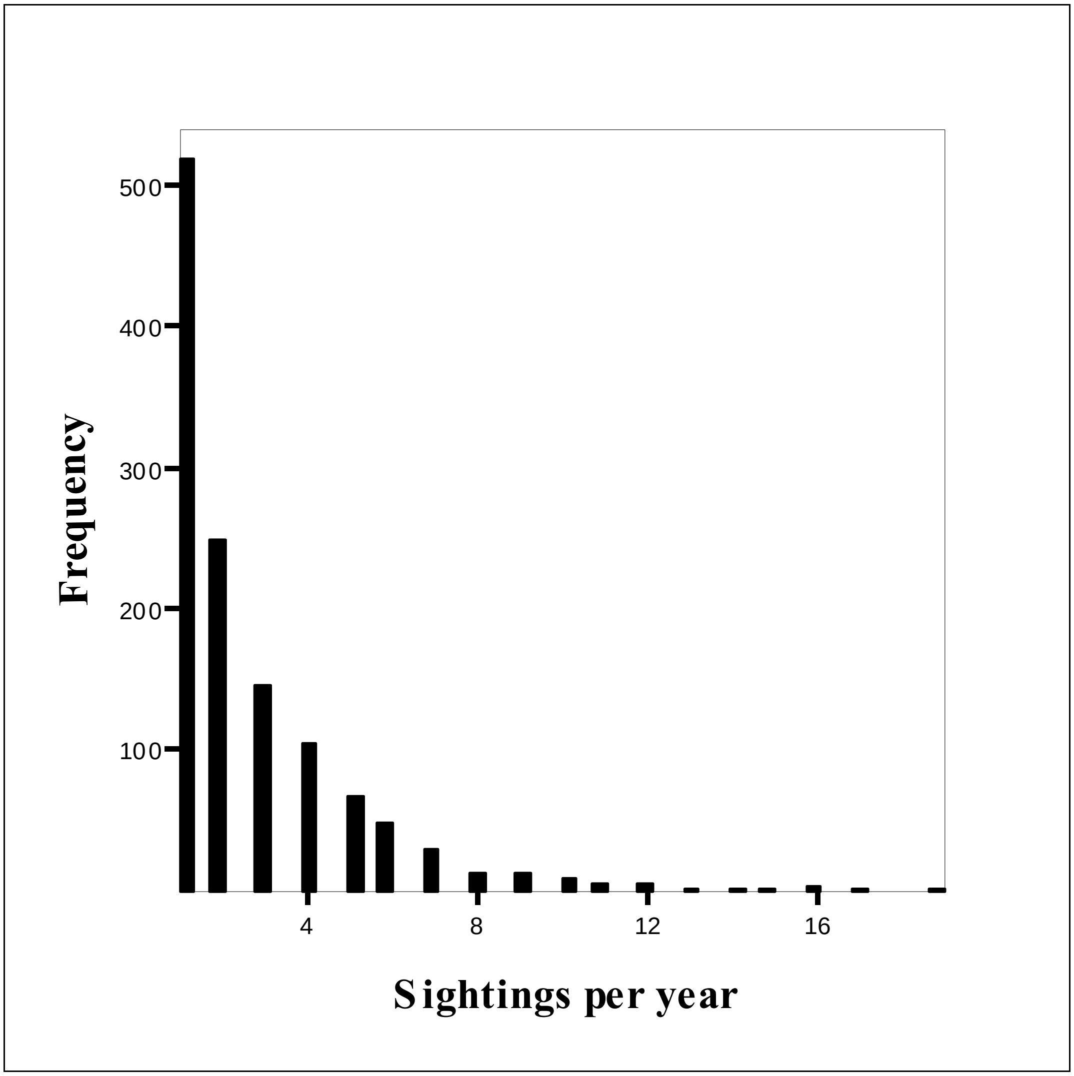

Fig. 12. Frequency distribution of the number of times a dusky dolphin was sighted in Admiralty Bay on average per year during 2001-2006 ($N = 741$).

and ranges from 0 (2 individuals were never sighted together) to 1 (2 individuals were always sighted together). Mean AI represents the mean proportion of time an individual is sighted with each individual in the sample population; maximum AI represents how affiliative an individual is with its closest associate.

AI's commonly used to analyze delphinid social structure are the half-weight index and the simple ratio. The choice of AI primarily depends on the bias present in sighting a dyad. If a dyad is more likely to be sighted separately than together, the half-weight index should be used (e.g., in very large groups when < 50% of individuals are photographed; Karczmarski et al. 2005). If no bias exists (e.g., most individuals in a group are photographed), the simple ratio should be used (Cairns and Schwager 1987). The simple ratio was used in the present study due to small group sizes (mean = 7 ± 6.0 SD; *N* = 4,702 2-min intervals; Chapter II, this volume) and the high mark rate, both of which enable greater photographic coverage of a group. In such cases, bias is unlikely to exist and the simple ratio is the most accurate AI (Ginsberg and Young 1992).

Temporal patterns

Standardized lagged association rates (SLAR) and standardized null association rates (SNAR) were analyzed for the period 2001-2006 (as in Gowans et al. 2001), and within the time period of one season by setting a maximum time lag of 200 d. The SLAR is appropriate when not all true associates of an individual are recorded during a sampling period in which it was seen. The SLAR refers to the probability that if two individuals are associated at one time point, the second will be a randomly chosen associate of the first at some later time point. For comparison, the SNAR refers to the probability that if two individuals are associated at one time point, the second is a randomly chosen associate of the first at a later time point, given that associations are completely random over that time period (Whitehead 1995). The SNAR does not change over time (Whitehead 2008).

Four models ("constant companions", "casual acquaintances", "constant companions and casual acquaintances", "two levels of casual acquaintances") were fitted to the SLAR to describe the temporal patterning of the society. Constant companions are stable associations over time and broken only by birth or death; casual acquaintances associate and then dissociate over time, but may reassociate at a later time point (Whitehead 1995). The "best fit" model had the lowest quasi Akaike Information Criterion (QAIC) (Whitehead 2007).

Preferred/avoided associates

To test for the presence of preferred/avoided associates, the permutation procedure described by Manly (1995) and Bejder et al. (1998) and later enhanced by Whitehead (1999) and Whitehead et al. (2005) was used. This procedure tests the randomness of association patterns by comparing the observed association matrix with a randomly-generated association matrix (a permutation). Random association matrices are generated through "flips", which are sequential inversions of the intersection of two rows and two columns of the observed association matrix. The use of 1,000 flips per permutation is considered optimum (Whitehead 2008) and was used in the present study. Permutations are then computed until the *p*-value stabilizes.

The permutation test option "permute groups within samples" was used. This procedure tests the null hypothesis of "no preferred or avoided companions given the number of groups each individual was seen in during each sampling period" (Whitehead 2008). This permutation method was chosen because it accounts for situations in which not all individuals are present during each sampling interval, as is the situation in Admiralty Bay where individuals move in and out of the bay during the course of a field season and many individuals are not seen over multiple years. Short-term (within sampling periods) preferred associations are indicated by a significantly smaller mean of the observed *vs*. random AI, while long-term (between sampling periods) preferred associations are indicated by a significantly larger standard deviation (SD) of the observed *vs*. random association index. Avoided associates are indicated by a significantly smaller proportion of non-zero AI's in the observed *vs*. random data (Whitehead 2008).

Based on resighting rates, average annual residency in Admiralty Bay from 2001 to 2006 was 15.6 d ± 21.77 SD ($N = 1212$, range = 1-136 d). Therefore, I set the sampling interval to 8 d, as approximately half of the individuals probably moved into or out of the bay during the 8 d sampling period. By constraining the permutations of the association matrix to 8 d intervals, the probability of committing a Type I error due to demographic effects (e.g., associations may appear different from random simply because individuals did not associate with individuals which were not present) is minimized (after Gowans et al. 2001).

<u>Behaviorally-specific association patterns</u>

Using the 2006 dataset (the most complete year), I examined whether individuals had different patterns of association according to behavioral state. For each focal group follow, the predominant behavioral state was obtained. If two activities were present in equal proportions during the group follow, I alternated between which activity took precedence (e.g., if forage and rest were present in equal proportions during a group follow, I coded the first focal group follow of forage and rest as "forage", the second focal group follow of forage and rest as "rest", etc.). Individuals sighted ≥ 5 times were included in these analyses.

SPSS 15.0 (SPSS Inc., Chicago, IL) was used to test for differences in mean and maximum AI's according to behavioral state. Due to non-normal distributions, overall differences were determined using the Kruskal-Wallis test. The Mann-Whitney U test was used for pair-wise comparisons. The two-tailed alpha level was set at $p < 0.05$ for the Kruskall-Wallis test. To adjust for multiple pair-wise comparisons, the alpha level for the Mann-Whitney U tests was set at $\alpha/6$, or $p < 0.008$.

Permutation tests were used to test for the presence of preferred/avoided associations in each of the four behavioral states (i.e., to test if associations were nonrandom). If associations within a behavioral state were nonrandom, the strength of association between dyad members within that behavioral state was tested according to techniques described in Gero et al. (2005) and Durrell et al. (2004). Dyad members were considered "preferred associates" if they had a behaviorally-specific AI ≥ twice the mean AI of the population, including zero values. Dyad members were considered “acquaintances” if they associated in ≥ 1 behavioral state but not at the level of “preferred associate” (after Gero et al. 2005).

Results

Research effort and resighting rate

Images of suitable quality for analysis were obtained during 215 d from 1998 to 2006 (Table 9). A total of 809 individuals were identified in 863 groups. The discovery curve of individuals identified *vs*. cumulative number of identifications indicates that new individuals continued to enter the population throughout the duration of the study (Fig. 13). Additionally, 66% (*n* = 537) of individuals were seen during one year, 17% (*n* = 141) were seen during two years, 7% (*n* = 60) were seen during three years, 4% (*n* = 31) were seen during four years, 3% (*n* = 24) were seen during five years, and 2% (*n* = 16) were seen during 6 years (Fig. 14). During 2001-2006, the mean number of sightings per individual was 4.4 ± 4.68 (*N* = 741, range = 1-28), and 34% (*n* = 251) of individuals were sighted once.

Table 9. Summary of research effort in Admiralty Bay from 1998 to 2006.

Year	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**Total**
Field season duration (d)	2	5	20	51	95	44	51	93	138	N/A
No. sampling days	1	2	7	25	35	18	17	47	63	215
No. groups	2	4	38	211	187	146	50	73	152	863

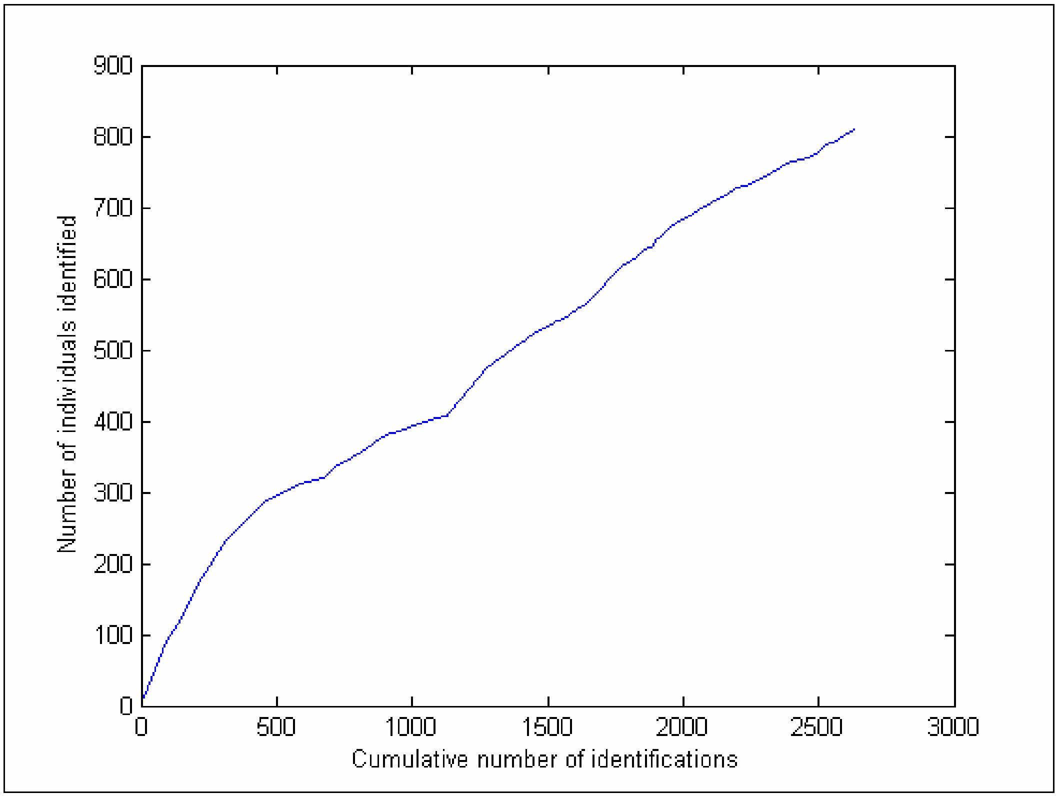

Fig. 13. Discovery curve of individuals identified *vs*. cumulative number of identifications in Admiralty Bay, 1998-2006.

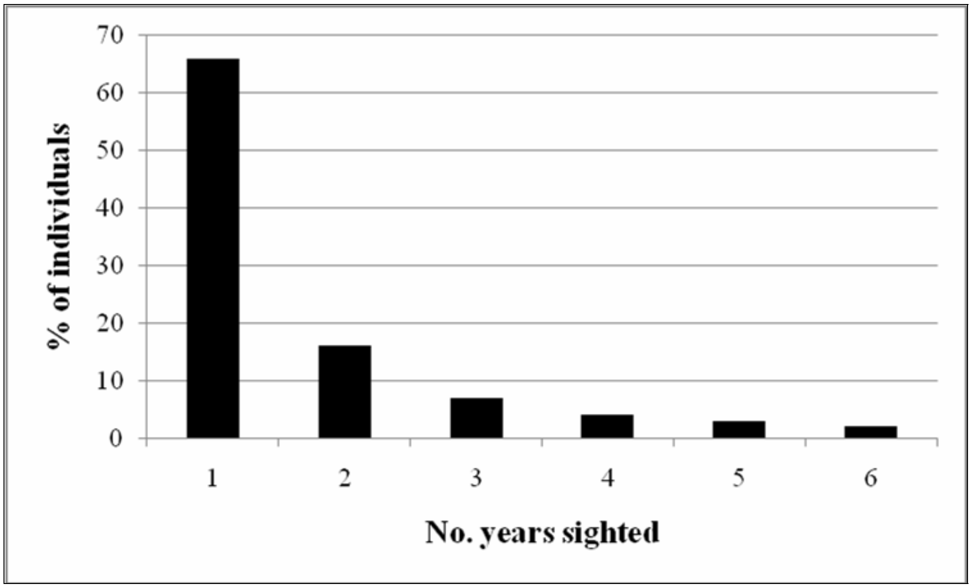

Fig. 14. Resighting rates of dusky dolphins in Admiralty Bay, 1998-2006 ($N = 809$).

Social fluidity

Distribution of AIs

From 2001 to 2006, 741 individuals were photographed and 228 individuals met selection criteria for inclusion in the final sample (i.e., were sighted ≥ 5 times). The distribution of observed (Fig. 15) and mean (Fig. 16) AI's per individual in the pooled sample shows that the majority of individuals formed weak associations.

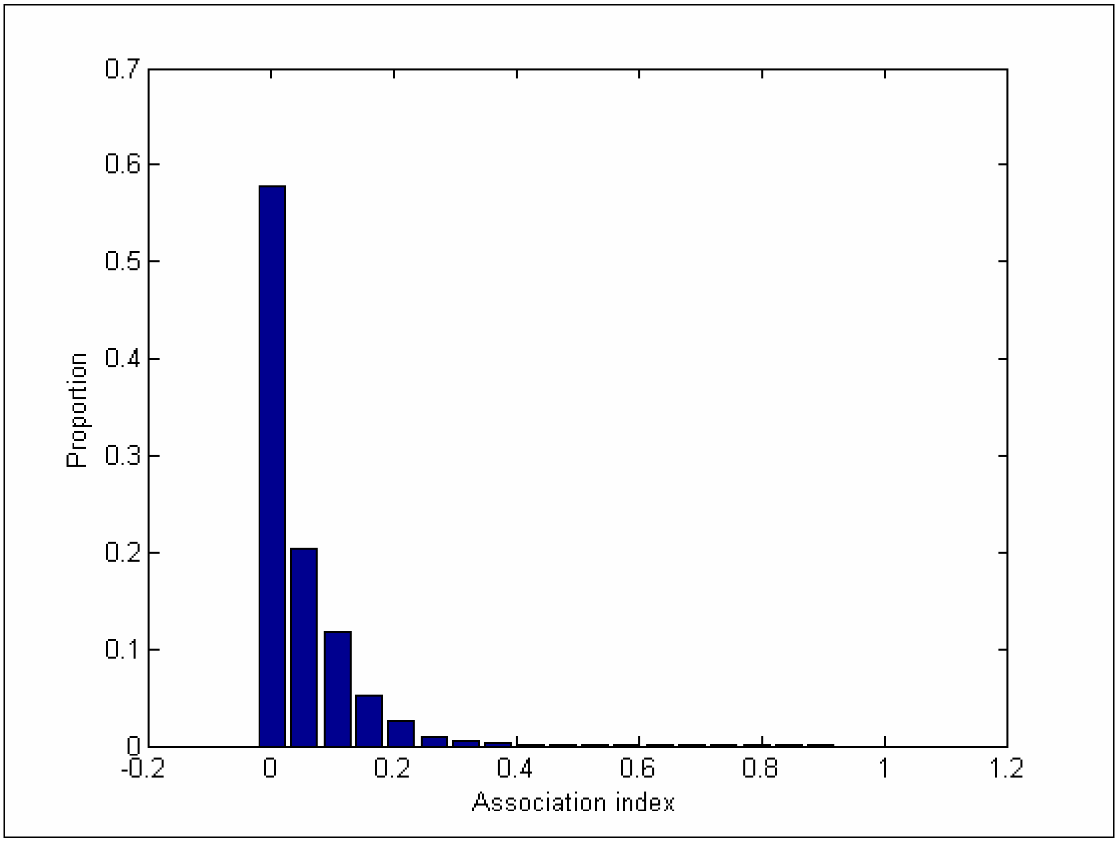

Fig. 15. Frequency distribution of observed association indices for dusky dolphins in Admiralty Bay during 2001-2006 ($N = 741$).

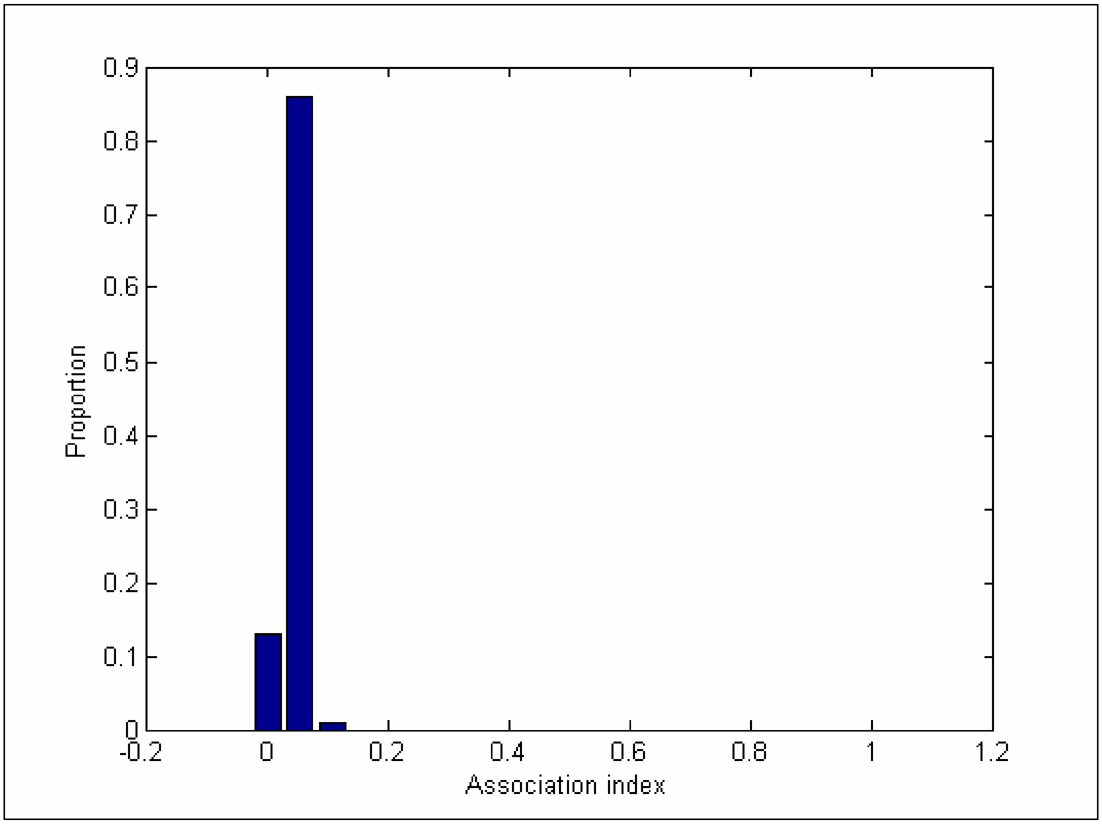

Fig. 16. Frequency distribution of mean association indices for dusky dolphins in Admiralty Bay during 2001-2006 (*N* = 741).

The mean AI of the pooled sample was 0.04 ± 0.07 SD (Table 10), indicating that, on average, any two individuals spent 4% of their time together. Mean AI's were higher when each year was considered individually, and ranged from 0.08 to 0.28 (Table 10). Mean values were also higher when AI's were calculated only for dyads which associated (i.e., excluding AI's = 0) (Table 10). Considering only those dyads which associated, mean AI of the pooled sample was 0.10 ± 0.08 SD, and mean AI's of the annual samples ranged from 0.18 to 0.35.

The distribution of maximum AI's per individual for the pooled sample indicates that some individuals formed strong bonds (Fig. 17). The mean maximum AI for the pooled sample was 0.45 ± 0.16, while mean maximum AI's for the annual analyses ranged from 0.48 to 0.75 (Table 10).

The proportion of non-zero AI's in the pooled sample was 0.42, indicating that less than half (42%) of all possible dyads were formed (Table 10). However, the proportion of non-zero AI's in all years but 2005 was higher. The highest proportion of non-zero AI's was in 2003 (0.79), when nearly 80% of all possible dyads associated.

Lagged association rate

Of the four models which were fitted to the 2001-2006 pooled data, the model "constant companions and casual acquaintances" had the lowest QAIC value and was therefore the best fit model (Table 11). While some individuals associated nonrandomly over short time periods ("casual acquaintances), others associated nonrandomly for *c.a.* 125 d ("constant companions"), as indicated by the point in Fig. 18 where the observed line drops below the null model line. Within a single season, the model "two levels of casual acquaintances" was the best fit model (Table 11), indicating shorter-lived associations than in the pooled sample (Fig. 19). Within a single field season, individuals associated nonrandomly for *c.a.* 60 d. The large jackknife error bars (estimates of 1 standard error) in each model indicate a lack of precision in estimating the observed patterns; however, the models may still be used as indicators of temporal stability in association patterns.

Table 10. Association index (AI) values for each annual sample and the pooled 2001-2006 sample.

Year	**2001** (*N* = 126)	**2002** (*N* = 84)	**2003** (*N* = 78)	**2004** (*N* = 11)	**2005** (*N* = 28)	**2006** (*N* = 118)	**Pooled** (*N* = 228)
All values, mean AI (SD)[a,b]	0.14 (0.14)	0.14 (0.13)	0.22 (0.17)	0.28 (0.17)	0.08 (0.14)	0.08 (0.12)	0.04 (0.07)
Non-zero values, mean AI (SD)[b]	0.21 (0.13)	0.19 (0.11)	0.27 (0.15)	0.35 (0.26)	0.23 (0.14)	0.18 (0.13)	0.10 (0.08)
All values, maximum AI (SD)[c]	0.69 (0.18)	0.57 (0.15)	0.75 (0.19)	0.70 (0.26)	0.48 (0.21)	0.60 (0.21)	0.45 (0.16)
Proportion of non-zero AI's	0.69	0.72	0.79	0.78	0.37	0.43	0.42

[a] SD = standard deviation

[b] Mean of the mean AI per individual

[c] Mean of the maximum AI per individual

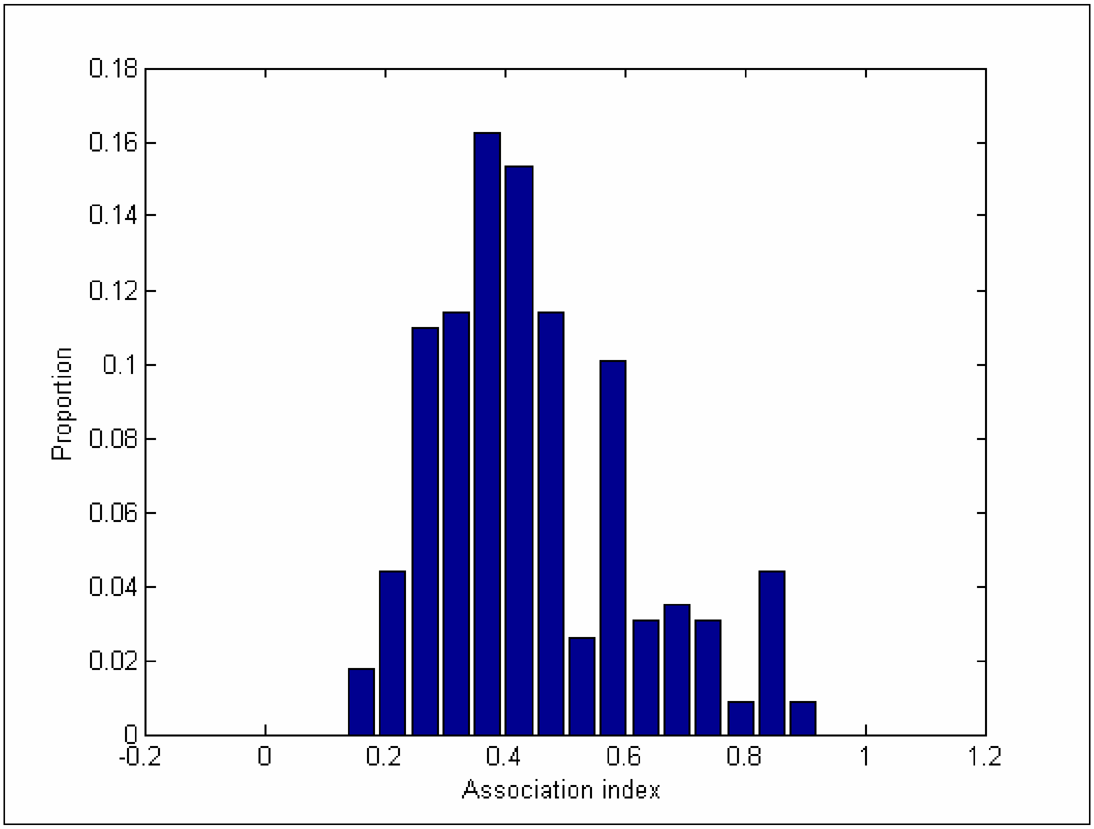

Fig. 17. Frequency distribution of maximum association indices for dusky dolphins in Admiralty Bay during 2001-2006 (*N* = 741).

Table 11. Quasi Akaike Information Criterion (QAIC) values for four standardized lagged association rate (SLAR) models, in the pooled sample and over a time period of one field season (200 d) (both $N = 228$). The model with the lowest QAIC value is the best fit model.

SLAR model	Constant companions	Casual acquaintances	Constant companions and casual acquaintances	Two levels of casual acquaintances
2001-2006	63,480	62,511	62,393	62,478
One field season	38,228	38,196	38,202	38,191

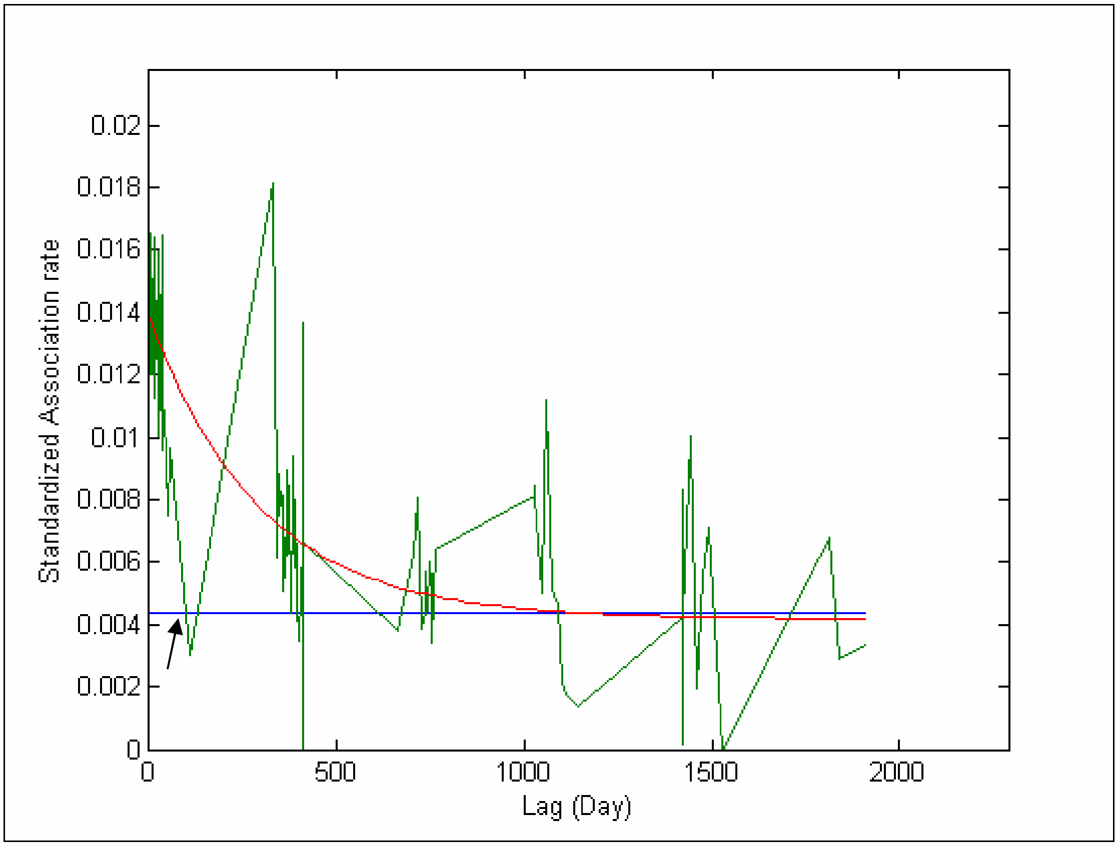

Fig. 18. Standardized lagged association rate (SLAR) for dusky dolphins in Admiralty Bay during 2001-2006 (*N* = 228). The straight blue line represents the standardized null association rate, and the jagged green line represents the SLAR with jackknifed error estimates (5 evenly-spaced vertical lines representing 1 standard error estimates). The curved red line represents the best fit model, “constant companions and casual acquaintances”. The arrow represents the time point at which associations become random.

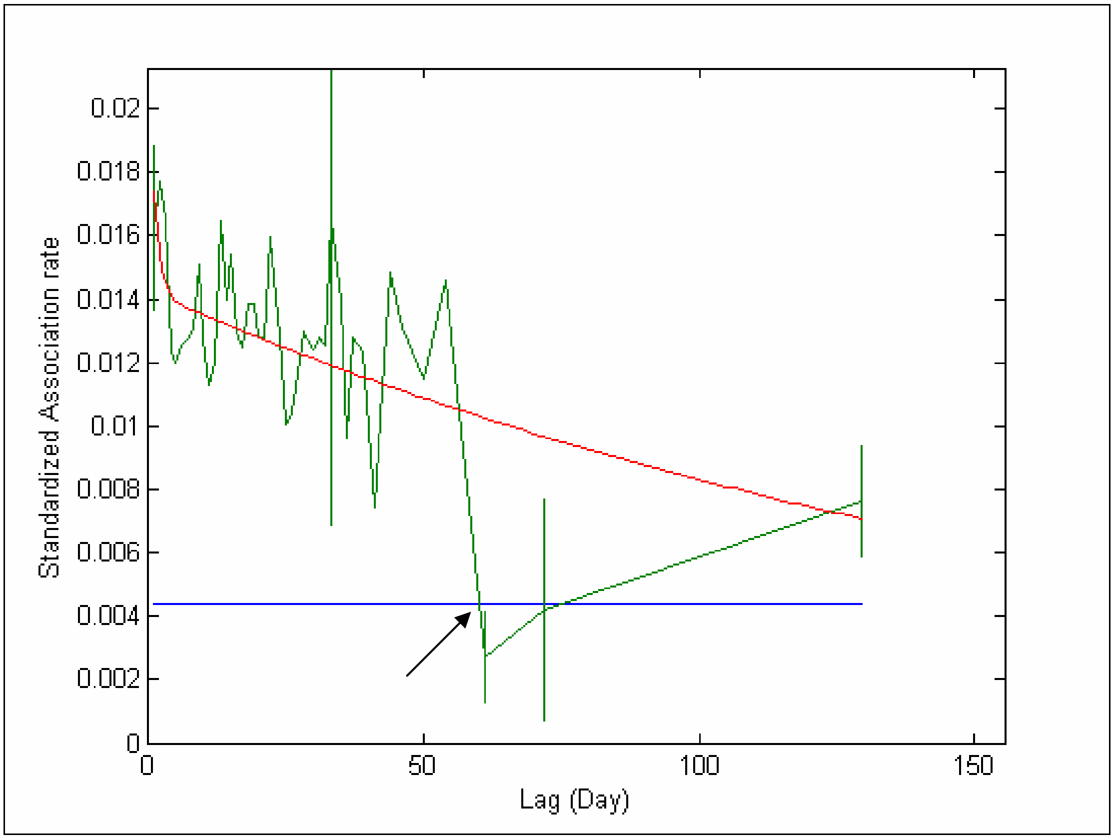

Fig. 19. Standardized lagged association rate (SLAR) for dusky dolphins in Admiralty Bay during one field season (200 d) (*N* = 228). The straight blue line represents the standardized null association rate, and the jagged green line represents the SLAR with jackknifed error estimates (5 evenly-spaced vertical lines representing 1 standard error estimates). The curved red line represents the best fit model, "two levels of casual acquaintances". The arrow represents the time point at which associations become random.

Preferred/avoided associates

Individuals did not associate at random, as indicated by the presence of short- and long-term preferred associations, and avoided associations (Table 12). Individuals formed preferred short-term associations in 2001, as indicated by a significantly smaller observed *vs*. random mean AI. Individuals formed preferred long-term associations during each individual year except 2004, as indicated by significantly higher SD's of the observed *vs.* random AI means. Individuals also formed preferred long-term associations in the 2001-2006 pooled sample. In 2001, 2003, 2005, 2006, and the pooled sample, some individuals avoided each other, as indicated by a significantly lower proportion of non-zero AI's in the observed *vs.* random sample.

Behaviorally-specific associations

Sixty individuals met selection criteria for inclusion in the analysis of behaviorally-specific associations during 2006 (i.e., they were sighted ≥ 5 times). Mean ($\chi^2 = 26.891$, df = 3, $p < .001$) and maximum ($\chi^2 = 19.663$, df = 3, $p < .001$) AI's differed according to behavioral state (Table 13). Mean AI during traveling was lower than during foraging (Z = -3.019, $p = .003$), socializing (Z = -4.569, $p = .000$), and resting (Z = -3.653, $p = .000$). Maximum AI during foraging was higher than during resting (Z = -2.753, $p =. 006$). Maximum AI during socializing was higher than during resting (Z = -3.721, $p = .000$) and traveling (Z = -3.373, $p = .001$).

Randomness of associations

There were no short-term preferred associations during any behavioral state (Table 14). Long-term preferred associations were present during all behavioral states except traveling. Avoided associations were present during foraging and resting.

Strength of associations

Mean AI's within each behavioral state were 0.13, 0.13, and 0.17 for foraging, resting, and socializing, respectively. Therefore, dyads with AI's ≥ 0.26, 0.26, and 0.34

Table 12. Annual and pooled (2001-2006) permutation test results to determine the presence of short- and long-term preferred associations, and avoided associations.

Year	**2001** (N = 126)	**2002** (N = 84)	**2003** (N = 78)	**2004** (N = 11)	**2005** (N = 28)	**2006** (N = 118)	**Pooled** (N = 228)
No. permutations required for *p*-values to stabilize	35,000	40,000	25,000	20,000	25,000	15,000	25,000
Preferred short-term associations							
Observed mean AI[a]	0.222	0.223	0.378	0.382	0.114	0.105	0.061
Random mean AI	0.227	0.222	0.377	0.383	0.114	0.105	0.062
P-value observed *vs*. random mean AI	<0.001	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05
Preferred long-term associations							
Observed AI SD [b]	0.894[c]	0.193	0.272	0.301	0.178	0.159	0.100
Random AI SD	0.858[c]	0.189	0.261	0.294	0.166	0.145	0.093
P-value observed *vs*. random AI SD	<0.001[c]	<0.05	<0.01	>0.05	<0.05	<0.001	<0.001
Avoided associations							
Observed proportion of non-zero AI's	0.689	0.717	0.791	0.782	0.373	0.426	0.423
Random proportion of non-zero AI's	0.704	0.723	0.813	0.799	0.400	0.452	0.434
P-value observed *vs*. random proportion of non-zero AI's	<0.01	>0.05	<0.01	>0.05	<0.01	<0.001	<0.001

[a] Association index

[b] Standard deviation of the mean

[c] The coefficient of variation of the AI mean was used to test for the presence of preferred long-term associations, which is a more accurate test statistic than the SD of the AI mean when there are preferred short-term associations (Whitehead 2008).

Table 13. Mean sample values for mean and maximum association index (AI) per individual according to behavioral state in 2006. Values with different letters are significantly different at $p < 0.008$.

Behavior	**Forage** ($N = 39$)	**Rest** ($N = 58$)	**Social** ($N = 34$)	**Travel** ($N = 56$)
Mean AI	0.13 (0.06)^{A}	0.13 (0.06)^{A}	0.17 (0.08)^{A}	0.09 (0.04)^{B}
Maximum AI	0.83 (0.25)^{AC}	0.68 (0.21)^{B}	0.87 (0.26)^{AD}	0.68 (0.24)^{BC}

Table 14. Permutation test results to determine the presence of preferred short- and long-term associations, and avoided associations, within each behavioral state during 2006.

Behavioral state	**Forage** ($N = 39$)	**Rest** ($N = 58$)	**Social** ($N = 34$)	**Travel** ($N = 56$)
No. permutations required for p-values to stabilize	20,000	10,000	20,000	25,000
Preferred short-term associations				
Observed mean AI[a]	0.132	0.157	0.177	0.104
Random mean AI	0.131	0.151	0.164	0.105
P-value observed *vs*. random mean AI	>0.05	>0.05	>0.05	>0.05
Preferred long-term associations				
Observed AI SD[b]	0.277	0.220	0.340	0.200
Random AI SD	0.269	0.193	0.318	0.201
P-value observed *vs*. random AI SD	<0.05	<0.001	<0.01	>0.05
Avoided associations				
Observed proportion of non-zero AI's	0.224	0.461	0.242	0.305
Random proportion of non-zero AI's	0.230	0.499	0.242	0.307
P-value observed *vs*. random proportion of non-zero AI's	<0.05	<0.001	>0.05	>0.05

[a] Association index

[b] Standard deviation of the mean

during foraging, resting, and socializing, respectively, were considered preferred associates. Traveling is not considered here as permutation tests revealed that associations during traveling were not different from random (Table 14).

A total of 741, 1653, and 561 possible dyads could be formed during foraging, resting, and socializing, respectively. Of these, 21% (*n* = 157), 19% (*n* = 309), and 10% (*n* = 56) were preferred associates during foraging, resting, and socializing, respectively. Additionally, 1% (*n* = 9), 27% (*n* = 453), and 50% (*n* = 182) of foraging, resting, and socializing dyads, respectively, were acquaintances (Fig. 20).

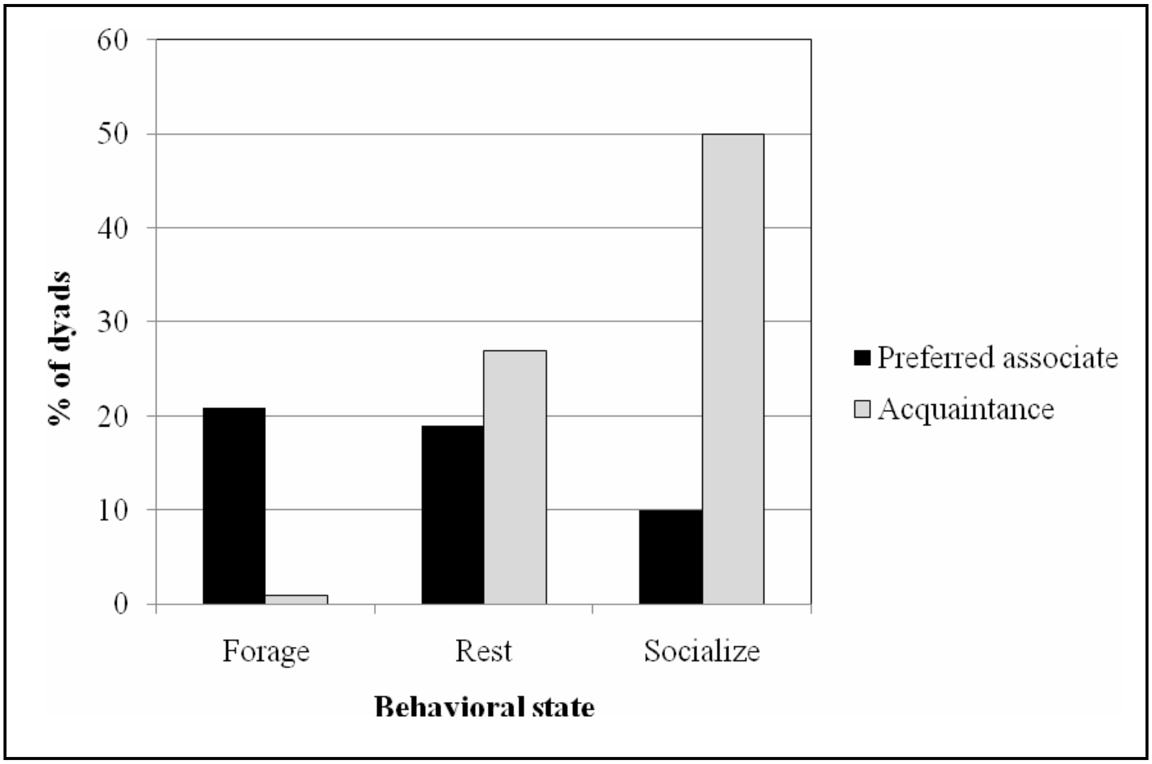

Fig. 20. Frequency distribution of dyads which were "preferred associates" and "acquaintances" during foraging (*N* = 741), resting (*N* = 1653), and socializing (*N* = 561). Traveling is not shown, as permutation tests revealed that associations were not different from random during traveling.

Discussion

Dusky dolphins in Admiralty Bay form a fluid society. However, within this fluid society, some individuals form relatively long-term bonds, form preferred and avoided associations, and associate preferentially during certain behaviors. While some findings corroborate previous reports (Markowitz 2004; Markowitz et al. 2004), this study also presents new results which provide insight into the evolution of fission-fusion sociality, and offers comparisons with other fission-fusion societies.

Spatio-temporal variability

On a spatial scale, nonrandom associations are of a longer duration in Kaikoura (200 d across seasons, 103 d within a season; Markowitz 2004) than in Admiralty Bay (125 d across seasons, 60 d within a season). This may be attributed to the low residency rates in Admiralty Bay. However, associations across and within seasons in Kaikoura are weaker (at the level of "casual acquaintances") than in Admiralty Bay. Differences in association patterns between Kaikoura and Admiralty Bay may be related to differences in predation pressure and prey availability.

In Kaikoura, large groups likely function in predator protection (Würsig et al. 1997). Additionally, individuals may "afford" to remain in large groups as they forage on the relatively evenly-distributed DSL. If individuals tend to remain in the same large grouping of animals, they are exposed to a larger number of potential associates and may thus interact less with any one individual (resulting in lower AI's). In Admiralty Bay during the winter and early spring, predation pressure is lower (C. Duffy, Marine Science Unit, New Zealand Department of Conservation; Chapter II, this volume) and thus individuals may "afford" to form smaller groups. Additionally, patchily-distributed prey may constrain group size. Therefore, individuals are not restricted to large groups and may join and split from smaller groups according to foraging and social pressures. In this manner, individuals may preferentially associate with partners during foraging or socializing (see below), but these associations may be relatively short-lived due to the transient nature of the Admiralty Bay population.

On a temporal scale, mean AI's and the proportion of non-zero AI's in Admiralty Bay were lower during 2005-2006 than during 2001-2004. This indicates that associations were weaker overall during 2005-2006, and fewer possible dyads were observed. These results coincide with a markedly reduced encounter rate (groups sighted/hour of survey effort) during 2005-2006 (H. Pearson, unpublished data) *vs*. 2001-2004 (Markowitz and Würsig 2004). Potential causes for the reduced encounter rate during 2005-2006 are currently being explored (e.g., reduction in prey availability; see Benoit-Bird et al. 2004 for details regarding the relationship between prey density and dusky dolphin distribution). These same causes may be related to the reduction in sociality during this period.

Social fluidity

The presence of many weak and few strong AI's is indicative of a fluid society with a high degree of "social mixing". This social mixing permits individuals to "meet" and interact with a wide variety of individuals in the community. Ultimately, this may facilitate coordinated foraging strategies in Admiralty Bay during the winter, and coordinated mating strategies for those individuals which associate in Admiralty Bay and then return to Kaikoura to mate during the summer.

Like dusky dolphins, common dolphins are oftentimes found in deep waters far from shore, but a nearshore population has been studied in the eastern Ionian Sea (Bruno et al. 2004). Here, common dolphins display a highly fluid society, marked by low AI's and few long-term associations. Low predation pressure and patchy food resources in Admiralty Bay (Chapter II, this volume) and the eastern Ionian Sea (Bruno et al. 2004) may be evolutionary pressures for a fluid society.

Social stability

There is some degree of social stability in the Admiralty Bay population, however. First, re-sighting rates indicate that 1/3 of individuals returned to Admiralty Bay during ≥ 2 years. This may indicate a cultural tradition of seasonal movement between Kaikoura and Admiralty Bay, as first proposed by Whitehead et al. (2004). Second, dusky dolphins formed preferred associations (i.e., associated nonrandomly) in the pooled and each annual sample except 2004; the lack of significance in 2004 may be due to small sample size. Finally, while the pooled SLAR indicates that some dyads disassociate quickly (“casual acquaintances”), other associations are stronger and persist throughout the duration of a field season (“constant companions”).

Behaviorally-specific preferred/avoided associations

Permutation test results revealed that individuals formed preferred associations during foraging, resting, and socializing. However, association patterns were not different from random during traveling, and the mean AI was lower during traveling than during all other behavioral states. Thus, traveling groups in Admiralty Bay may be viewed as non-mutualistic aggregations of individuals, requiring little social coordination.

Similar to bottlenose dolphins in Shark Bay, Australia (Gero et al. 2005), bonding during foraging and socializing appears to be important to dusky dolphin society. Maximum AI’s were strongest during foraging and socializing. Additionally, during foraging, the frequency of preferred associates was highest and the frequency of acquaintances was lowest, indicating that foraging associates may “know” each other well. In contrast, during socializing, the frequency of preferred associates was lowest and the frequency of acquaintances was highest, indicating that individuals may “meet” and “get to know” a variety of individuals through socializing. Thus, foraging and socializing may form the “core” of dusky dolphin society. Although dusky dolphins spend just 1/3 of the day foraging and socializing (Chapter II, this volume), this “quality” time may be used to form and renew bonds.

Social bonding may have ultimate fitness benefits, as individuals may more effectively coordinate or cooperate to herd fish if they are more familiar with each other. This “social facilitation” explanation has also been used to explain the relationship between social behavior and cooperative foraging for dusky dolphins in Golfo San José, Argentina (Würsig and Würsig 1980). Similarly, in Shark Bay, Australia, formation of preferred associations during socializing may enhance predator defense and parenting skills (Gero et al. 2005).

Social bonding is also crucial to fission-fusion sociality in primates, and may permeate many aspects of society. For example, grooming is an important means of bond formation and maintenance, and may have far-reaching effects. Male chimpanzees may reinforce alliance relationships through grooming, and these alliances may then be used to secure food and mates (Nishida and Hiraiwa-Hasegawa 1987). Social bonding may also serve to alleviate tension between individuals, as exhibited by female bonobos which are highly social and exhibit genital-rubbing behavior prior to competitive interactions over food or mates (Kano 1980).

Fission-fusion sociality in other species

A primary adaptive value of fission-fusion sociality is that it enables individuals to adjust their association patterns according to changing socioecological conditions. For example, African elephants form complex multi-tiered societies in which associations change seasonally. While the composition of second-tier “family” units is generally stable, higher-level tiers of “core” and “bond” groups are more loosely structured and seasonally associate when benefits (e.g., receptive females) outweigh costs (e.g., competition for food) (Wittemyer et al. 2005; Couzin 2006). Although dusky dolphin associations change much more rapidly than elephant associations, individual sociality in both species is likely to be driven by similar socioecological pressures (e.g., food availability, mating opportunities, predation risk).

Overall, fission-fusion societies may range along a continuum of being fluid and loosely bonded to being cohesive and strongly bonded. Hector’s dolphins off Banks Peninsula, New Zealand (Slooten et al. 1993), common dolphins in the eastern Ionian Sea (Bruno et al. 2004), and Indo-Pacific humpback dolphins in Algoa Bay, South Africa (Karczmarski 1999) lie at one end of this continuum, exhibiting fluid societies with short-lived associations. On the opposite end of the spectrum are bottlenose dolphins in Doubtful Sound, New Zealand (Lusseau et al. 2003); spinner dolphins off Midway Atoll, Hawaii (Karczmarski et al. 2005); and chimpanzees of the Taï forest, Ivory Coast (Boesch and Boesch-Acherman 2000). The latter three societies are bisexually-bonded societies, characterized by strong group cohesion and strong AI’s within and between sexes. These highly cohesive communities may be a result of relatively small community size, geographic isolation, and high predation pressure.

New Zealand dusky dolphins appear to fit in the middle of this continuum. Weaker bonds of longer duration which are present within large groups in Kaikoura are replaced by stronger bonds of shorter duration within small groups in Admiralty Bay. Some individuals return to Admiralty Bay year after year and form preferred social and foraging associations. As photo-identification studies continue in Admiralty Bay, we will enhance our knowledge of association patterns formed within this potential cultural unit.

In a comparative context, continued comparisons between marine and terrestrial fission-fusion societies are warranted. A lower cost of transport in the marine environment (Williams et al. 1992), may cause terrestrial fission-fusion societies to be less fluid than marine systems. For example, living in a weightless environment with a fusiform body shape may “enable” dolphins (*vs.* great apes) to associate with a wider variety of individuals, and to join and split from parties more rapidly; however, this remains to be tested. In general, further comparisons between dolphin and great ape fission-fusion sociality will provide insight into the evolutionary forces leading to social convergence between these taxa (see Connor et al 1998; Marino 2002; Bearzi and Stanford 2008; Chapters I and V, this volume).

CHAPTER V

SOCIAL CONVERGENCE BETWEEN BOTTLENOSE DOLPHINS (*Tursiops spp.*) AND CHIMPANZEES (*Pan troglodytes*): FOCUS ON FEMALE SOCIALITY

Introduction

Since the 1970's, when cetacean field studies began to flourish, behavioral ecologists have commented on the social convergence between cetaceans and primates (e.g., Tayler and Saayman 1972), and delphinids and pongids in particular (e.g., Würsig 1978; Saayman and Tayler 1979; Herman 1980). Despite being evolutionarily separated for 95 million years (Jurmain and Nelson 1994; Bromham, et al. 1999; Marino 2002) and inhabiting vastly different environments, delphinids and pongids share striking similarities such as: high cognition (including large brains with high encephalization quotients, self-recognition, and long-term memory; summarized in Reiss and Marino 2001; Marino 2002), slow life histories (summarized in Morin 1993; Whitehead and Mann 2000), fission-fusion societies (summarized in Smolker et al. 1992), sympatric associations (Bearzi and Stanford 2007), cooperative hunting which may involve role-specialization (Boesch and Boesch-Acherman 2000; Gazda et al. 2005), multi-mate mating systems often involving sexual coercion (Scott et al. 2005; Muller et al. 2007), male alliances (Goodall 1986; Connor et al. 1992), alloparental care (Nishida 1983; Wells et al. 1987; Shane 1990), tool use (e.g., Smolker, et al. 1997; Pruetz and Bertolani 2007), and culture (e.g., Rendell and Whitehead 2001).

When examining the delphinid-pongid social convergence, a good starting point is to determine what influences female behavior. In mammals, female reproductive success is primarily influenced by food and predation pressures, while male reproductive success is primarily influenced by gaining access to receptive females (Emlen and Oring 1977; Greenwood 1980; van Schaik 1989; Morin 1993; Sterck et al. 1997). Therefore, by understanding what factors influence females, insight may be gained regarding the evolutionary pressures which drive the social and mating systems of a species as a whole. While more detailed comparisons between delphinids and pongids have been made regarding topics such as cognition (Marino 1996; Marino 1998a; Marino 1998b; Reiss and Marino 2001; Marino 2002), sympatric associations (Bearzi and Stanford 2007), and culture (Rendell and Whitehead 2001; Whitehead et al. 2004), to my knowledge no review has focused explicitly on comparing the female sociality.

In this review, I compare sociality between adult female bottlenose dolphins (*Tursiops* sp.; hereafter referred to as "dolphins") and chimpanzees (*Pan troglodytes*), two of the best-studied delphinids and pongids, respectively. Additionally, as understanding determinants of reproductive success, and dispersal and ranging patterns, is fundamental to understanding a species' social organization, I also compare these characteristics between female dolphins and chimpanzees. Overall, I focus on results reported from long-term dolphin and chimpanzee field sites that have been published in journal articles and book chapters. In this manner, I provide a cohesive summary of female sociality in order to increase our understanding of social convergence between dolphins and chimpanzees.

As the field of cetology lags behind the field of primatology by 20-30 years (Connor et al. 2000a), and the longest running dolphin field study is shorter than the longest running chimpanzee field study by about 15 years, there is a tendency for more detailed information to be available for chimpanzees than dolphins. Therefore, more chimpanzee field sites than dolphin field sites are represented in each section of this review. Dolphin field sites include: Sarasota, Florida, USA; Shark Bay, Australia; New South Wales, Australia; and Doubtful Sound, New Zealand (Figure 21). Chimpanzee field sites include: Gombe, Tanzania (Kasakela community); Mahale, Tanzania (M-group community); Kibale, Uganda (Kanyawara community); the Taï forest, Ivory Coast; and Bossou, Guinea. These dolphin and chimpanzee sites were chosen because, in addition to being long-term study sites (each dolphin and chimpanzee site has been studied for > 10 and > 25 years, respectively), they collectively represent a wide variety of socioecologic factors (e.g., habitat type, predation risk, community size and

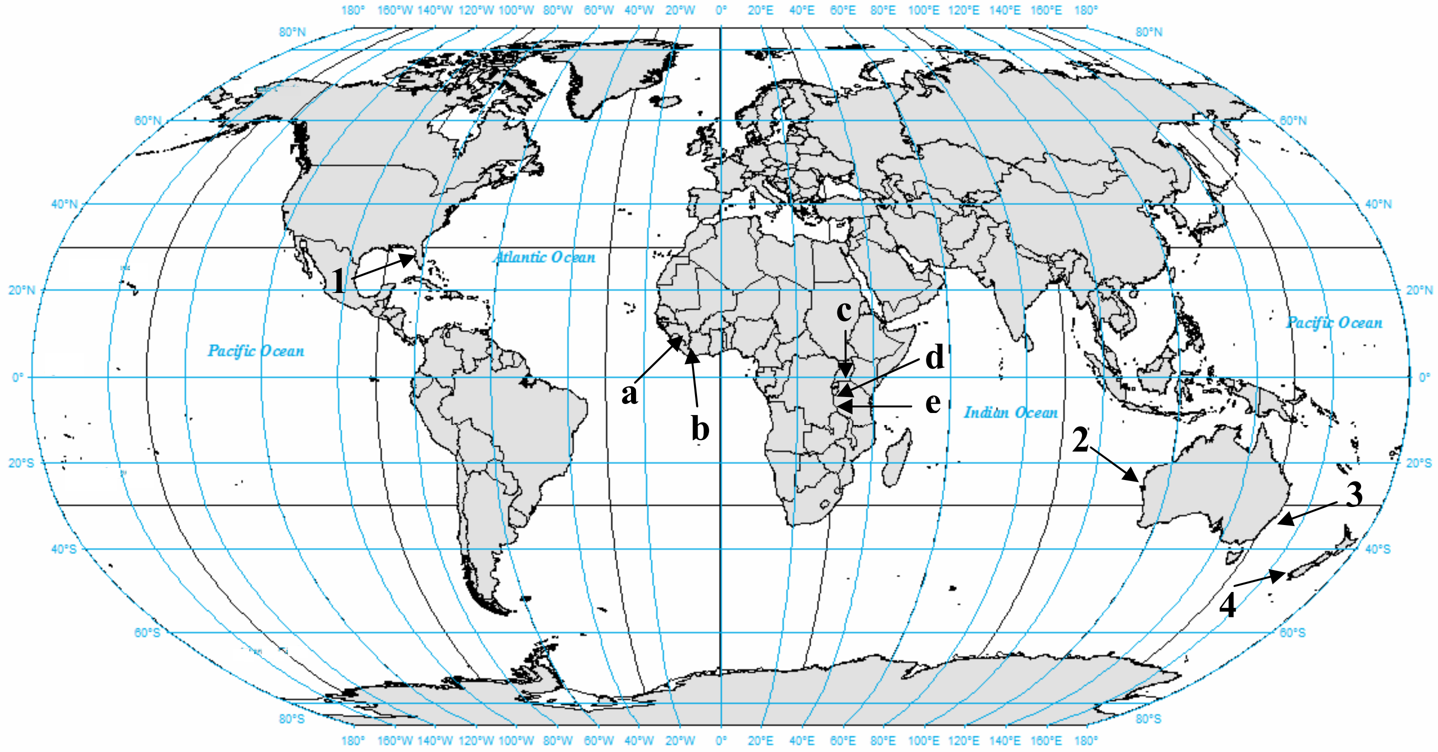

Fig. 21. Map of long-term bottlenose dolphin (*Tursiops* spp.) and chimpanzee (*Pan troglodytes*) field sites. Dolphin field sites include: 1) Sarasota, Florida, USA; 2) Shark Bay, Australia; 3) New South Wales, Australia; and 4) Doubtful Sound, New Zealand. Chimpanzee sites include: a) Bossou, Guinea; b) the Taï forest, Ivory Coast; c) Kibale, Uganda; d) Gombe, Tanzania; and e) Mahale, Tanzania. Map created using ArcView 9.2 (ESRI, Redlands, CA).

demographics) which may influence each species.

In this review, determinants of reproductive success, dispersal and ranging patterns, association patterns, and patterns of sociality are compared between the aforementioned sites. As comparable results are not available on each topic for all sites, all sites will not be discussed in each section. Before focusing on specific sites, however, I discuss potential costs and benefits of grouping for female dolphins and chimpanzees, and female life history characteristics.

Costs and benefits of grouping

Costs

Dolphins and chimpanzees live in fission-fusion societies which enable community members to join and leave groups. Optimality models would predict an individual to join a group when it is beneficial, and leave a group when it is costly; in this manner, the maximum net fitness benefit may be obtained (after Krebs and Davies 1993).

Increased competition for food is one ecologic cost of grouping. This may also be viewed in terms of scramble competition, meaning that when food sources occur in depleting patches, larger group size leads to increased feeding competition, and as a result individuals must range farther to satisfy their food requirements (Wrangham 2000). Thus, smaller group size during foraging may alleviate scramble competition for some dolphins (Möller et al. 2006; Gowans et al. 2008) and chimpanzees (Wrangham and Smuts 1980).

A possible social cost of grouping is increased conspecific aggression. In both species, intersexual aggression may take the form of harassment or sexual coercion. At Shark Bay, Australia, male dolphin alliances may herd receptive females through the use of aggressive behaviors such as chasing, “pop” vocalizations, and physical attacks (Connor et al. 1992). Additionally, cycling females have more tooth rakes than non-cycling females (Connor et al. 1996; Scott et al. 2005). Similarly, male chimpanzees at Kibale direct more aggression towards cycling females than non-cycling females (Muller et al. 2007). Intrasexual aggression may also be high for female chimpanzees which disperse from their natal communities. In such cases, immigrant females may experience high rates of aggression from resident females (Wrangham and Smuts 1980; Goodall 1986; Nishida 1990; Morin 1993).

Conspecific aggression may also be directed towards a female's offspring in the form of infanticide. For dolphins, evidence of infanticide has been reported from the Moray Firth, Scotland (Patterson et al. 1998); off St. Augustine, Florida, USA (Kaplan 2007); and off the Virginia coast, USA (Dunn et al. 2002). For chimpanzees, infanticide is widespread and was reported at all but one site mentioned in a recent review (Stumpf and Boesch 2005). Chimpanzee infanticide may occur by males from neighboring communities, or within the community by males or females (summarized in Arcadi and Wrangham 1999; Murray et al. 2007).

Benefits

Ecologic benefits of grouping may include increased access to rich food resources and predator protection. Increased access to food resources may occur through shared knowledge or cooperation in locating rich food patches (e.g., Goodall 1986; Würsig 1986), or through cooperative hunting (e.g., Boesch 1994; Gazda et al. 2005). Predator protection may occur via the dilution effect (Krause and Ruxton 2002) or via group mobbing or chasing of the predator (Boesch and Boesch-Acherman 2000; Mann and Watson-Capps 2005). For cetaceans living in the marine environment with little refuge from predators, protection from predators is believed to be a primary influence on group formation (Norris and Dohl 1980).

Offspring socialization is one possible social benefit of grouping, and may be especially important for young males, as males in both species form alliances as adults (Pusey 1983; Goodall 1986; Connor et al. 1992; Mann et al. 2000; Mitani et al. 2002). Another possible social benefit of grouping is decreased male aggression via the dilution effect whereby females in groups may receive less male aggression than when they are alone (e.g., Mann et al. 2000). Females of both species may also thwart male aggression by opportunistically forming coalitions (Nishida et al. 1990; Boesch and Boesch-

Acherman 2000; Mann et al. 2000; Newton-Fisher 2006). However, these coalitions appear to be less prevalent in dolphins than in chimpanzees.

Alloparental care is another potential social benefit of grouping, which may benefit the mother, alloparent, and/or the infant. Mothers may forage when alloparents provide relief from infant caregiving (Shane 1990), and may also profit by being groomed by alloparents (Nishida 1983). Allomothers may benefit by "learning to parent" and forging social bonds with the infant's mother, while infants may benefit from alloparenting by receiving protective care, learning about edible food items, and expanding their social network (Nishida 1983; Mann and Smuts 1998).

Finally, chimpanzee grooming and its corollary in dolphins, petting and rubbing, are another benefit of grouping. These behaviors may provide a hygienic function (e.g., parasite removal) in addition to having an affiliative social function (Goodall 1986; Mann 1997; Mann et al. 2000; Connor et al. 2006).

Overview of life history strategies

Like other large-brained species, dolphins and chimpanzees have slow life histories. Slow life history traits of females include a long lifespan, slow maturation, increased age at first parturition, a long lactation period and interbirth interval, and a low lifetime reproductive output (Table 15). In particular, a prolonged period of maternal dependence may provide time for offspring to learn the complex social, foraging, and predator avoidance strategies inherent to both species (Pusey 1983; Wells et al. 1987).

Prolonged offspring dependence on the mother subsequently leads to a long interbirth interval and a limited number of offspring that a female can physically produce in her lifetime. When combined with high rates of offspring mortality at some sites, the actual reproductive output of a female is much lower than the theoretical lifetime reproductive potential. Some chimpanzee sites report median or mean values of 2-3 offspring per female, which survive to adolescence (Tutin 1980; Nishida et al. 1990;

Table 15. Life history characteristics of female bottlenose dolphins (*Tursiops* spp.) and chimpanzees (*Pan troglodytes*).

Characteristic	Dolphins	References	Chimpanzees	References
Longevity	> 50 y [a]	(Mann et al. 2000)	> 45 y [a]	(Tutin 1979; Nishida et al. 1990)
Age at 1st parturition	5-13 y [b]	(Connor et al. 2000b)	13-15 y [c]	(Wallis 1997; Boesch and Boesch-Acherman 2000; Hill et al. 2001)
Gestation	12 mo [d]	(Whitehead and Mann 2000)	7.5 mo [d]	(Wallis 1997)
Interbirth interval	3-6 y [b]	(Wells et al. 1987; Mann et al. 2000; Haase and Schneider 2001; Grellier et al. 2003; Wells 2003)	5-6 y [c]	(Tutin 1979; Wallis 1997; Boesch and Boesch-Acherman 2000; Deschner and Boesch 2007)
Theoretical maximum no. births/lifetime	5-6	(Mann et al. 2000)	5-6	(Tutin 1979; Boesch and Boesch-Acherman 2000)
Reproductive senescence?	N	(Wells and Scott 1990; Wells et al. 2005)	Y	(Sugiyama 1994; Boesch and Boesch-Acherman 2000; Nishida et al. 2003)

a Maximum value
b Range of values reported from various sites
c Range of mean values reported from Taï and Gombe
d Mean value

Boesch and Boesch-Acherman 2000), while over a 10-year period in Shark Bay, the majority (68%) of females had 0-1 surviving calves (Mann et al. 2000). In turn, low reproductive output for both species has direct implications for conservation management strategies because it may take years for a declining population to start increasing in numbers (e.g., Hill et al. 2001).

While there is evidence for reproductive senescence at some chimpanzee sites (Nishida et al. 2003; Sugiyama 2004), this has not yet been reported for dolphins. However, as longitudinal field studies continue and individual life histories are tracked, conclusive data may be obtained regarding reproductive senescence in dolphins.

Reproductive success

Determinants of female reproductive success have been reported for some sites (Table 16). A positive relationship between age and reproductive success has been reported for Sarasota (Wells 2003) and Mahale (Nishida et al. 1990). A lack of maternal experience in primiparous females may largely contribute to high rates of infant mortality in young mothers. Additionally, at Sarasota, the high infant mortality rate for primiparous female dolphins may also be attributed to high contaminant loads which are transferred from a female to her firstborn calf (Wells et al. 2004; Wells et al. 2005).

The relationship between party size and reproductive success has been reported for dolphins but not chimpanzees. At Shark Bay, the mean or median party size of females was unrelated to reproductive success over a 10-year period (Mann et al. 2000). However, at Sarasota, females that raised calves in larger and more stable parties had higher reproductive success, likely through benefits of grouping such as increased predator protection, allomaternal care, and experience “learning to parent” (Wells 1993; Wells 2003).

Reproductive success has also been linked to habitat. At Shark Bay, female dolphins that were found more often in shallow waters had increased reproductive success. This was likely due to increased prey availability in shallow waters (Mann et al. 2000) which may have resulted in better maternal body condition (Mann and Watson-Capps 2005). At Kibale, female chimpanzees in higher quality core areas had increased

Table 16. Determinants of reproductive success for female bottlenose dolphins (*Tursiops truncatus*) and chimpanzees (*Pan troglodytes*).

Characteristic	Chimpanzee site	References	Dolphin site	References
Age/maternal experience	Mahale	(Nishida et al. 1990)	Sarasota	(Wells 1993; Wells 2003)
Habitat	Kibale	(Emery Thompson et al. 2007	Shark Bay	(Mann et al. 2000)
Dominance rank	Gombe	(Pusey et al. 1997)	N/A[a]	N/A
Party size	N/A	N/A	Sarasota	(Wells 1993; Wells 2003)

[a] Data not available

reproductive success, likely mediated by access to higher quality food in higher quality core areas (Emery Thompson et al. 2007).

Dominance rank was positively related to reproductive success at Gombe. Similar to Kibale, this relationship is likely mediated by food availability, as higher ranking females typically have access to better core areas with higher quality food while lower ranking females may be "forced" into lower quality core areas (Pusey et al. 1997). As dominance relationships have not been reported for female dolphins in the wild, any relationship between dominance rank and reproductive success for dolphins is currently unknown.

Dispersal and ranging patterns

Dispersal

The dispersal of one sex from the natal area may function to avoid deleterious effects of inbreeding. The typical mammalian dispersal pattern is for females to remain in their natal community (i.e., female philopatry) and for males to emigrate (Greenwood 1980). However, among the dolphin and chimpanzee sites included in this review, only one site (dolphins in New South Wales Australia, Möller and Beheregaray 2004) adheres to this pattern (Table 17).

At some dolphin sites, neither sex disperses from the natal community. Natal philopatry by both male and female dolphins has been reported at Shark Bay (Krützen et al. 2004), Sarasota (Wells et al. 1987), and Doubtful Sound (Lusseau et al. 2003). The low cost of transport in dolphins may enable community members to temporarily search for mates in neighboring communities without permanently emigrating from their natal area (after Connor 2000).

In contrast, male philopatry and female dispersal during adolescence is typical for chimpanzees (Mitani et al. 2002). Cooperative territory defense by males may be among the evolutionary pressures for males to remain in their natal area (Morin 1993). By remaining in their natal communities, males may increase familiarity with their territory. In addition, male philopatry may facilitate alliance formation between males (who are oftentimes kin); alliances may then result in increased dominance rank and

Table 17. Dispersal and ranging patterns for female bottlenose dolphins (*Tursiops* spp.) and chimpanzees (*Pan troglodytes*).

Site	Dispersing sex	♀ home range smaller than ♂ home range?	♀ core areas?	References
Dolphins				
Shark Bay	Neither	Y	Y	(Smolker et al. 1992; Krützen et al. 2004)
Sarasota	Neither	Y	Y	(Wells et al. 1987; Wells and Scott 1990; Wells 1991)
Doubtful Sound	Neither	N/A [a]	N/A	(Lusseau et al. 2003)
New South Wales	♂	N/A	Y	(Möller and Beheregaray 2004; Möller et al. 2006)
Chimpanzees				
Gombe	♀	Y	Y	(Goodall 1986; Pusey et al. 1997; Williams et al. 2002b)
Mahale	♀	Y	Y	(Hasegawa 1990; Nishida et al. 1990; Matsumoto-Oda and Oda 1998)
Kibale	♀	Y	Y	(Chapman and Wrangham 1993)
Taï	♀	Y	Y	(Boesch 1997; Lehmann and Boesch 2005)
Bossou	♀	— [b]	N	(Sugiyama 1988; Sugiyama 1999)

[a] Data not available

[b] Due to the small number of adult males present at Bossou, comparisons between males and females are not possible.

access to resources such as meat and estrous females (Boesch and Boesch-Acherman 2000). Thus, as compared to females, there may be more pressure for males to remain within their natal communities. This is apparent at Taï, where 95% of females dispersed from their natal community, all as adolescents (Boesch and Boesch-Acherman 2000).

However, a lack of neighboring communities may cause some female chimpanzees to remain in their natal communities. At Gombe, 50% of females have remained in their natal community, which is likely due to isolation of the Gombe community due to deforestation (Goodall 1986; Pusey et al. 1997; Constable et al. 2001; Williams et al. 2002b). In contrast, at Bossou, 88% of females and 40% of males have remained in their natal community. Bossou has historically been a small community of 15-20 individuals containing only 1-2 adult males, and high rates of aggression from the alpha male may be responsible for the high rate of male dispersal (Sakura 1994; Sugiyama 1999).

Ranging

For most dolphin and chimpanzee sites, female home ranges are smaller than male home ranges (Table 17). At Shark Bay and Sarasota where both sexes exhibit natal philopatry, males range farther than females and are thus vectors of genetic exchange between communities (Wells et al. 1987; Wells and Scott 1990; Krützen et al. 2004). At Gombe, the day range of males was reported to be 48% longer than the day range of females (Wrangham and Smuts 1980) while at Kibale male home ranges may be twice as large as female home ranges (Chapman and Wrangham 1993).

Females of both species spend most of their time in overlapping core areas (Table 17). Core areas likely provide several benefits to females, such as increased knowledge of an area which may lead to increased foraging efficiency and offspring safety (Williams et al. 2002b). Additionally, both female chimpanzees (Williams et al. 2002b; Pontzer and Wrangham 2006) and dolphins (Noren 2008) incur additional costs of transport when accompanied by dependent offspring and thus remaining in smaller known core areas may lessen travel costs for mothers.

Taï and Bossou are exceptions to these general ranging patterns. While male chimpanzees at Taï have larger home ranges than females, intersexual differences in home range size are not as pronounced as at other sites (Lehmann and Boesch 2005). At Bossou, the community occupies a small area (8-10 km^2), and thus there is little space available for females to have individual core areas (Sakura 1994). Additionally, distinctions between male and female home ranges at Bossou are not possible because there are so few adult males in the community (Sugiyama 1988; Sugiyama 1999).

Association patterns

There is a general pattern across all dolphin and chimpanzee sites for adult male-male bonds to be the strongest, followed by female-female bonds, and then male-female bonds (Table 18). At Shark Bay, the mean coefficient of association (COA) between top-ranking female associates was nearly 40% weaker than the mean COA between top-ranking male associates (Smolker et al. 1992). Strong bond formation between males is likely related to alliance formation, and in dolphins, some male alliance partners may exhibit COAs that are similar in strength to COAs between females and their young offspring (Wells, et al. 1987; Smolker et al. 1992).

Although bonds between females may be weaker than bonds between adult males, females typically form larger social networks than males. At Sarasota, female dolphins were observed to associate with nearly every other female in the community at some point (Wells et al. 1987), and the majority of females at Shark Bay were linked to each other either directly or through a common third-party associate (Smolker et al. 1992). However, within the larger social network, female dolphins may associate more strongly within "bands" or "cliques" (Wells et al. 1987; Smolker et al. 1992). Furthermore, within female bands at Sarasota, dolphins of similar reproductive state (i.e., pregnant, receptive, resting) are often found together, likely because they shared similar energetic requirements (Wells 2003). Overall, female dolphin social networks may remain fairly constant. For example, at Shark Bay, associations in cliques remained stable across a 5-year period (Smolker et al. 1992).

Table 18. Frequency of association (rank order) for bottlenose dolphins (*Tursiops truncatus*) and chimpanzees (*Pan troglodytes*).

Site	♂-♂	♀- ♀	♀-♂	References
Dolphins				
Shark Bay	1	2	3	(Smolker et al. 1992)
Sarasota	1	2	3	(Wells et al. 1987; Wells 2003)
Doubtful Sound [a]	1	2	3	(Lusseau et al. 2003)
Chimpanzees				
Gombe	1	2	3	(Goodall 1986; Symington 1990)
Mahale	1	2	3	(Nishida 1990)
Kibale	1	3	2	(Wrangham et al. 1992)
Taï	1	2	3	(Boesch and Boesch-Acherman 2000; Wittig and Boesch 2003)
Bossou	—— [b]	——	——	(Sugiyama and Koman 1979; Sakura 1994; Sugiyama 1981,1999)

[a] Differences between male-male, female-female, and male-female bonds are not significantly different.

[b] Due to the small community size and small number of adult males within this community, intra- and inter-sexual comparisons in association patterns are not possible.

While female chimpanzees also form larger social networks than males, when compared to female dolphins, female chimpanzees generally associate less consistently with certain other females (Smolker et al. 1992). Consistent associations between females at Gombe may be limited to mothers and daughters; otherwise, females typically associate sparsely and inconsistently with other females (Goodall 1986). At Kibale, female-female relationships may be exceptionally weak. The mean COA between female chimpanzees at Kibale was less than half as strong as that between males, and female-female bonds were also weaker than male-female bonds (Wrangham et al. 1992).

The Doubtful Sound and Taï communities have been described as "bisexually bonded" because of strong intersexual bonds and the high frequency of parties containing adult males and adult females (i.e., mixed parties). At Doubtful Sound, while male-male bonds were stronger than female-female or male-female bonds, differences between the three groups were not significant (Lusseau et al. 2003). Additionally, members of the Doubtful Sound community generally occurred in large mixed schools in which a large number of strong and lasting bonds were formed. At Taï, while female-female bonds were not as strong as male-male bonds, bonds between Taï females were higher than at any other chimpanzee sites. Male-male and male-female bonds were also higher at Taï than at other sites (Boesch and Boesch-Acherman 2000; Wittig and Boesch 2003). Furthermore, Taï chimpanzees were found in mixed parties 52% of the time, and 82% of the time that females were observed, they were with males (Boesch 1996, but see Doran 1997).

Patterns of sociality

Males vs. females

Females at most sites are typically less social than males; that is, females spend more time alone and/or occur in smaller parties than males (Table 19). As male reproductive success primarily depends on obtaining access to receptive females and this may be accomplished through alliance formation, integration into the social network is important for males. On the other hand, as female reproductive success depends more on food availability and predation risk, maintaining a high level of sociability may not be

Table 19. Patterns of sociality for female bottlenose dolphins (*Tursiops truncatus*) and chimpanzees (*Pan troglodytes*). Table modeled after Wrangham (2000).

	Males *vs*. females			Mothers *vs*. non-mothers		Cycling *vs*. non-cycling females		
Site	♀ less social than ♂?	♀ mostly associate with ♀?	Coalitions or alliances?	Mothers often alone?	Mothers associate less with ♂?	Non-cycling ♀ in smaller parties?	Non-cycling ♀ associate less with ♂?	References
Dolphins								
Shark Bay	Y	Y	♂-♂, ♀-♀	Y	N/A [a]	Y	Y	(Connor et al. 1992; Smolker et al. 1992; Mann and Smuts 1999; Sargeant et al. 2005; Gibson an Mann 2008)
Sarasota	Y	Y	♂-♂	N	Y	N	Y	(Wells et al. 1987; Wells 1993)
Chimpanzees								
Gombe	Y	Y	♂-♂	Y	Y	Y	Y	(Halperin 1979; Wrangham and Smuts 1980; Goodall 1986; Pusey 1990; Williams et al. 2002a)

Table 19. Continued.

	Males *vs.* females			Mothers *vs.* non-mothers		Cycling *vs.* non-cycling females		
Site	♀ less social than ♂?	♀ mostly associate with ♀?	Coalitions or alliances?	Mothers often alone?	Mothers associate less with ♂?	Non-cycling ♀ in smaller parties?	Non-cycling ♀ associate less with ♂?	References
Mahale	Y	Y	♂-♂, ♀-♀	Y	Y	Y	Y	(Nishida et al. 1990; Takahata 1990; Matsumoto-Oda and Oda 1998; Matsumoto-Oda 1999)
Kibale	Y	Y	♂-♂	Y	Y	N/A	Y [b]	(Wrangham et al. 1992; Chapman and Wrangham 1993; Muller et al. 2006; Otali and Gilchrist 2006)
Taï	Y/N [c]	Y/N	♂-♂, ♀-♀, ♂-♀	Y	N/A	N/A	N/A	(Boesch 1996; Doran 1997; Boesch and Boesch-Acherman 2000)
Bossou	— [d]	N	— [e]	Y/N [c]	N	Y	N	(Sugiyama and Koman 1979; Sugiyama 1981, 1999; Sakura 1994)

[a] Data not available for this site

[b] The comparison for this site is between estrous *vs*. anestrous females.

[c] Results vary according to study; see text for details

[d] Due to the small number of adult males present at Bossou, comparisons between males and females are not possible.

[e] Due to the small number of adult males present at Bossou, males do not form alliances.

critical for females unless this functions to increase access to high quality food or reduce predation risk (after van Schaik 1989; Pusey 1990; Chapman and Wrangham 199;).

At Shark Bay, a mother spends approximately 50% of her time alone with her calf (Mann and Smuts 1999; Gibson and Mann 2008) while at Gombe and Kibale, females spent more than twice as much time alone (or with their offspring only) than adult males (Wrangham and Smuts 1980; Symington 1990; Wrangham et al. 1992). In contrast, it would be rare for an adult male to spend a significant amount of time alone, as many males form alliances where the partners spend the majority of their time together (Goodall 1986; Connor et al. 1999; Wells 2003).

Individual females may vary more widely in their sociality than males, with some females being quite gregarious and others being more solitary (Smolker et al. 1992). This may be partially attributed to reproductive state, as cycling females are generally more social than non-cycling females (see below). For chimpanzees, variation in sociability may also be related to immigrant status. Immigrant (*vs*. resident) females are more social with males as they integrate into the social network of the new community (Goodall 1986).

Female foraging specializations may favor a more solitary lifestyle (Mann et al. 2000). Female dolphins at Shark Bay which specialize in sponging (Smolker et al. 1997) or beach-hunting (Sargeant et al. 2005) are more solitary than other females. For example, spongers were with other dolphins an average of 7% of observation days (Smolker et al. 1997), while beach-hunters spent approximately 30% less time with other dolphins than non-beach-hunters (Sargeant et al. 2005). Similarly, at Gombe, there is a relationship between the amount of time mothers spend alone (with their dependent offspring) and the amount of time they engage in termite fishing (Lonsdorf 2006). Additionally, nut-cracking at Taï is a solitary activity which is engaged in more frequently and more proficiently by females (Boesch and Boesch-Acherman 2000).

When females are social, they typically associate with females instead of males (Table 19). Mothers and calves at Shark Bay preferentially associated with females but avoided adult males (Gibson and Mann 2008). At Gombe, mothers with young were observed alone with their offspring on 65% of observation intervals, in all-female nursery groups on 25% of observation intervals, and with males on 10% of observation intervals (Halperin 1979).

At Taï, one study found that female chimpanzees were as social as males and associated with males and females equally, while a subsequent study found the opposite (Table 19). These conflicting results may be an artifact of differing study methods. Boesch's (1996) study was: 1) conducted during 11 months spanning a 19-month period, 2) focused on observing the behavior of individuals in groups, and 3) biased to sample males more than females (summarized in Doran 1997). In contrast, Doran's (1997) study was: 1) conducted over the course of 7 consecutive months, 2) based on observing behavior of individuals in groups and alone, and 3) unbiased in equal samples of males and females.

Coalition or alliance formation is another way to assess sociality. Female alliances or coalitions are rare and have only been reported at two of the chimpanzee sites included in this review (Table 19). Females at Mahale and Taï may form coalitions against aggressive males, or immigrant females (Boesch and Boesch-Acherman 2000). Taï females may also form alliances with adult males (Boesch and Boesch-Acherman 2000). At Shark Bay, female dolphins may opportunistically cooperate against aggressive males (Connor et al. 1992; Connor et al. 1996; Connor et al. 2000b; Gero et al. 2005; Scott et al. 2005), but it is a rare occurrence (J. Mann, personal communication). Male coalitions or alliances are present at sites presented in Table 19, except for Bossou. Male coalitions or alliances have not been observed at Bossou, likely due to the historically low number of adult males in this community (Sakura 1994; Sugiyama 1999; Sugiyama 2004).

Mothers vs. non-mothers

At most sites, mothers are often alone or with their offspring only and associate (in terms of percent time spent with males or COAs between mothers and males) with males less often than do non-mothers (Table 19). For example, at Shark Bay, mothers were observed to be alone an average of 51% of the time and to associate with males significantly less than expected (Gibson and Mann 2008), while chimpanzee mothers at Gombe were alone 65% of the time (Wrangham 1986).

Mothers may spend more time alone, which may reduce scramble competition. As both species primarily feed on patchy food which occurs in depleting patches (e.g., fruit, non-schooling fish), increasing group size will reduce per capita food intake, resulting in increased time spent traveling between food patches (Wrangham 2000; Gowans et al. 2008). At Shark Bay, maternal foraging time was positively related to the proportion of time mothers and calves spent alone (Gibson and Mann 2008). Similarly, female chimpanzees at Gombe spent more time feeding when alone than when in parties, and feeding bout length was inversely related to length of time spent in a party (Wrangham and Smuts 1980).

Mothers may be more affected by scramble competition than non-mothers because mothers incur an increased cost of transport when accompanied by dependent offspring. Until they are weaned (Whitehead and Mann 2000), dolphin calves spend 30-45% of their time swimming alongside their mothers in echelon (parallel swimming just above the mother's midline) or infant position (swimming under the mother's tailstock with its head lightly touching the mother's abdomen). This "infant carrying" behavior increases the drag force on the mother, and reduces the mean maximum swim speed of a female by nearly 25% (Noren 2008). Likewise, a chimpanzee mother travels more slowly when carrying an infant (Wrangham 2000; Williams, et al. 2002a), and has a reduced day range when constrained by the slow walking speed of a juvenile (Pontzer and Wrangham 2006). Therefore, travel costs associated with scramble competition may be lessened for dolphin and chimpanzee mothers that spend more time alone.

Reduced sociality between mothers and males may be related to lower infanticide risk. While evidence for infanticide has not been reported for either dolphin site listed in Table 19, it has been documented at several other dolphin sites (see "Costs of grouping" above). However, infanticide has been documented for all chimpanzee sites in Table 19 (summarized by Arcadi and Wrangham 1999; Murray et al. 2007). According to the infant safety hypothesis, females with young may protect against infanticide by avoiding males. At Kibale, mothers (*vs.* non-mothers) had a lower probability of occurring in groups containing ≥ 1 male, but this probability increased with offspring age. However, the number of males with which a female associated did not differ between mothers and non-mothers (Otali and Gilchrist 2006).

At Bossou, there are conflicting results regarding the sociality of mothers. While Sakura (1994) reported that lactating females often foraged alone with their offspring and appeared to avoid large sexual parties, Sugiyama and Koman (1979) and Sugiyama (1981) stated that mothers with infants spent more time in larger parties with other mothers and had stronger associations with males than when they did not have young infants.

Although mothers in general may spend a significant portion of their time alone, mothers may adjust their sociability according to offspring age. At Sarasota (Wells et al. 1987; Scott et al. 1990) and Shark Bay (Mann et al. 2000; Mann and Sargeant 2003), mothers with young calves occur in larger groups than females with older calves, One function of large nursery groups may be to protect against predators (e.g., Wells 2003). Large nursery groups may also result from "natal attraction", when inexperienced or nulliparous females are attracted to infants (after Mann and Smuts 1998).

The sociability of female chimpanzees with infants varies between sites. At Kibale (Otali and Gilchrist 2006), there was a significant negative relationship between offspring age and the number of female associates that a mother had, a pattern seemingly similar to that found at Shark Bay and Sarasota. However, these results must be interpreted cautiously, as the predicted decrease in number of female associates with increasing offspring age was 0.71 and is thus unlikely to be biologically meaningful (Otali and Gilchrist 2006). In contrast, Gombe females with infants were less likely to be with other females, but mothers with juveniles were attracted to each other (Williams et al. 2002a). These results suggest that different socioecological factors (e.g., protection from male aggression, scramble competition) are influencing the sociability of mothers with infants at Kibale and Gombe.

Cycling vs. non-cycling females

In general, there is a pattern for non-cycling females to occur in smaller parties and to associate with males less than cycling females (Table 19). This result is expected, because cycling females are attractive to males seeking mating opportunities. At Shark Bay, male dolphin subgroups had higher associations with females when they were cycling *vs*. when they were pregnant (Connor et al. 1992; Smolker et al. 1992). At Mahale, non-cycling female chimpanzees were in large mixed parties less often and in female parties more often than cycling females, and there was a positive correlation between the number of estrous females and males in a group (Matsumoto-Oda 1999). In some cases, the increased gregariousness of cycling females may be largely attributed to their increased association with males, at the expense of associating with other females. At Kibale, females increased their association with males when in estrous but had decreased rates of association with other females (Otali and Gilchrist 2006).

At Gombe, in years in which a female is cycling, she has a wider variety of associates and spends much more time in mixed parties than years in which she is not cycling. Additionally, as over half of Gombe females do not emigrate and females tend to associate primarily with their offspring, a female may also become much more social when her daughter comes into estrus (Goodall 1986). In contrast, cycling (*vs*. non-cycling) females at Bossou do not associate more with adult males (Sakura 1994), perhaps because this is already such a small, cohesive community with few adult males.

Matsumoto-Oda (1999) stated that non-cycling female chimpanzees should adopt a “falling out” strategy by avoiding large groups in order to avoid increased travel costs, increased scramble competition, and increased male aggression. In both species, cycling females receive more male aggression than non-cycling females (see “Costs of grouping” above). Thus, observations of increased sociality of cycling *vs*. non-cycling dolphins and chimpanzees may be an artifact of non-cycling females avoiding the costs associated with “rowdy” sexual groups, as opposed to estrous females being atypically social.

Sarasota is the only site shown in Table 19 where females do not occur in smaller parties when they are cycling, and where mothers are not often alone (Wells et al. 1987). As reproductive success for Sarasota females increases with party size (Wells 1993; Wells 2003), females may remain in groups, regardless of maternal or reproductive status. Additionally, elevated predation risk or reduced scramble competition may lead to increased gregariousness for all females at Sarasota.

Synthesis

The complex cognition and social structure inherent to dolphins and chimpanzees makes it difficult to generalize patterns of female sociality within a species or even a site. However, based on the patterns presented in Tables 18-19, there are several broad generalizations that can be made regarding female dolphin and chimpanzee sociality: 1) social bonds between females are not as strong as social bonds between males; 2) overall, females are less social (e.g., occur in smaller groups, associate with fewer conspecifics) than males; 3) females associate mostly with other females; 4) mothers are often alone with their offspring; 5) mothers (*vs*. non-mothers) associate less with males; 6) non-cycling (*vs*. cycling) females are found in smaller parties; and 7) non-cycling (*vs*. cycling) females associate less with males.

Some of the key factors associated with these patterns likely include scramble competition, predation risk, and the cost of transport. Reduced scramble competition, increased predation risk, and a lower cost of transport may “allow” females to be more social. In contrast, increased scramble competition, reduced predation risk, and a higher cost of transport may restrict female sociality. The interplay between the costs and benefits of grouping (e.g., predation risk, resource availability) and their influence on female sociality has been well-described in conceptual models proposed by Krebs and Davies (1993) and van Schaik (1989). More recently, the cost of transport has been used to explain differences in sociality within (e.g., chimpanzee females of various reproductive states; Wrangham 2000; Williams et al. 2002) and between (e.g., cetaceans *vs*. primates; Connor 2000) species. The intensity of the aforementioned factors is likely to vary between dolphins and chimpanzees, and there may be a tendency for female dolphins to be more social than female chimpanzees. Below are several predictions and hypotheses which should be further explored and tested.

First, there may be less scramble competition for dolphins foraging on mobile prey resources than for chimpanzees foraging on static fruit and plant resources. Therefore, female dolphins may "afford" to form larger groups. Second, predation risk is likely to be higher, or at least more variable, in the marine than terrestrial environment due to the lack of refuge from predators in a marine environment. Thus grouping is the primary defense against predation for dolphins (Norris and Dohl 1980), and female dolphins may tend to form larger groups than female chimpanzees.

Third, for both dolphins and chimpanzees, the act of leaving and joining parties (i.e., "fission" and "fusion") according to the shifting balance of costs and benefits associated with grouping is a behavioral adaptation to rapidly changing socioecological conditions. However, anatomical (e.g., fusiform body shape) and behavioral (e.g., wave-riding) adaptations of dolphins facilitate locomotion at a low energetic cost (Williams et al. 1992, 1993). The cost of transport for a chimpanzee moving at a walking gait of 1 m s^{-1} is 3.82 J kg^{-1} m^{-1} (Sockol et al., 2007), while the cost of transport for a dolphin swimming at "preferred" speeds of 2.1–2.5 m s^{-1} is 1.16-1.29 J kg^{-1} m^{-1} (Williams et al. 1993; Yazdi et al. 1999). Thus, the cost of transport for chimpanzees is more than three times higher than for dolphins.

The reduced cost of transport for dolphins may enable female dolphins to join and split from groups more rapidly than is physically possible for chimpanzees (after Connor 2000). For example, dolphins may spread out in areas and times of low prey abundance, but may quickly and "cheaply" rejoin a party at the conclusion of a feeding bout. In contrast, female chimpanzees which disperse from a party to feed must expend more energy to rejoin a party; as a result, they may remain solitary or in smaller parties for longer periods of time. Additionally, a reduced cost of transport may lead to a larger social network in dolphins than chimpanzees, as dolphins exhibit a high degree of social "mixing" as they rapidly join and split from parties.

Future research directions

In order to test the aforementioned predictions and hypotheses regarding the effects of scramble competition, predation risk, and the cost of transport on female sociality, continued comparisons should be made both within and between dolphins and chimpanzees. To understand which evolutionary pressures are influencing female sociality within a species, sites that differ in levels of food availability and predation risk should be compared. Some chimpanzee studies have already done this by broadly comparing female sociality between Taï and their East African counterparts at Gombe and Mahale (e.g., Boesch and Boesch-Acherman 2000). As more forested environments are expected to have a more abundant food supply than less forested environments (Boesch and Boesch-Acherman 2000), the increased sociality of Taï females may be attributed to increased forest cover (and the supposed increase in food availability) as compared to Gombe and Mahale.

For dolphins, patterns of sociality may be compared between communities inhabiting enclosed or protected areas (e.g., small shallow bays and estuaries) *vs.* open or less protected areas (e.g., deep bays and pelagic waters), which differ in levels of predation risk and prey abundance (summarized in Möller et al. 2002). However, in order to test specific hypotheses regarding the relationship between food availability and female dolphin sociality, more data are needed on prey availability (see Heithaus and Dill 2002 for one example) and scramble competition (Michaud 2005) in the marine environment.

Continued studies on travel costs (e.g., travel speed, day range) for mothers with offspring of different ages are needed to determine if and how travel costs restrict mother sociality in both species. Chimpanzee mothers carrying infants travel more slowly (Williams et al. 2002a) and mothers with juveniles have a reduced day range (Pontzer and Wrangham 2006), indicating that the costs of transport are high for chimpanzee mothers. This may be related to the increased energetic cost of carrying an infant, or the reduced travel speed of independently-traveling dependent offspring. For dolphins, although it has been shown that mothers travel more slowly when accompanied by an infant (Noren 2008), more data are needed regarding the day range of dolphin mothers with infants.

Furthermore, more data are needed to test the null hypothesis that juveniles do not increase travel costs for mothers in an aquatic environment (Pontzer and Wrangham 2006). Measuring the day range and travel speed of single females *vs*. mothers with juveniles would be one way to assess travel costs between these two types of females. If no differences are found, this may indicate that an aquatic environment releases dolphin mothers from an increase in travel costs due to an accompanying juvenile. In turn, dolphin mothers with juveniles may be more social than chimpanzee mothers with juveniles, and this should also be tested.

In general, the assimilation of data from a variety of chimpanzee and dolphin sites will enhance hypothesis testing. Data obtained from longitudinal sites will be most useful, as these data will account for inter-year variability in female sociality which may result from changes in food availability (e.g., Otali and Gilchrist 2006), community demographics (e.g., Lehmann and Boesch 2004), predation levels, or habitat loss/interference. However, so as to more fully account for inter-site variation within dolphins and chimpanzees, data from more recently established sites will also be important so as to represent a wider variety of habitats.

Increased consistency in methods will also increase the efficacy of comparative research. The discrepancies in female sociality reported for the Taï chimpanzees (Boesch 1996; Doran 1997) highlight the need for consistent methods so that comparable results may be obtained, both within and between sites. Additionally, similar definitions of a “group” and the use of similar behavioral sampling methods are warranted for intra-species comparisons. Increased consistency in methods within each species will then enhance the accuracy of inter-species comparisons.

There are inherent difficulties associated with studying cognitively and socially complex animals such as chimpanzees and dolphins. However, if careful comparisons are made within and between species, we will increase our understanding of the evolutionary pressures leading to social convergence between delphinids and pongids.

Additionally, increased collaborative efforts between cetologists and primatologists will bolster comparative research. As “integrative” and cross-disciplinary science becomes more widespread, we may soon see an increase in cross-taxa research between terrestrial and marine mammals. For example, striking parallels have been noted for another pair of marine and terrestrial mammals – sperm whales (*Physeter macrocephalus*) and African elephants (*Loxodonta africana*) (Weilgart et al. 1996; Whitehead and Weilgart 2000). As we continue to study species which are evolutionary distant but socially alike, we will increase our understanding of how similar adaptations to socioecological pressures may lead to similar types of social organization in species that, at first glance, may appear to have little in common.

CHAPTER VI

SUMMARY

Although Admiralty Bay is typically inhabited by dusky dolphins for less than six months each year, this is an important habitat. Through the use of behavioral observations and photo-identification, this study provided a detailed examination of the social lives of dusky dolphins in Admiralty Bay. Specifically, this study examined influences on fission-fusion sociality such as coordinated foraging, predation pressure, and social pressures to "meet" and interact with other members of the community. Overall, dusky dolphins in Admiralty Bay exhibited complex sociality through coordinated foraging strategies, facilitated by leaping and short- and long-term bond formation; and formation of preferred companions during foraging and socializing. By understanding how these traits influence dusky dolphin fission-fusion sociality, our understanding of the evolution of this type of society in other delphinids and great apes has been furthered.

Low predation pressure in Admiralty Bay appears to have "released" dusky dolphins from enacting defensive mechanisms such as forming large parties during resting, and resting near shore. Consequently, party size appears to be primarily influenced by foraging strategies. Party size increased during foraging, and parties were the most "fluid" (i.e., a large proportion of individuals joined and split from groups) during foraging.

Dusky dolphins are known for their acrobatic leaping behaviors. This study found that leaping primarily occurs in large parties and during foraging. In particular, "clean" head-first re-entry leaps were the most common, and appeared to aid in prey capture. This is in contrast to dusky dolphins in Kaikoura, where leaping appears to function in social facilitation (Markowitz 2004), and dusky dolphins in Golfo San José, where leaping appears to function in both prey capture and social facilitation (Würsig and Würsig 1980).

While dusky dolphin parties may at times appear to be little more than a flurry of frenzied behavior with individuals continually joining and leaving in no real pattern, closer analyses reveal a more structured society. Dusky dolphins in Admiralty do not associate at random but form short- and long-term preferred associations. Additionally, individuals appear to form strong bonds during foraging and socializing. Bond formation during these behaviors appears to be particularly important in this society, as individuals which "meet and get to know" each other during socializing may be able to more closely coordinate behaviors during foraging in Admiralty Bay.

Observations of dusky dolphins in Admiralty Bay, and comparisons with dusky dolphin populations in Kaikoura (Markowitz 2004) and Golfo San José (Würsig and Würsig 1980), reveal that dusky dolphins may use their large brains to solve complex ecological and social problems. In the open waters off Kaikoura, large parties provide the benefit of predator protection (Würsig et al. 1997), at the cost of increased cognitive demands to keep track of potential social and mating partners within a wide social network. Social complexity is also high in the more enclosed environments of Admiralty Bay and Golfo San José (Würsig and Würsig 1980), where individuals form and reinforce social bonds to facilitate coordinated foraging strategies on patchy prey items.

The social brain hypothesis helps us to understand that it is the need to keep track of social relationships in a fluid environment, and not ecological complexity alone, which demands high cognition (e.g., Dunbar and Shultz 2007). Of course, the social brain hypothesis applies not only to dusky dolphins, but also to other highly-encephalized species living in complex social environments, such as bottlenose dolphins and chimpanzees. Complex sociality (i.e., fission-fusion) and large brains with complex cognition may have co-evolved in delphinids and pongids, both likely driven by ecological unpredictability.

To further examine aspects of social convergence between delphinids and pongids, I examined social strategies of female bottlenose dolphins and chimpanzees. Females of both species are affected by similar ecological (e.g., food availability, predator pressure) and social (e.g., male harassment, infanticide risk, offspring socialization, allomaternal care) pressures. In general, females tend to be less social than males, associate primarily with other females, and change patterns of sociality according to changes in reproductive state. However, there may be a tendency for female dolphins to be more social than female chimpanzees, due to decreased scramble competition, increased predation risk, and a decreased cost of transport for dolphins *vs.* chimpanzees.

Science is a perpetual process whereby one answer leads to many more questions; this study is no exception. As we now have a better understanding of fission-fusion sociality for dusky dolphins in Kaikoura and Admiralty Bay, an important next step will be to determine "how" individuals learn the cultural tradition of migrating between the two areas. A comparison of the Kaikoura and Admiralty Bay image catalogues may provide insight into which individuals are responsible for the spread of this cultural tradition. As the majority of individuals in Admiralty Bay are male (Shelton 2006), it is likely that this is an example of horizontal or oblique culture (i.e., transmission of knowledge between members of the same generation) rather than vertical culture (i.e. transmission of knowledge from parent(s) to offspring, see (Whitehead et al. 2004).

Another promising line of research will be to better understand interactions between individuals, and not simply associations (*sensu* Hinde 1976). This will take our understanding of dusky dolphin sociality to the "next level", on par with detailed behavioral studies of wild bottlenose dolphins and chimpanzees (e.g., Goodall 1986, Boesch and Boesch-Achermann 2000, Connor et al 2006). Additionally, interaction data will enable a better understanding of the cognitive basis of animal bonds in terms of the social brain hypothesis.

More generally, as the importance of long-term study is widely recognized (e.g., Wells 1991), it is important that research continues on the New Zealand dusky dolphin population, both in Kaikoura and Admiralty Bay. Continued behavioral and photo-identification studies will be important in assessing long-term patterns of sociality.

Ultimately, a better understanding of social convergence between delphinids and pongids will only be possible through further detailed comparisons between these two groups, which will be facilitated through collaborations between cetologists and primatologists. In particular, the predictions and hypotheses proposed in Chapter V need to be tested. There is also a need for greater consistency in research methods, within and between taxonomic groupings, so that more detailed, quantitative comparisons may be made.

Overall, this research shows that Admiralty Bay is an important foraging habitat for dusky dolphins, and warrants protection. While the full impact of mussel farms on dusky dolphins is still not clear, it is evident that dusky dolphins forage near, but not in, mussel farms. Therefore, careful consideration should be given to proposals to increase the size and/or number of mussel farms in this area. As researcher presence may also advance conservation efforts, the continuation of dusky dolphin studies in Admiralty Bay will help in managing this population for "robustness" (after Wursig et al. 2002).

Although the dusky dolphin population is currently healthy, I would be remiss if I did not draw attention to the perilous conservation status of other odontocetes, and great apes (see below). Thus, while we may be just on the cusp of our knowledge of social convergence between these two taxonomic groupings, time may be running out to fully understand just how similar these incredible minds are.

Concluding thoughts: Conservation of "intelligent" species — combating the "Not me" attitude

With mounting evidence for high intelligence and complex cognition in taxonomic groups as diverse as primates (e.g., Dunbar 2003), cetaceans (e.g., Marino 2002), social carnivores (e.g., Holekamp et al. 2007), corvids (e.g., Emery and Clayton 2004), and insects (e.g., Coolen et al. 2005), one might reasonably surmise that practical outcomes of this would be global enhancement and prioritization of species conservation efforts. For who wants to be responsible for driving a "smart" species to extinction? I suspect the response would be an overwhelming, "Not me!" However, primarily through habitat interference and destruction, we as a human race seem to be doing a pretty good job of wiping out the “superstars” of high intelligence, the great apes (pongids) and the toothed whales (odontocetes). All of the world’s pongids are either endangered or critically endangered, and face a very high probability of extinction within the next 50 years (Walsh et al. 2003; IUCN 2007). Sadly, it may already be too late for some odontocetes such as the baiji (*Lipotes vexillifer*) and the vaquita (*Phocoena sinus*) (IUCN 2007; Turvey et al. 2007).

I remember reading the Family Circus cartoons by Bill Keane in the Sunday paper (before I was a graduate student and had time to read the newspaper!), and laughing at the ones which depicted “Not Me” as a character. This character flitted from place to place, creating messes in the family house and wreaking havoc in the neighborhood. When the boy in the cartoon was questioned by his parents as to who had done these things, he would answer, “Not Me!” In the real world, “Not Me” is responsible for environmental crimes such as deforestation, melting of the polar icecaps, pollution and overfishing of the seas, poaching, illegal trading of endangered species, and the list goes on.

I am not advocating that only “intelligent” species be conserved. Far from it. The way I see it, there is evidence for “intelligent” behavior in just about any species if one mindfully engages in careful and patient observation (Griffin 1976). Evolution has selected for behaviors which enable animals to survive in their ecological niche, and each animal thus has the necessary capabilities or “smarts” to survive in that niche. Instead of adopting the null hypothesis that animals are not intelligent, we as scientists should initially acknowledge that we *do not know* if an animal is intelligent or not, and then our alternative hypothesis should be to ask if an animal is intelligent or not (Gadagkar 1995). In many cases, the most parsimonious explanation may be to assume high cognition in animals (van Schaik and van Hooff 1989).

The crux of my argument, however, is that if we cannot even find a way to protect chimpanzees (*Pan troglodytes*), which are perhaps the most blatantly intelligent species and also so like ourselves, what hope is there for preserving species like the beluga whale (*Delphinapterus leucas*) or blue whale (*Balaenoptera musculus*), which are so morphologically unlike us and whose entire world occurs primarily in the foreign realm of ultra- and infra-sound? Thus, it is time for this "not me" *attitude* to turn into the *action* of "why not me"? While it is apparent that most natural scientists are well-aware of the amazing cognitive complexity exhibited by our closest primate relatives and distant cetacean relatives, the conservation message is not reaching the audience which has the potential for making the greatest difference – the general public and, importantly, policy makers (Bearzi 2007).

Another important conduit for disseminating the conservation message is the education of upcoming generations, which I believe is the best hope for ingraining environmental values into society as a whole. This may occur formally in school, informally at home, or via community activities. Jane Goodall's "Roots and Shoots" program (http://www.rootsandshoots.org/) is an excellent example of how engaging youth in community- and environmentally-minded activities can instill conservation values that will hopefully last a lifetime and eventually "trickle-up" to policy-makers. When I visited the savanna chimpanzees (*P. t. verus*) of southeast Sénégal in 2006, I befriended a Peace Corps volunteer who was operating a similar program by educating schoolchildren on the value of protecting the chimpanzees living near their villages.

According to the 2007 World Conservation Union (IUCN) Redlist, we are facing a "global extinction crisis". Unfortunately, action within the scientific community and "conservation on paper" (Bearzi 2007) are not enough. As stated by Julia Marton-Lefèvre, the director of the IUCN, the only hope for combating this crisis is to act at the level of the society (http://www.iucn.org). Thus, in addition to continuing our conservation-minded research and teachings, we as scientists can help those around us to engage in "Why not me?" actions by setting good examples through everyday activities such as recycling and driving fuel-efficient vehicles. Indeed, it is worrisome to think that this global extinction crisis may not be limited to non-human species.

When I was 15 years old, I thought I was the luckiest kid in the world because my parents generously allowed me to go on a month-long safari in East Africa. The clear highlight of this adventure was visiting the mountain gorillas (*Gorilla beringei*

beringei) in Virunga National Park in what was then Zaïre. I do not think it is possible to look into the eyes of such a gentle and beautiful creature and not vow to take action to ensure its survival. While walking though the rainforest back down the mountain after spending just one hour with these wondrous creatures, I vowed to do just that. We are at a pivotal point in our society, and have the power to be the part of the greatest generation ever by using our own species' high intelligence and complex cognition to solve this extinction crisis. Or, we can simply sit back and allow "Not Me" to run around and continue to make things worse.

REFERENCES

Acevedo-Gutiérrez A (1999) Aerial behavior is not a social facilitator in bottlenose dolphins hunting in small groups. J Mammal 80:768-776

Anderson DP, Nordheim EV, Boesch C, Moermond TC (2002) Factors influencing fission-fusion grouping in chimpanzees in the Taï National Park, Côte d'Ivoire. In: Boesch C, Hohmann G, Marchant LF (eds) Behavioural diversity in chimpanzees and bonobos. Cambridge University Press, Cambridge, pp 90-101

Araabi BN, Kehtarnavaz N, McKinney T, Hillman G, Würsig B (2000) String matching computer-assisted system for dolphin photoidentification. Ann Biomed Eng 28:1269-1279

Arcadi AC, Robert D, Mugurusi F (2004) A comparison of buttress drumming by male chimpanzees from two populations. Primates 45:135-139

Arcadi AC, Wrangham RW (1999) Infanticide in chimpanzees: review of cases and a new within-group observation from the Kanyawara study group in Kibale National Park. Primates 40:337-351

Au D, Weihs D (1980) At high speeds dolphins save energy by leaping. Nature 284: 548-550

Baker AN (1972) Reproduction, early life history, and age-growth relationships of the New Zealand Pilchard, *Sardinops neopilchardus* In: Fisheries Research Bulletin, vol 5, Fisheries Research Division, New Zealand Marine Department, Wellington, pp 1-64

Bearzi G (2007) Marine conservation on paper. Conserv Biol 21:1-3

Bearzi G, Agazzi S, Bonizzoni S, Costa M, Azzellino A (2007) Dolphins in a bottle: abundance, residency patterns and conservation of bottlenose dolphins *Tursiops truncatus* in the semi-closed eutrophic Amvrakikos Gulf, Greece. Aquat Conserv: Mar Freshw Ecosyst 17:1-17

Bearzi G, Di Sciara GN, Politi E (1997) Social ecology of bottlenose dolphins in the Kvarnerić (northern Adriatic Sea) Mar Mamm Sci 13:650-668

Bearzi G, Politi E, Agazzi S, Bruno S, Costa M, Bonizzoni S (2005) Occurence and present status of coastal dolphins (*Delphinus delphis* and *Tursiops truncatus*) in the eastern Ionian Sea. Aquat Conserv: Mar Freshw Ecosyst 15: 243-257

Bearzi G, Quondam F, Politi E (2004) Bottlenose dolphin foraging alongside fish farm cages in eastern Ionian Sea coastal waters. In: European Research on Cetaceans: Proceedings of the Annual Conference of the European Cetacean Society, vol 15, pp 292-293

Bearzi M, Stanford CB (2007) Dolphins and great apes: comparisons of sympatric socio-ecology. Contrib Zool 76:235-254

Bearzi M, Stanford CB (2008) Beautiful minds: the parallel lives of great apes and dolphins. Harvard University Press, Cambridge

Bejder L, Fletcher D, Bräger S (1998) A method for testing association patterns of social animals. Anim Behav 56:719-725

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. Mar Mamm Sci 20:215-231

Blake, RW (1983) Energetics of leaping in dolphins and other aquatic animals. J Mar Biolog Assoc UK 63: 61-70

Boesch C (1991) The effects of leopard predation on grouping patterns in forest chimpanzees. Behaviour 117:220-242

Boesch C (1994) Cooperative hunting in wild chimpanzees. Anim Behav 48:653-667

Boesch C (1996) Social grouping in Taï chimpanzees. In: McGrew WC (ed) Great ape societies. Cambridge University Press, Cambridge, pp 101-113

Boesch C (1997) Evidence for dominant wild female chimpanzees investing more in sons. Anim Behav 54:811-815

Boesch C, Boesch-Acherman H (2000) The chimpanzees of the Taï forest. Behavioural ecology and evolution. Oxford University Press, Oxford

Bromham L, Phillips MJ, Penny D (1999) Growing up with dinosaurs: molecular dates and the mammalian radiation. Trend Ecol Evol 13:113-118

Bruno S, Politi E, Bearzi G (2004) Social organisation of a common dolphin community in the eastern Ionian Sea: evidence of a fluid fission-fusion society. Eur Res Cet 15:49-51

Cairns SJ, Schwager SJ (1987) A comparison of association indices. Anim Behav 35:1454-1469

Caraco T (1979) Time budgeting and group size: a test of theory. Ecology 60:618-627

Caraco T, Martindale S, Pulliam HR (1980) Avian flocking in the presence of a predator. Nature 285:400-401

Cassens I, van Waerebeek K, Best PB, Tzika A, van Helden AL, Crespo EA, Milinkovitch MC (2005) Evidence for male dispersal along the coasts but no migration in pelagic waters in dusky dolphins (*Lagenorhynchus obscurus*). Mol Ecol 14:107-121

Chapman CA, White FJ, Wrangham RW (1993) Defining subgroup size in fission-fusion societies. Folia primatologica 61:31-34

Chapman CA, Wrangham RW (1993) Range use of the forest chimpanzees of Kibale: Implications for the understanding of chimpanzee social organization. Am J Primatol 31:263-273

Chapman CA, Wrangham RW, Chapman LJ (1995) Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. Behav Ecol Sociobiol 36:59-70

Chilvers LB, Corkeron PJ (2002) Association patterns of bottlenose dolphins (*Tursiops aduncus*) off Point Lookout, Queensland, Australia. Can J Zool 80:973-979

Cipriano F (1992) Behavior and occurrence patterns, feeding ecology, and life history of dusky dolphins (*Lagenorhynchus obscurus*) off Kaikoura, New Zealand. Ph.D. dissertation, Texas A&M University, College Station

Clutton-Brock TH, Albon SD (1979) The roaring of red deer and the evolution of honest advertisement. Behaviour 59, 145-170

Clutton-Brock TH, Harvey PH (1980) Primates, brains and ecology. Journal of Zoology 190:390-323

Connor RC (2000) Group-living in whales and dolphins. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds) Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago, pp 199-218

Connor RC, Heithaus MR, Barre LM (1999) Superalliance of bottlenose dolphins. Nature 397:571-572

Connor RC, Heithaus MR, Barre LM (2001) Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance'. Proc R Soc Lond B Biol Sci 268: 263-267

Connor RC, Mann J, Tyack PL, Whitehead H (2000a) The social lives of whales and dolphins. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds) Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago, pp 1-6

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 RC, Richards AF, Smolker RA, Mann J (1996) Patterns of female attractiveness in Indian Ocean bottlenose dolphins. Behaviour 133:37-69

Connor RC, Smolker RA, Richards AF. 1992. Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). Proc Natl Acad Sci USA 89:987-990

Connor RC, Mann J, Tyack PL, Whitehead H (1998) Social evolution in toothed whales. Trends in Ecology and Evolution 13:228-232

Connor RC, Wells RS, Mann J, Read AJ (2000b) The bottlenose dolphin: social relationships in a fission-fusion society. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds) Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago, pp 91-126

Constable JL, Ashley MV, Goodall J, Pusey AE (2001) Noninvasive paternity assignment in Gombe chimpanzees. Mol Ecol 10:1279-1300

Coolen I, Dangles O, Casas J (2005) Social learning in noncolonial insects? Curr Biol 15:1931-1935

Couzin ID (2006) Behavioral ecology: social organization in fission-fusion societies. Current Biology 16:R169-R171

Cross PC, Lloyd-Smith JO, Getz WM (2005) Disentangling association patterns in fission-fusion societies using African buffalo as an example. Anim Behav 69: 499-506

Deschner T, Boesch C (2007) Can the patterns of sexual swelling cycles in female Taï chimpanzees be explained by the cost-of-sexual-attraction hypothesis? Int J Primatol 28:389-406

Díaz López B (2006) Bottlenose dolphin (*Tursiops truncatus*) predation on a marine fish farm: some underwater observations. Aquat Mamm 32: 305-310

Díaz López B, Bernal Shirai JA (2007) Bottlenose dolphin (*Tursiops truncatus*) presence and incidental capture in a marine fish farm on the north-eastern coast of Sardinia (Italy). J Mar Biolog Assoc UK 87:113-117

Díaz López B, Marini L, Polo F (2005) The impact of a fish farm on a bottlenose dolphin population in the Mediterranean Sea. Thalassas 21:65-70

Doran D (1997) Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Taï chimpanzees. Int J Primatol 18:183-206

Dunbar RI (2003) The social brain: mind, language, and society in evolutionary perspective. Annu Rev Anthropol 32:163-181

Dunbar RIM, Shultz S (2007) Evolution in the social brain. Science 317:1344-1347

Dunn DG, Barco SG, Pabst DA, McLellan WA (2002) Evidence for infanticide in bottlenose dolphins of the western North Atlantic. J Wildl Dis 38:505-509

Durrell JL, Sneddon IA, O'Connell NE, Whitehead H (2004) Do pigs form preferential associations? Appl Anim Behav Sci 89:41-5

Emery NJ, Clayton NS (2004) The mentality of crows: convergent evolution of intelligence in corvids and apes. Science 306:1903-1907

Emery Thompson M, Kahlenberg SM, Gilby IC, Wrangham RW (2007) Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. Anim Behav 73:501-512

Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223

FAO (2007) The state of world fisheries and aquaculture 2006. In: FAO Fisheries and Aquaculture Department. Food and Agriculture Organization of the United Nations, Rome, pp 180

Finneran JJ, Oliver CW, Schaefer KM, Ridgway SH (2000) Source levels and estimated yellowfin tuna (*Thunnus albacares*) detection ranges for dolphin jaw pops, breaches, and tail slaps. J Acoust Soc Am 107:649-665

Fish FE, Nicastro AJ, Weihs, D (2006) Dynamics of the aerial maneuvers of spinner dolphins. J Exp Biol 209:590-598

Gadagkar, R (1995) Observational study of animal behaviour: from instinct to intelligence. Curr Sci 68:185-196

Gaskin DE (1968) Distribution of Delphinidae (Cetacea) in relation to sea surface temperatures off eastern and southern New Zealand. N Z J Mar Freshwater Res 2:527-534

Gazda SK, Connor RC, Edgar RK, Cox F (2005) Division of labour with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. Proc R Soc Lond B Biol Sci 272:135-140

Gero S, Bejder L, Whitehead H, Mann J, Connor RC (2005) Behaviourally specific preferred associations in bottlenose dolphins, *Tursiops* spp. Can J Zool 83:1566-1573

Gibson QA, Mann J (2008) The size, composition and function of wild bottlenose dolphin (*Tursiops* sp.) mother-calf groups in Shark Bay, Australia. Anim Behav 76:389-405

Gilkinson AG, Pearson HC, Weltz F, Davis RW (2007) Photo-identification of sea otters using nose scars. J Wild Manage 71:2045-2051

Ginsberg JR, Young TP (1992) Measuring association between individuals or groups in behavioural studies. Anim Behav 44:377-379

Goodall J (1986) The chimpanzees of Gombe. Patterns of behavior. The Belknap Press of Harvard University Press, Cambridge

Gowans S, Whitehead H, Hooker SK (2001) Social organization in northern bottlenose whales, *Hyperoodon ampullatus*: not driven by deep-water foraging? Anim Behav 62:369-377

Gowans S, Würsig B, Karczmarski L (2008) The social structure and strategies of delphinids: predictions based on an ecological framework. Adv Mar Biol 53: 195-294

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140-1162

Grellier K, Hammond PS, Wilson B, Sanders-Reed CA, Thompson PM (2003) Use of photo-identification to quantify mother-calf association patterns in bottlenose dolphins. Can J Zool 81:1421-1427

Griffin, DR (1976) The question of animal awareness: evolutionary continuity of mental experience. Rockefeller University Press, New York

Haase PA, Schneider K. 2001. Birth demographics of bottlenose dolphins, *Tursiops truncatus*, in Doubtful Sound, Fiordland, New Zealand - preliminary findings. N Z J Mar Freshwater Res 35:675-680

Halperin SD (1979) Temporary association patterns in free ranging chimpanzees: an assessment of individual grouping preferences. In: Hamburg DA, McCown ER, (eds) The great apes. Benjamin/Cummings Publishing Company International, Menlo Park, pp 491-499

Hasegawa T (1990) Sex differences in ranging patterns. In: Nishida T (ed) The chimpanzees of the Mahale Mountains. University of Tokyo Press. Tokyo, pp 99-114

Hashimoto C, Furuichi T, Tashiro Y (2001) What factors affect the size of chimpanzee parties in the Kalinzu Forest, Uganda? Examination of fruit abundance and number of estrous females. Int J Primatol 22:947-959

Heithaus MR, Dill LM (2002) Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83:480-491

Herman LM (1980) Cognitive characteristics of dolphins. In: Herman LM (ed) Cetacean behavior: mechanisms and functions. Robert. E. Krieger Publishing Company, Malabar, pp 363-429

Hill K, Boesch C, Goodall J, Pusey A, Williams J, Wrangham R (2001) Mortality rates among wild chimpanzees. J Hum Evol 40:437-450

Hillman GR, Würsig B, Gailey GA, Kehtarnavaz N, Drobyshevsky A, Araabi BN, Tagare HD, Weller DW (2003) Computer-assisted photo-identification of individual marine vertebrates: a multi-species system. Aquat Mamm 29:117-123

Hinde RA (1976) Interactions, relationships and social structure. Man 11:1-17

Holekamp KE, Sakai ST, Lundrigan BL (2007) The spotted hyena (*Crocuta crocuta*) as a model system for study of the evolution of intelligence. J Mammal 88:545-554

Humphrey NK (1976) The social function of intellect. In: Bateson PPG, Hinde RA (eds) Growing points in ethology: based on a conference sponsored by St. John's College and King's College, Cambridge. Cambridge University Press, Cambridge, pp 303-317

IUCN (2007) 2007 IUCN Red List of Threatened Species. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland. Available from http://www.iucnredlist.org (accessed May 25, 2008)

Janson CH (1998) Testing the predation hypothesis for vertebrate sociality: prospects and pitfalls. Behaviour 135:389-410

Jefferson TA (2000) Population biology of the Indo-Pacific hump-backed dolphin in Hong Kong Waters. Wildl Monogr 144:1-65

Jerison HJ (1973) Evolution of the brain and intelligence. Academic Press, New York

Jolly A (1966) Lemur social behavior and primate intelligence. Science 153: 501-506

Jurmain R, Nelson H (1994) Introduction to physical anthropology. West Publishing, St Paul

Kano T (1980) The social behavior of wild pygmy chimpanzees (*Pan paniscus*) of Wamba: a preliminary report. J Hum Evol 9:243-260

Kaplan JD (2007) Possible evidence for infanticide among bottlenose dolphins (*Tursiops* *truncatus*) off St. Augustine, Florida. (poster) 17th Biennial Conference on the Biology of Marine Mammals, Cape Town, South Africa, Nov 29-Dec 3

Karczmarski L (1999) Group dynamics of humpback dolphins (*Sousa chinensis*) in the Algoa Bay region, South Africa. J Zool (Lond) 249:283-293

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

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

Krebs JR, Davies NB (1993) An introduction to behavioral ecology. Third edn. Blackwell Scientific Publications, Oxford

Krützen M, Sherwin WB, Berggren P, Gales N (2004) Population structure in an inshore cetacean revealed by microsatellite and mtDNA analysis: bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia. Mar Mamm Sci 20:28-47

Kummer H (1968) Social organization of Hamadryas baboons: a field study. S. Karger, New York

Lehmann J, Boesch C (2004) To fission or to fusion: effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organisation. Behav Ecol Sociobiol 56:207-216

Lehmann J, Boesch C (2005) Bisexually bonded ranging in chimpanzees (*Pan troglodytes verus*). Behav Ecol Sociobiol 57:525-535

Lehmann J, Korstjens AH, Dunbar RIM (2007) Fission-fusion social systems as a strategy for coping with ecological constraints: a primate case. Evol Ecol 21:613-634

Lehner PN (1996) Handbook of ethological methods, Second edn. Cambridge University Press, Cambridge

Lloyd BD (2003) Potential effects of mussel farming on New Zealand's marine mammals and seabirds: a discussion paper. New Zealand Department of Conservation, Wellington

Lonsdorf EV (2006) What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? Anim Cogn 9:36-46

Lusseau, D (2006)Why do dolphins jump? Interpreting the behavioural repertoire of bottlenose dolphins (*Tursiops* sp.) in Doubtful Sound, New Zealand. Behav Processes 73:257-265

Lusseau D, Schneider K, Boisseau OJ, Haase P, Slooten E, Dawson SM (2003) The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations. Behavioral Ecology and Sociobiology 54:396-405

Manly BJF (1995) A note on the analysis of species co-occurrences. Ecology 76:1109-1115

Mann J (1997) Individual differences in bottlenose dolphin infants. Fam Syst 4:34-48

Mann J (1999) Behavioral sampling methods for cetaceans: a review and critique. Mar Mamm Sci 15:102-122

Mann J (2000) Unraveling the dynamics of social life. In: Mann J, Connor RC, Tyack PL,Whitehead H (eds) Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago, pp 45-64

Mann J, Connor RC, Barre LM, Heithaus MR (2000) Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. Behav Ecol 11:210-219

Mann J, Sargeant B (2003) Like mother, like calf: the ontongeny of foraging traditions in wild Indian ocean bottlenose dolphins (*Tursiops* sp.). In: Fragaszy DM, Perry S (eds) The biology of traditions. Cambridge University Press, Cambridge, pp 236-266

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

Mann J, Smuts B. 1999. Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). Behaviour 136:529-566

Mann J, Watson-Capps JJ (2005) Surviving at sea: ecological and behavioural predictors of calf mortality in Indian Ocean bottlenose dolphins, *Tursiops* sp. Anim Behav 69:899-909

Margurran AE, Seghers BH (1991) Variation in schooling and aggression amongst guppy (*Poecilia reticulata*) populations in Trinidad. Behaviour 118:214-234

Marino L (1996) What can dolphins tell us about primate evolution? Evol Anthropol 5: 81-86

Marino L (1998) A comparison of encephalization between odontocete cetaceans and anthropoid primates. Brain Behav Evol 51:230-238

Marino L (2002) Convergence of complex cognitive abilities in cetaceans and primates. Brain Behav Evol 59:21-32

Marino L, McShea DW, Uhen MD (2004) Origin and evolution of large brains in toothed whales. The Anatomical Record Part A 281A:1247-1255

Markowitz TM (2004) Social organization of the New Zealand dusky dolphin. Ph.D. dissertation, Texas A&M University, College Station

Markowitz TM, Harlin AD, Würsig B (2003) Digital photography improves efficiency of individual dolphin identification. Mar Mamm Sci 19:217-223

Markowitz TM, Harlin AD, Würsig B, McFadden CJ (2004) Dusky dolphin foraging habitat: overlap with aquaculture in New Zealand. Aquat Conserv: Mar Freshw Ecosyst 14:133-149

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

Matsumoto-Oda A (1999) Mahale chimpanzees: grouping patterns and cycling females. Am J Primatol 47:197-207

Matsumoto-Oda A, Oda R (1998) Changes in the activity budget of cycling female chimpanzees. Am J Primatol 46:157-166

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

Michaud R (2005) Sociality and ecology of the odontocetes. In: Ruckstuhl KE, Neuhaus P (eds) Sexual segregration in vertebrates: ecology of the two sexes. Cambridge University Press, Cambridge, pp 303-326

Mitani JC, Watts DP, Muller MN (2002) Recent developments in the study of wild chimpanzee behavior. Evol Anthropol 11:9-25

Möller LM, Allen SJ, Harcourt RG (2002) Group characteristics, site fidelity and seasonal abundance of bottlenose dolphins *Tursiops aduncus* in Jervis Bay and Port Stephens, south-eastern Australia. Australian Mammalogy 24:11-21

Möller LM, Beheregaray LB (2004) Genetic evidence for sex-biased dispersal in resident bottlenose dolphins (*Tursiops aduncus*). Mol Ecol 13:1607-1612

Möller LM, Beheregaray LB, Allen SJ, Harcourt RG (2006) Association patterns and kinship in female Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. Behav Ecol Sociobiol 61:109-117

Morin PA (1993) Reproductive strategies in chimpanzees. Yearb Phys Anthropol 36:179-212

Morrisey DG, Cole RG, Davey NK, Handley SJ, Bradley A, Brown SN, Madarasz AL (2006) Abundance and diversity of fish on mussel farms in New Zealand. Aquaculture 252:277-288

Muller MN, Kahlenberg SM, Thompson ME, Wrangham RW (2007)Male coercion and the costs of promiscuous mating for female chimpanzees. Proc R Soc Lond B Biol Sci 274:1009-1014

Muller MN, Thompson ME, Wrangham RW (2006) Male chimpanzees prefer mating with old females. Curr Biol 16:2234-2238

Murray CM, Wroblewski E, Pusey AE (2007) New case of intragroup infanticide in the chimpanzees of Gombe National Park. Int J Primatol 28:23-30

Newton-Fisher NE (2006) Female coalitions against male aggression in wild chimpanzees of the Budongo Forest. Int J Primatol 27:1589-1599

Nishida T (1983) Alloparental behavior in wild chimpanzees of the Mahale Mountains, Tanzania. Folia Primatol 41:1-33

Nishida T (1990) A quarter century of research in the Mahale Mountains: An overview. In: Nishida T (ed) The chimpanzees of the Mahale Mountains. University of Tokyo Press, Tokyo, pp 3-35

Nishida T, Corp N, Hamai M, Hasegawa T, Hiraiwa-Hasegawa M, Kazuhiko H, Hunt KD, Itoh N, Kawanaka K, Matsumoto-Oda A, Mitani JC, Nakamura M, Norikoshi K, Sakamaki T, Turner L, Uehara S, Zamma K (2003) Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. Am J Primatol 59:99-121

Nishida T, Hiraiwa-Hasegawa M (1987) Chimpanzees and bonobos: cooperative relationships among males. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago pp 165-177

Nishida T, Takasaki H, Takahata Y (1990) Demography and reproductive profiles. In: Nishida T (ed) The chimpanzees of the Mahale Mountains. University of Tokyo Press, Tokyo, pp 63-97

Noren SR (2008) Infant carrying behaviour in dolphins: costly parental care in an aquatic environment. Funct Ecol 22:284-288

Norris KS, Dohl TP (1980a) Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. Fish Bull 77: 821–849

Norris KS, Dohl TP (1980b) The structure and function of cetacean schools. In: Herman LM (ed) Cetacean behavior: mechanisms and functions. Wiley Interscience, New York, pp 211-261

Norris, K. S., Würsig, B. & Wells, R. S. 1994: Aerial Behavior. In: The Hawaiian spinner dolphins. Norris KS, Würsig B, Wells RS, Würsig M (eds) University of California Press, Los Angeles, pp 103-121

Otali E, Gilchrist JS (2006) Why chimpanzee (*Pan troglodytes schweinfurthii*) mothers are less gregarious than nonmothers and males: the infant safety hypothesis. Behav Ecol Sociobiol 59:561-570

Packer C, Scheel D, Pusey, AE (1990) Why lions form groups: food is not enough. Am Nat 126:1-19

Patterson IAP, Reid RJ, Wilson B, Grellier K, Ross HM, Thompson PM (1998) Evidence for infanticide in bottlenose dolphins: an explanation for violent interactions with harbour porpoises? Proc R Soc Lond B Biol Sci 265:1167-1170

Pontzer H, Wrangham RW (2006) Ontogeny of ranging in wild chimpanzees. Int J Primatol 27:295-309

Pruetz JD, Bertolani P (2007) Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. Curr Biol 17:412-417

Pusey A, Williams JM, Goodall (1997) The influence of dominance rank on the reproductive success of female chimpanzees. Science 277:828-831

Pusey AE (1983) Mother-offspring relationships in chimpanzees after weaning. Anim Behav 31:363-377

Pusey AE (1990) Behavioural changes at adolescence in chimpanzees. Behaviour 115:203-246

Quintana-Rizzo E, Wells RS (2001) Resighting and association patterns of bottlenose dolphins (*Tursiops truncatus*) in the Cedar Keys, Florida: insights into social organization. Can J Zool 79:447-456

Randall JA (1989) Individual footdrumming signatures in banner-tailed kangaroo rats *Dipodomys spectabilis*. Anim Behav 38: 620-630

Randall JA (2001) Evolution and function of drumming as communication in mammals. Am Zool 41:1143-1156

Reeves RR, Stewart BS, Clapham PJ, Powell JA (2002) National Audubon Society guide to marine mammals of the world. Chanticleer Press, New York

Reiss D, Marino L (2001) Mirror self-recognition in the bottlenose dolphin: a case of cognitive convergence. Proc Natl Acad Sci USA 98:5937-5942

Rendell L, Whitehead H (2001) Culture in whales and dolphins. Behav Brain Sci 24:309-382

Ribeiro S, Viddi FA, Cordeiro JL, Freitas TRO (2007) Fine-scale habitat selection of Chilean dolphins (*Cephalorhynchus eutropia*): interactions with aquaculture activities in southern Chiloé Island, Chile. J Mar Biolog Assoc UK 87:119-128

Rogers CA, Brunnick, BJ, Herzing DL, Baldwin JD (2004) The social structure of bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. Mar Mamm Sci 20:668-708

Sakura O (1994) Factors affecting party size and composition of chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea. Int J Primatol 15:167-183

Sargeant BL, Mann J, Berggren P, Krützen M (2005) Specialization and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (*Tursiops* sp.). Can J Zool 83:1400-1410

Saayman GS, Tayler CK (1979) The socioecology of humpback dolphins (*Sousa* sp.). In: Winn HE, Olla BL (eds) Behaviour of marine animals. Current perspectives in research. Volume 3: cetaceans. Plenum Press, New York, pp 165-226

van Schaik CP (1989) The ecology of social relationships amongst female primates. In: Standen V, Foley RA (eds) Comparative socioecology: the behavioural ecology of humans and other mammals. Blackwell Scientific Publications, Boston, pp 195-218

van Schaik CP (1999) The socioecology of fission-fusion sociality in orangutans. Primates 41: 69-96

van Schaik CP, van Hooff JARAM (1983) On the ultimate causes of primate social systems. Behaviour 85:91-117

van Schaik CP, van Hooff JARAM (1989) Why simians are smart. Nature 337:700-700

Scott EM, Mann J, Watson-Capps JJ, Sargeant BL, Connor RC (2005) Aggression in bottlenose dolphins: evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behaviour. Behaviour 142:21-44

Scott MD, Wells RS, Irvine AB (1990) A long-term study of bottlenose dolphins on the west coast of Florida. In: Leatherwood S, Reeves RR (eds) The bottlenose dolphin. Academic Press, New York, pp 235-243

Shane SH (1990) Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. In: The bottlenose dolphin. Leatherwood S, Reeves RR (eds) Academic Press, San Diego, pp 245-265

Shelton DE (2006) Dusky dolphins in New Zealand: group structure by sex and relatedness. M.S. thesis, Texas A&M University, College Station

Slooten E (1994) Behavior of Hector's dolphin: classifying behavior by sequence analysis. J Mammal 75:956-964

Slooten E, Dawson SM, Lad F (1992) Survival rates of photographically identified Hector's dolphins from 1984 to 1988. Mar Mamm Sci 8:327-343

Slooten E, Dawson SM, Whitehead H (1993) Associations among photographically identified Hector's dolphins. Can J Zool 71:2311-2318

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

Sockol MD, Raichlen DA, Pontzer H (2007) Chimpanzee locomotor energetics and the origin of human bipedalism. Proceedings of the National Academy of Sciences 104: 12265–12269

Steele (1985) A comparison of terrestrial and marine ecological systems Nature 313: 355-358

Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. Behav Ecol Sociobiol 41:291-309

Stumpf RM, Boesch C (2005) Does promiscuous mating preclude mate choice? Female sexual strategies in chimpanzees (*Pan troglodytes verus*) of the Taï National Park, Côte d'Ivoire. Behav Ecol Sociobiol 57:511-524

Sugiyama Y (1981) Observations on the population dynamics and behavior of wild chimpanzees at Bossou, Guinea, in 1979-1980. Primates 22:435-444

Sugiyama Y (1988) Grooming interactions among adult chimpanzees at Bossou, Guinea, with special reference to social structure. In J Primatol 9:393-407

Sugiyama Y (1994) Age-specific birth rate and lifetime reproductive success of chimpanzees at Bossou, Guinea. Am J Primatol 32:311-318

Sugiyama Y (1999) Socioecological factors of male chimpanzee migration at Bossou, Guinea. Primates 40:61-68

Sugiyama Y (2004) Demographic parameters and life history of chimpanzees at Bossou, Guinea. Am J Phys Anthropol 124:154-165

Sugiyama Y, Koman J (1979) Social structure and dynamics of wild chimpanzees at Bossou, Guinea. Primates 20:323-339

Sundaresan SR, Fischhoff IR, Dushoff J, Rubenstein DI (2007) Network metrics reveal differences in social organization between two fission-fusion species, Grevy's zebra and onager. Oecologia 151:140-149

Szykman M, Engh AL, Van Horn RC, Funk SM, Scribner KT, Holekamp KE (2001) Association patterns among male and female spotted hyenas (*Crocuta crocuta*) reflect male mate choice. Behav Ecol Sociobiol 50:231-238

Symington MM (1988) Food competition and foraging party size in the black spider monkey (*Ateles paniscus chamek*). Behaviour 1-2: 117-134

Symington MM (1990) Fission-fusion social organization in *Ateles* and *Pan*. Int J Primatol 11:47-61

Takahata Y (1990) Adult males' social relations with adult females. In: Nishida T (ed) The chimpanzees of the Mahale Mountains. University of Tokyo Press, Tokyo, pp 133-148

Tayler CK, Saayman GS (1972) The social organisation and behaviour of dolphins (*Tursiops aduncus*) and baboons (*Papio ursinus*): some comparisons and assessments. Ann Cape Prov Mus (Nat His) 9:11-49

Turvey ST, Pitman RL, Taylor BL, Barlow J, Akamatsu T, Barrett LA, Zhao X, Reeves RR, Stewart BS, Wang K, Wei Z, Zhang X, Pusser LT, Richlen M, Brandon JR, Wang D (2007) First human-caused extinction of a cetacean species? Biol Lett 3:537-540

Tutin CEG (1979) Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). Behav Ecol Sociobiol 6:29-38

Tutin CEG (1980) Reproductive behavior of wild chimpanzees in the Gombe National Park, Tanzania. J Reprod Fertil Suppl 28:43-57

Vaughn RL, Shelton DE, Timm LL, Watson LA, Würsig B (2007) Dusky dolphin (*Lagenorhynchus obscurus*) feeding tactics and multi-species associations. N Z J Mar Freshwater Res 41:391-400

van Waerebeek K, Read AJ (1994) Reproduction of dusky dolphins, *Lagenorhynchus obscurus*, from coastal Peru. J Mammal 75:1054-1062

Wallis J (1997) A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. J Reprod Fertil 109:297-307

Walsh PD, Abernethy KA, Bermejo M, Beyers R, De Wachter P, Akou ME, Huijbregts B, Mambounga DI, Toham AK, Kilbourn AM, Lahm SA, Latour S, Maisels F, Mbina C, Mihindou Y, Obiang SN, Effa EN, Starkey MP, Telfer P, Thibault M, Tutin CEG, White LJT, Wilkie DS (2003) Catastrophic ape decline in western equatorial Africa. Nature 422:611-614

Watson-Capps JJ, Mann J (2005) The effects of aquaculture on bottlenose dolphin (*Tursiops* sp.) ranging in Shark Bay, Western Australia. Biol Conserv 124: 519-526

Weihs D, Fish FE, Nicastro AJ (2007) Mechanics of remora removal by dolphin spinning. Mar Mamm Sci 23:707-714

Weilgart L, Whitehead H, Payne K (1996) A colossal convergence. Am Sci 84: 278-287

Weinrich MT, Belt CR, Morin D (2001) Behavior and ecology of the Atlantic white-sided dolphin (*Lagenorhynchus acutus*) in coastal New England waters. Mar Mamm Sci 17:231-248

Wells RS (1991) The role of long-term study in understanding the social structure of a bottlenose dolphin community. In: Pryor K, Norris KS (eds) Dolphin societies: discoveries and puzzles. University of California Press, Los Angeles, pp 199-225

Wells RS (1993)Parental investment patterns of wild bottlenose dolphins. In: Hecker NF (ed) Proceedings of the 18th International Marine Animal Trainers Association Conference, Chicago, pp 58-64

Wells RS (2003) Dolphin social complexity: lessons from long-term study and life history. In: de Waal FBM, Tyack PL (eds) Animal social complexity: intelligence, culture, and individualized societies. Harvard University Press, Cambridge, pp 32-56

Wells RS, Rhinehart HL, Hansen LJ, Sweeney JC, Townsend FI, Stone R, Casper DR, Scott MD, Hohn AA, Rowles TK (2004) Bottlenose dolphins as marine ecosystem sentinels: developing a health monitoring system. EcoHealth 1:246-254

Wells RS, Scott MD (1990) Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. In: Hammond PS, Mizroch SA, Donovan GP (eds) Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. Reports of the International Whaling Commission, Special Issue No. 12, International Whaling Commission, Cambridge, pp 407-415

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

Wells RS, Tornero V, Borrell A, Aguilar A, Rowles TK, Rhinehart HL, Hofmann S, Jarman WM, Hohn AA, Sweeney JC (2005) Integrating life-history and reproductive success data to examine potential relationships with organochlorine compounds for bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. Sci Total Environ 349:106-119

Whitehead H (1995) Investigating structure and temporal scale in social organizations using identified individuals. Behav Ecol 6:199-208

Whitehead H (1997) Analysing animal social structure. Anim Behav 53:1053-1067

Whitehead H (1998) Cultural selection and genetic diversity in matrilineal whales. Science 282:1708-1711

Whitehead H (1999) Testing association patterns of social animals. Anim Behav 57:F26-F29

Whitehead H (2004) The group strikes back: follow protocols for behavioral research on cetaceans. Mar Mamm Sci 20:664-670

Whitehead H (2007) Selection of models of lagged identification rates and lagged association rates using AIC and QAIC. Commun Stat Simul Comput 36:1233-1246

Whitehead H (2008) Programs for analyzing social structure. Available at: http://whitelab.biology.dal.ca/index.html. Accessed May 19, 2008.

Whitehead H, Bejder L, Ottensmeyer CA (2005) Testing association patterns: issues arising and extensions. Anim Behav 69:e1-e6

Whitehead H, Dufault S (1999) Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. Adv Study Behav 28:33-74

Whitehead H, Mann J (2000) Female reproducive strategies of cetaceans: life histories and calf care. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds) Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago, pp 219-246

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. Biol Conserv 120:427-437

Whitehead H, Weilgart L (2000) The sperm whale. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds) Cetacean societies: field studies of dolphins and whales. The University of Chicago Press, Chicago, pp 154-172

Williams JM, Hsein-Lang L, Pusey AE (2002a) Costs and benefits of grouping for female chimpanzees at Gombe. In: Marchant LF, Boesch C, Hohmann G (eds) Behavioural diversity in chimpanzees and bonobos. Cambridge University Press, Cambridge, pp 192-203

Williams JM, Pusey AE, Carlis JV, Farm BP, Goodall J (2002b) Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. Anim Behav 63:347-360

Williams TM, Friedl WA, Fong ML, Yamada RM, Sedivy P, Haun JE (1992) Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. Nature 355:821-823

Williams TM, Friedl WA, Haun JE (1993) The physiology of bottlenose dolphins (*Tursiops truncatus*): heart rate, metabolic rate and plasma lactate concentration during exercise. J Exp Biol 179:31-46

Wittemyer G, Douglas-Hamilton I, Getz WM (2005) The socioecology of elephants: analysis of the processes creating multitiered social structures. Anim Behav 69:1357-1371

Wittig RM, Boesch C (2003) Food competition and linear dominance hierarchy among female chimpanzees of the Taï National Park. Int J Primatol 24:847-867

Wrangham R, Smuts BB (1980) Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. J Reprod Fertil Suppl 28:13-31

Wrangham RW (1986) Ecology and social relationships in two species of chimpanzee. In: Rubenstein DI, Wrangham RW (eds) Ecology and social evolution: birds and mammals. Princeton University Press, Princeton, NJ pp 352-378

Wrangham RW (2000) Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In: Kappeler PM (ed) Primate males: causes and consequences of variation in group composition. Cambridge University Press, Cambridge, pp 248-258

Wrangham RW, Clark AP, Isabirye-Basuta G (1992) Female social relationships and social organization of Kibale Forest chimpanzees. In: Nishida T, McGrew WC, Marler P, Pickford M, De Waal FBM (eds) Topics in primatology, volume I: Human origins. University of Tokyo, Tokyo, pp 81-9

Würsig B (1978) Occurrence and group organization of Atlantic bottlenose porpoises (*Tursiops truncatus*) in an Argentine Bay. Biol Bull 154:348-359

Würsig B (1986) Delphinid foraging strategies. In: Schusterman RJ, Thomas JA, Wood FG (eds) Dolphin cognition and behavior: a comparative approach. Lawrence Erlbaum Associates, Hillsdale, NJ, pp 347-359

Würsig, B (2002) Leaping behavior. In: Perrin WF Würsig B, Thewissen JGM (eds) Encyclopedia of marine mammals. Academic Press, San Diego, pp 689-692

Würsig B, Cipriano F, Slooten E, Constantine R, Barr K, Yin S (1997) Dusky dolphins (*Lagenorhynchus obscurus*) off New Zealand: status of present knowledge. Rep Int Whal Comm 47: 715-722

Würsig B, Duprey N, Weir J (2007) Dusky dolphins (*Lagenorhynchus obscurus*) in New Zealand waters. Present knowledge and research goals. DOC Research and Development Series 270:1-28

Würsig B, Gailey GA (2002) Marine mammals and aquaculture: conflicts and potential resolutions. In: Stickney RR, McVey JP (eds) Responsible marine aquaculture. CABI Publishing, Cambridge, pp 45-59

Würsig B, Jefferson TA (1990) Methods of photo-identification for small cetaceans. Rep Int Whaling Comm Spec Issue 12:17-78

Würsig B, Reeves RR, Ortega-Ortiz JG (2002) Global climate change and marine mammals. In: Evans PGH, Raga JA (eds) Marine mammals: biology and conservation. Plenum Press, New York, pp 589-608

Würsig B, Wells RS, Würsig M, Norris KS (1994) Population structure. In: Norris KS, Würsig B, Wells RS, Würsig M (eds) The Hawaiian spinner dolphin. University of California Press, Los Angeles, pp 122-140

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. Fish Bull 77:871-890

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

Yazdi P, Kilian A, Culik BM (1999) Energy expenditure of swimming bottlenose dolphins (*Tursiops truncatus*). Mar Biol 134:601-607

VITA

Name: Heidi Christine Pearson

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

Email Address: heidipearson@tamu.edu

Education: B.S., Double major in Biological Anthropology and Anatomy, and Biology, Duke University, 1998

Peer-reviewed publications:

Gilkinson AK, Pearson HC, Weltz F, Davis RW (2007) Photo-identification of sea otters using nose scars. J Wildlife Manage 71: 2045-2051

Kornblau IS, Pearson HC, Radecki Breitkopf C (2007) Demographic, behavioral, and physical correlates of body esteem among low-income female adolescents. J Adolesc Health 41: 566-570

Navarro Rubio, R., Pearson, H.C., Clark, A.A., and Radecki Breitkopf, C (2007) Satisfaction with care among low-income female outpatients. Psychol Health Med 12: 334-345

Pearson HC, Davis RW (2005) Behavior of territorial male sea otters in Prince William Sound, Alaska. Aquat Mamm 31: 226-233

Pearson HC, Packard JM, Davis RW (2006) Territory quality of male sea otters in Prince William Sound, Alaska: relation to body and territory maintenance behaviors. Can J Zool 84: 939-946

Radecki Breitkopf C, Pearson HC, Breitkopf DM (2005) Poor knowledge regarding the Pap test among low-income women undergoing annual screening. Perspect Sex Repro Health 37: 78-84

Slomovitz BM, Sun CC, Frumovitz M, Soliman PT, Schmeler KM, Pearson HC, Berenson A, Ramirez PT, Lu KH (2006) Are women ready for the HPV vaccine? Gynecol Oncol 103: 151-154