

2014

The Social Structure and Mating Strategies of Bottlenose Dolphins (*Tursiops truncatus*) in the St. Johns River

Jessica Lea Ermak

University of North Florida, jessie@udel.edu

Follow this and additional works at: <https://digitalcommons.unf.edu/etd>



Part of the [Biology Commons](#), and the [Marine Biology Commons](#)

Suggested Citation

Ermak, Jessica Lea, "The Social Structure and Mating Strategies of Bottlenose Dolphins (*Tursiops truncatus*) in the St. Johns River" (2014). *UNF Graduate Theses and Dissertations*. 533.

<https://digitalcommons.unf.edu/etd/533>

This Master's Thesis is brought to you for free and open access by the Student Scholarship at UNF Digital Commons. It has been accepted for inclusion in UNF Graduate Theses and Dissertations by an authorized administrator of UNF Digital Commons. For more information, please contact [Digital Projects](#).

© 2014 All Rights Reserved

THE SOCIAL STRUCTURE AND MATING STRATEGIES OF BOTTLENOSE DOLPHINS
(*TURSIOPS TRUNCATUS*) IN THE ST. JOHNS RIVER

by

Jessica Lea Ermak

A thesis submitted to the Department of Biology
in partial fulfillment of the requirements for the degree of

Master of Science in Biology

UNIVERSITY OF NORTH FLORIDA

COLLEGE OF ARTS AND SCIENCES

2014

Unpublished work c Jessica Lea Ermak

CERTIFICATE OF APPROVAL

The thesis “The Social Structure and Mating Strategies of Bottlenose Dolphins (*Tursiops truncatus*) in the St. Johns River” submitted by Jessica Lea Ermak

Approved by the thesis committee:

Date

Dr. Quincy Gibson
Committee Chair Person

Dr. Julie Avery

Dr. Eric Johnson

Accepted for the Department:

Dr. Dan Moon
Chairperson

Accepted for the College of Arts and Sciences:

Dr. Barbara Hetrick
Dean

Accepted for the University:

Dr. John Kantner
Dean of the Graduate School

ACKNOWLEDGEMENTS

This thesis would have been impossible without the support of a handful of individuals. I would first like to thank all the volunteers and undergraduates who have made my research possible. I'd also like to extend a warm thanks to Dr. Eric Johnson for his patience and statistical insight- I know you've learnt a lot about dolphins these past two years! Also, Dr. Julie Avery, not only for her many thoughtful discussions but also for the moral support she has provided in my time at the University of North Florida. Not least of all, I'd like to thank my advisor Dr. Quincy Gibson for her patience and thought-provoking comments on all my work. I am a better writer and scientist for it.

More than just colleagues, I would like to thank all my friends within the Marine Mammal lab, particularly Rachael Dailey, Samantha Nekolny, and Kristy Karle. Rachael, you have offered nothing but support and encouragement to me as I adjusted to graduate school and your acceptance of me under your wing made all the difference in my time here. To Samantha, you have always offered an optimistic, if not comedic, look at graduate life. I think I would have gone crazy in the lab if not for your company, though perhaps we're both a little crazier for it. Kristy, part therapist and part friend, thank you for overlooking all my crazy and always offering a listening ear and a warm hug. The chocolate and puppies didn't hurt either.

To my family, Mom, thank you for the weekly phone chats and care packages. Though I didn't always show it, I was glad someone was thinking of me. Your unwavering belief in me and continuous prayers must have worked. It's probably safe to tell you now that I didn't always rest my eyes. To my boyfriend Andrew, thanks for taking a chance on me when the vast majority of our relationship took place a thousand miles apart. I'm not quite sure how you've

put up with me the past two years, but your patience and support has made all the difference. I can't wait to be a "real person" with you! And finally, I'd like to thank my father, Rick Ermak. Dad, I know none of this would have been possible without you. I can't count the number of tearful phone calls you patiently answered over the past two years or the number of times you motivated and steered me back onto track. For that, I dedicate this thesis to you.

TABLE OF CONTENTS

List of Tables.....	v
List of Figures.....	vi
Abstract.....	viii
Introduction.....	1
Chapter 1	
Social structure analysis reveals the presence of multi-level alliances within estuarine bottlenose dolphins (<i>Tursiops truncatus</i>) in Northeast Florida.....	4
Abstract.....	4
Introduction.....	5
Methods.....	8
Results.....	11
Discussion.....	13
Acknowledgements.....	17
Chapter 2	
The use of ecological and demographic variables to predict alliance formation.....	24
Abstract.....	24
Introduction.....	25
Results and discussion.....	30
Acknowledgements.....	35
Chapter 3	
Quantification of seasonal aggression in bottlenose dolphins (<i>Tursiops truncatus</i>) through the use of tooth rakes.....	40
Abstract.....	40
Introduction.....	41
Methods.....	45
Results.....	49
Discussion.....	51
Acknowledgments.....	54
References.....	62
Vita.....	72

LIST OF TABLES

Chapter 1

Table 1. Mean zero, non-zero, and maximum half-weight indices (HWI) within and between the sexes. A Mantel test revealed that within-sex bonds were significantly greater than between-sex bonds ($p = 1.000$).....19

Table 2. A comparison of bottlenose dolphin social structure studies world-wide.....22

Chapter 2

Table 1. Comparison of the population density and male social complexity across study sites world-wide. Study sites in which alliances are present are shaded.....36

Table 2. Predation rate as measured by the proportion of shark bites across populations. Study sites that support male alliances are highlighted.....38

Table 3. Length and mass measurements of male and female bottlenose dolphins across study sites, with the proportion of female to male length/mass noted in parentheses. Study sites at which male alliances have been recorded are highlighted.....39

Chapter 3

Table 1. Hypotheses regarding sex and seasonal patterns in rake mark presence. Note that hypotheses are non-mutually exclusive in nature.....55

Table 2. A significantly smaller proportion of females had rake marks and new rake marks, as well as extensive coverage in comparison to unknown individuals in both the breeding and non-breeding seasons ($p < 0.050$).....61

LIST OF FIGURES

Chapter 1

Figure 1. Data were collected through weekly photo-identification surveys from the mouth of the St. Johns River to downtown Jacksonville, with the direction of travel alternating weekly.....18

Figure 2. Sociogram of all allied males. First-order alliances ($HWI \geq 0.80$) are represented by thick lines while intermediate bonds between alliances ($HWI \geq 0.32$) are represented by thin lines.....20

Figure 3. Mean top associations of females and unknown sex individuals. Female top associations ranged from HWI of 0.13 to 0.62 but fell primarily within HWI of 0.20 to 0.30. Unknown sex top associations ranged from HWI of 0.15 to 1.00 but were more variable than those of females.....21

Chapter 2

Figure 1. Mean and standard deviation of inter-birth intervals for available study sites. Study sites that support male alliances are noted in red. Data presented from: Adelaide, Australia (Steiner and Bossley 2008), North Carolina (Thayer 2008), Natal, South Africa (Cockcroft and Ross 1990), Moray Firth, Scotland (Mitcheson 2008), Tokyo, Japan (Kogi et al. 2004), Bay of Islands, New Zealand (Tezano-Pinto 2009), Doubtful Sound, New Zealand (weighted IBI from the work of Henderson et al. 2014), Shark Bay, Australia (Mann et al. 2000), and Sarasota, Florida (Wells 1993).....37

Chapter 3

Figure 1. Rake marks were categorized by recency as A) new, B) obvious, and C) faint.....56

Figure 2. There was a significant difference in the presence of new rake marks both across the four seasons ($p = 0.026$) and between the breeding and non-breeding season ($p = 0.007$). The greatest proportion of new rake marks occurred in the non-breeding season, and more specifically in the winter and spring.....57

Figure 3. Extensive coverage, defined as rake mark coverage $\geq 50\%$ within a body section, was significantly different across seasons ($p = 0.003$), with winter coverage significantly greater than in spring.....58

Figure 4. Female extensive coverage was significantly different across seasons ($p = 0.037$), with peaks in winter and summer, while unknown sex extensive coverage exhibited a trend ($p = 0.052$) towards decreased extensive coverage in the spring. A greater proportion of unknown sex individuals had extensive coverage in comparison to females in spring, summer, and fall ($p < 0.050$).....59

Figure 5. Across all seasons, a significantly greater proportion of unknown sex individuals had new rake marks compared to females ($p < 0.050$).....	60
---	----

Abstract

Across populations, bottlenose dolphins (*Tursiops* sp.) exhibit a fission-fusion pattern of associations, in which group size and composition change fluidly throughout the day. Beneath this seemingly ephemeral social structure, considerable variation exists across study sites. While females typically have moderate bonds with one another within a large social network, male-male bonds are variable, though males typically take one of two strategies; some males encounter females individually for opportunities to breed while others cooperate within a first-order alliance to collectively herd females. In addition, multi-tiered alliances in which two first-order alliances cooperate to defend or assist in the theft of a female have been documented within Shark Bay, Australia. However, these patterns do not apply to all study sites, as intersexual bonds are strong within several bottlenose dolphin populations. Given the variation in the presence and complexity of male alliances, greater documentation of social structure and male mating strategies across study sites is needed to draw conclusions as to the ultimate factors behind alliance formation. As such, chapter one documents the inclusion of a new study site in the St. Johns River (SJR) in Northeast Florida where males form first and second-order alliances. In addition, variables from the SJR are included within a meta-analysis in chapter two, the first systematic examination of what variables correlate with alliance presence and complexity, with the conclusion that male-male competition best describes the patterns seen in male alliance formation. Chapter three builds upon this conclusion by examining seasonal trends in tooth rake marks, a proxy for aggression, across the sexes and males of two different mating strategies, ultimately highlighting the potential for non-reproductive aggression. Together, this work provides greater insight as to the social structure and mating patterns of bottlenose dolphins, as well as to the ecological pressures that result in complex sociality.

Introduction

All bottlenose dolphin (*Tursiops* sp.) populations studied to date exhibit a fission-fusion pattern of associations, in which individuals fluidly leave or join groups throughout the day. However, underneath this seemingly transitory social structure, there is considerable variation across study sites, with many populations forming strong bonds within or across the sexes. In most populations that have been thoroughly examined, females are found to have moderate bonds with one another within a large network of associates (Wells et al. 1987; Smolker et al. 1992; Möller et al. 2006). Though these female bonds may be stable over years, they are often focused around similar reproductive states (Wells et al. 1987; Möller and Harcourt 2008). Male-male bonds are more variable across populations. Some males employ a solitary strategy and encounter females individually for access to breeding. Other males form strong bonds with one or two males in the shape of a first-order alliance used to cooperatively herd females for mating. Some locations lack alliances entirely (Doubtful Sound, New Zealand [Lusseau et al. 2003], Moray Firth, Scotland [Eisfeld and Robinson 2004]), some utilize alliances primarily (Sarasota, Florida [Owen et al. 2002], Shark Bay, Australia [Smolker et al. 1992]), and in other locations males are found to utilize both strategies (Port Stephens, Australia [Wiszniewski et al. 2012], Bahamas [Parsons et al. 2003]). In addition, first-order alliances have been observed cooperating with other first-order alliances in the defense or theft of females, indicative of a second level of organization (Connor et al. 1992*a,b*). These second-order alliances are thought to be limited to Shark Bay, Australia, as is a complex super-alliance in which fourteen males pair off into smaller sub-alliances while maintaining strong bonds and preferences within the larger group. In contrast to the strong male-male bonds found in several study sites are Moray Firth, Scotland, and Doubtful Sound, New Zealand (Lusseau et al. 2003; Eisfeld and Robinson 2004). In both

locations the pattern of strong intra-sexual bonds is broken, as bonds between the sexes are of comparable strength (Lusseau et al. 2003; Eisfeld and Robinson 2004).

However, bottlenose dolphins are a cosmopolitan species and it is unlikely that the social structure of any one study site is unique. Rather, documentation of bottlenose dolphin associations across a variety of habitats is needed to draw conclusions as to what factors drive the organization of social structures, specifically the formation of male alliances. Chapter one adds to the current literature by presenting the association values of females and unknowns/presumable males within the St. Johns River (SJR), Jacksonville, Florida, with the conclusion that males within the SJR form first and second-order alliances.

The inclusion of a second study site which supports second-order male alliances allows for further comparison of what factors drive first and second-order alliance formation. If paired and solitary males are pursuing alternative strategies, what variables determine which tactic is best? Several hypotheses have been suggested, but no systematic examination of what variables may correlate with alliance presence or complexity has been pursued. Chapter two provides the first comparison of pertinent ecological variables relative to alliance status across 20 study sites worldwide, with the conclusion that direct male-male competition best predicts alliance formation.

Chapter three builds upon chapter two by examining the level of aggression within and between the sexes via the quantification of rake marks. As noted in chapter two, the level of male-male competition, and thus aggression, is a good predictor of male alliance formation, while the proportion of male-female aggression within a population reveals what kind of strategy males take to gain breeding access. Consortships of females in Shark Bay, Australia, are often violent (Connor et al. 1992*b*; Connor and Vollmer 2009) while long-term male-female

interactions in Doubtful Sound, New Zealand, may be based upon affiliative relationships (Lusseau et al. 2003). Contrary to the patterns found in Shark Bay, Australia, the greatest rake mark prevalence in both males and females within the SJR community was found outside the breeding season, when conception is unlikely. This highlights the potential of sexual behavior outside of a reproductive context.

Together, this work documents the presence of a previously male mating strategy previously documented in only one study site, second-order alliances, within a relatively unstudied population of bottlenose dolphins in the St. Johns River, Jacksonville, Florida. It is also the first in-depth examination of what ecological variables drive male alliance formation. As such, it is a step towards determining what ecological pressures shape the need for male-male cooperation. Further insight is added as patterns of male-male and male-female aggression are examined, shedding light on seasonal patterns of male-male competition and the use of coercive mating as a male mating strategy. Overall, this work evokes greater insight as to the social structure and mating patterns of bottlenose dolphins as well as to the ecological parameters that result in alternative mating strategies. The complex social structure of bottlenose dolphins shows marked convergence to several other species, including primates (Symington 1990; Watts 1998; Pearson 2011), elephants (Wittemyer et al. 2005), and humans (DeScioli and Kurzban 2009). As such, this work highlights what shared evolutionary pressures shape sociality across a variety of taxa.

Chapter 1

Social structure analysis reveals the presence of multi-level alliances within estuarine bottlenose dolphins (*Tursiops truncatus*) in Northeast Florida

Abstract

Within many mammals, the advantages of group living outweigh the costs, and sociality emerges. Bottlenose dolphins (*Tursiops* sp.) live in fission-fusion societies, where female and male bonds are shaped by different ecological pressures. Across most study sites females form moderate within-sex bonds, while males bonds are extremely variable; males range from primarily solitary to allied within first-order alliances to collectively herd females. Multi-tiered alliances have thus far been limited to Shark Bay, Australia. Given the variation in male bonds, analysis of the social structure of bottlenose dolphins within Northeast Florida adds to current knowledge of male mating strategies. Data was collected from March 2011-March 2013 via boat-based weekly photo-identification surveys in the St. Johns River (SJR), Jacksonville, Florida. Data analysis was limited to individuals sighted ten or more times (n=117) and each individual was categorized as a known female (FEM, n=37) or of unknown sex (UNK, n=80), which included several known males (n=8). The UNK category was further divided into allied vs. unallied individuals based upon high level associations. Coefficients of association via the half-weight index, a test for preferred and avoided associations, and a Mantel test were calculated within SOCPROG 2.5 to examine within and between sex bonds. The population as a whole was found to interact non-randomly ($p=0.001$) with the formation of long-term preferred associations. Within-sex bonds were significantly stronger than between-sex bonds (Mantel test,

$p=1.000$), with FEM-FEM top associations averaging 0.27 ± 0.11 and UNK-UNK top associations averaging 0.60 ± 0.27 . Twenty-six UNK individuals met the criteria for male alliance status within 11 dyads and one quad. In addition, 12 of these individuals had high level associations with other alliances, indicative of second-order alliances. This is the first documentation of second-order alliances within bottlenose dolphins outside of Shark Bay, Australia, suggesting similar ecological pressures shape male mating strategies in the SJR.

Introduction

As first explained in Alexander's seminal paper, sociality evolves when the benefits of association are greater than the costs (1974). The most apparent advantages of group living are decreased predation and the increased transfer of information, while the most commonly cited disadvantage is that of intragroup competition, both for feeding and reproduction (See Krause and Ruxton 2002 for a review). Optimal group size is ultimately determined by balancing the costs and benefits of grouping. However, spatial and temporal variability in environmental conditions may stimulate the need for group size to change dynamically (Sueur et al. 2011). Several authors have suggested that fission-fusion grouping patterns, in which animals fluidly leave and rejoin groups of varying size and composition, is an adaptation to allow species to optimally adjust group size according to the flux of costs and benefits (Lehmann et al. 2007; Smith et al. 2008; Schreier and Swedell 2012).

Bottlenose dolphins are one species that live in fission-fusion societies. However, they share this characteristic with several other species, including elephants (Wittemyer et al. 2005), hyenas (Smith et al. 2008), baboons (Kummer 1971), spider monkeys, and chimpanzees (Symington 1990) (see review in Aureli et al. 2008). But not all fission-fusion societies are alike. Elephants (Wittemyer et al. 2005) and hamadryas baboons (Kummer 1968) repeatedly fission into the same basic units,

mother-calf pairs and male-based breeding units, respectively. But other species, such as spotted hyenas, chimpanzees, and dolphins, demonstrate atomistic fission-fusion patterns, in that individuals form the primary units of fission and fusion events, allowing greater flexibility in group identity (Rodseth et al. 1991). Bottlenose dolphin associations are most similar to those of chimpanzees in that they are a male-bonded species that use consortships to gain access to females (Connor and Vollmer 2009), the more solitary sex (Wrangham and Smuts 1980; Smolker et al. 1992). Also similar to chimpanzees (Wrangham and Smuts 1980; Lehmann and Boesch 2008; Langergraber et al. 2009), female-female bottlenose dolphin bonds are weaker and females spend less time in groups than males (Smolker et al. 1992; Pearson 2011), perhaps due to foraging constraints (Mann and Sargeant 2003).

Within social species females and males are often governed by different pressures. Exploring the social structure of a species allows us to examine and potentially quantify the benefits of relationships given the different needs of the sexes. According to socio-ecological theory, females are usually limited by resources (Wrangham 1980). When food resources are dispersed and hard to defend, as is the case for bottlenose dolphins, females gain little from forming dominance relations or coalitions to compete for food (Sterck et al. 1997). Males, however, are limited by access to females, discrete entities that can be defended (Wrangham 1980). This may lead to mate guarding, which includes the short-term cooperative coalitions of chimpanzees (Nishida 1983) and lions (Packer et al. 1991), and also the long-term alliance system used by some male bottlenose dolphins. Given their differing priorities, the sexes are expected to exhibit different activity budgets which may generate a level of social segregation (Conradt and Roper 2000; Fury et al. 2013). This prediction is upheld in bottlenose dolphin societies where the strongest bonds, defined using coefficients of association, are typically found within the sexes (Smolker et al. 1992; Wells 2003; Wiszniewski et al. 2009; Tsai and Mann 2013). As predicted, some female dolphins devote a large amount of time to foraging potentially limiting their time spent socializing (Gibson and Mann 2008; Mann et al. 2008). Female bonds also tend to be more ephemeral than males', and they typically maintain a larger network of

associates and a greater number of indirect links to other associates (Wells et al. 1987; Smolker et al. 1992). Their strongest bonds are typically with females of a similar reproductive state (Möller and Harcourt 2008). Male fitness, on the other hand, is dictated less by foraging and more by the distribution of females (Wrangham 1980), perhaps freeing them to nurture intra-sexual bonds (Mann 2006). In addition, males form stronger and more long-term relationships than females. These bonds can take the shape of first-order alliances between two to three males or second-order alliances between two or more first-order alliances (Connor et al. 1992*a,b*). These alliances cooperate to herd females for mating purposes and defend against thefts by other alliances (Connor et al. 1992*a,b*).

However, the strength of male bonds varies between populations (See Connor et al. 2000 for a review). For example, bottlenose dolphins in Moray Firth, Scotland (Lusseau et al. 2003), and Doubtful Sound, New Zealand (Eisfeld and Robinson 2004), demonstrate moderately strong associations both within and between the sexes. In contrast, first-order alliances are evident in Sarasota, Florida (Owen et al. 2002), the Bahamas (Parsons et al. 2003), and Port Stephens, Australia (Möller et al. 2001), while both first and second-order alliances are documented in Shark Bay, Australia (Connor et al. 1992*a,b*; Smolker et al. 1992). Whether these differences in social structure are a factor of population dynamics, habitat structure, resource availability, predation, or an unknown variable remains to be determined (Smolker et al. 1992; Wilson et al. 1993; Connor et al. 2000).

The St. Johns River (SJR) in Jacksonville, Florida, U.S.A., is an urban estuary utilized by over 300 dolphins annually. Of these, at least 70 individuals are year-round residents (Gibson, unpublished data), which may facilitate the formation of preferred, long-term associations. Though previous research has defined the community structure of dolphins inhabiting the Jacksonville area (Caldwell 2001), little research has been done to examine individual or sex-specific association patterns. Additionally, because the SJR is a highly trafficked and expanding

international shipping port, identification of fine-scale population structure in the SJR is important in order to monitor anthropogenic impacts on the dolphin community.

The primary goal of this research is to document the social structure of male and female dolphins within the SJR and specifically determine whether bottlenose dolphins in the SJR demonstrate strong intra-sexual bonds, as seen within other study sites. We also investigated whether first or second-order alliances, defined by coefficients of association, were present. Associations in the SJR can then be compared to other field sites and may highlight what common ecological pressures shape recurrent patterns in male and female relationships.

Methods

Data Collection

The St. Johns River (SJR) is a large blackwater river that drains into the Atlantic Ocean at Mayport Inlet (N30.39904, W-81.39396), approximately 40 km east of downtown Jacksonville (N30.31479, W-81.62987) (Figure 1). It is characterized by brackish water, depths of up to 18m within dredging zones, and extensive boat traffic (DeMort 1991; Benke and Cushing 2005). Previous work indicates several distinct communities of bottlenose dolphins inhabit the estuarine waters near Jacksonville (Caldwell 2001). However, this community has not been studied since 1997 and the social structure of these individuals needs to be addressed at a finer scale.

Data collection took place via weekly photo-identification surveys from March 2011-March 2013 along a fixed 40km transect from Mayport Inlet to downtown Jacksonville, with the direction of travel alternating each week. Researchers conducted surveys from a 7.9-m Twin Vee Catamaran or 6.4-m Carolina Skiff and traveled at a consistent speed of 10-12 km/hr until

dolphins were sighted, at which time the vessel approached and maintained proximity to the dolphin group until all individuals were photographed, typically over a span of 5-30 minutes. Behavioral information (dive type, predominant group activity, and the occurrence of specific behaviors) and environmental variables (water depth, water temperature, and salinity) were collected in addition to group composition. The dorsal fins of all dolphins within the group (defined using a conservative 10m-chain rule as in Smolker et al. 1992) were photographed using a professional grade digital camera with 400mm telephoto lens. All data were collected under the authorization of NOAA Fisheries GA LOC 14157 and UNF IACUC 10-013.

Data Analysis

Over 25 months, data were gathered from 96 surveys and 835 group sightings. All photographs were analyzed using standard photo-identification techniques (see Mazzeil et al. 2004), in which the best photograph of each individual within a sighting was compared to a master catalogue for identification. Dorsal fin shape, nick pattern, and scars were utilized to uniquely identify individuals. All unmatched dolphins were added to the catalogue as new individuals. Only identified, non-calf individuals sighted ten or more times were used for data analyses. All incomplete sightings, sightings that were less than 30% different from a previous group that day, and sightings that violated the 10-m chain rule (Smolker et al. 1992) were excluded from data analyses, for a total of 660 sightings included within the analysis. Of a total of 301 individual dolphins encountered, 117 met the sighting history criteria and were sighted 10+ times.

Although the current study was focused on two years of data, sex determination was based on all available sighting data collected from March 2011 – August 2014. Poor water clarity inhibits frequent direct observation of the genitals within the SJR. Alternatively, individuals

were categorized as female (FEM) if they had been sighted with a calf in infant position (Mann et al. 2000) in at least two sightings ($n = 37$). All other individuals were categorized within an unknown sex category (UNK) ($n = 80$). It should be noted that some males have been sexed based on direct observation of the genitals ($n = 8$). However, known males were included in the unknown sex category to increase sample size. As such, the unknown sex category included several known males, behaviorally-presumed males, and non-reproductive females. Due to our inability to sex non-reproductive females, the unknown category is probably confounded by approximately 20 true females, given the assumption that the sex ratio of our sample is 1:1. Despite this caveat, the mean top coefficients of association of UNK individuals were identical to the mean top associations of known, unallied males, suggesting that the UNK category is comprised largely of true males.

Coefficients of association (COAs), specifically half-weight indices (HWIs), were used as a proxy for the strength of social bonds among individuals (Cairns and Schwager 1987). The HWI is the most commonly used association index with bottlenose dolphin associations, allowing for comparison between study sites (See Table 2). The half-weight index also accounts for the bias that photo-identification surveys tend to underestimate joint sightings (Smolker et al. 1992). The HWI is defined as $HWI = 2N_T / (N_a + N_b)$, in which N_T represents the number of times two individuals are seen in the same sighting and N_a and N_b represent the total number of times each individual is sighted, respectively (Cairns and Schwager 1987). Half-weight indices range from 0 (animals never seen together) to 1 (animals consistently seen together) (Cairns and Schwager 1987). HWIs were calculated within SOCPROG version 2.5 to quantify the level of association between individuals and also within and between sex classes, the latter via a Mantel test (Whitehead 2009). A two-tailed permutation test (20,000 permutations) for preferred and

avoided associates was also performed to test for dyads that associate non-randomly ($\alpha = 0.050$; Bejder et al. 1998). Results from the above analyses were then used to further divide the unknown sex category into allied and unallied individuals. In this study, “allied” status was given to groups of unknown sex individuals that: 1) Had $\text{HWI} \geq 0.80$, 2) Had greater than random associations, and 3) Were reciprocal top associates or second top associates with a HWI within 20 % of the top association. These criteria were adapted from previous work (Connor et al. 1992b,1999; Möller et al. 2001; Parsons et al. 2003; Wiszniewski et al. 2012). Smolker et al. (1992) defined second-order alliances as those in which individuals within separate first-order alliances maintained average coefficients of association greater than 0.20 with one another. Because the average non-zero HWI between individuals of unknown sex in the SJR community was 0.16, we conservatively raised our criterion for second-order alliance affiliation to first-order alliances that shared $\text{HWI} \geq 0.32$, twice the average, as seen in Elliser and Herzing (2014). Although the unknown sex category inevitably contains non-reproductive females, the stringent criteria used to define allied individuals almost certainly excludes all females, as no known female approached a top association of $\text{HWI} \geq 0.80$. In addition, fourteen of the allied individuals have been observed herding females and five are confirmed males. As such, allied individuals are further referred to in the text as males, while unallied individuals of the unknown sex are referred to as unallied presumed males.

Results

Analysis revealed a social differentiation, via the likelihood method, of 0.951, suggesting a moderately differentiated population. Further analysis revealed an overall HWI of 0.05 ± 0.02 , a non-zero HWI of 0.13 ± 0.11 , and a mean maximum HWI of 0.51 ± 0.27 across the

community. A test for preferred associations revealed that both the standard deviation and coefficient of variation within the real data were greater than in the random data, indicating the presence of long-term preferences within the SJR population ($p=0.001$). In addition, the proportion of real non-zero elements was lower than the number of random non-zero elements, indicating avoidances between individuals.

When examining inter- and intra-sexual associations, mean HWIs within the sexes were significantly greater than those between them (Mantel test, $p = 1.000$). This was especially apparent when examining the maximum HWIs of the sexes. FEM-all and FEM-FEM maximum bonds averaged 0.29 ± 0.10 and 0.27 ± 0.11 , respectively (range: 0.13 to 0.62), while maximum UNK-all and UNK-UNK bonds averaged 0.61 ± 0.26 and 0.60 ± 0.27 , respectively (range: 0.15 to 1.00) (see Figure 3). For comparison, known male-UNK maximum bonds averaged 0.71 ± 0.18 . UNK had their highest association with another UNK in 91 % of cases, while FEM had their highest association with another FEM in 69 % of cases. Neither sex exhibited any evidence of subgroup division after community division by modularity. Between sex bonds were lower, with non-zero HWIs at $\bar{x} = 0.10 \pm 0.05$. See Table 1 for a complete list of HWIs within and between the sexes.

When addressing male alliance status, 26 individuals of unknown sex (including five known males) met our criteria for first-order alliances, including 11 dyads and one quad (see Figure 2). Of these males, 12 individuals had $\text{HWI} \geq 0.32$ with another alliance, indicative of a second-order alliance. In all, five second-order alliances were found; two first-order alliances participated in two different second-order alliances and one first-order alliance participated in three separate second-order alliances. Bonds across the five second order alliances averaged a

HWI of 0.52 ± 0.12 . Of the 80 unknown sex individuals within the study, 33 % ($n = 26$) were considered allied and 15 % ($n = 12$) exhibited second-order alliances.

Both allied males and unallied presumed males interacted with one another at approximately baseline levels (non-zero HWI $\bar{x} = 0.13 \pm 0.10$) and even formed preferential associations. In addition, unallied presumed males were found to interact as often with females as did allied males (allied non-zero HWI $\bar{x} = 0.11 \pm 0.05$, unallied non-zero HWI $\bar{x} = 0.10 \pm 0.05$).

Discussion

Overall, these data describe a community where female relationships are low to moderate in strength and a portion of males participate in first and second-order alliances, a level of bottlenose dolphin social complexity previously limited to Shark Bay, Australia (Connor et al. 1992*a,b*). The community as a whole interacts non-randomly ($p = 0.001$), with the formation of long-term preferential associations and avoidances, a pattern noted across the majority of well-studied populations (Smolker et al. 1992; Lusseau et al. 2003; Rogers et al. 2004; Wiszniewski et al. 2009). Prior to drawing comparisons, it should be noted that group definitions, and thus association calculations, vary across study sites with most studies utilizing a 100-m diameter rule for inclusion. Despite using a more conservative 10-m chain rule, our population exhibits high levels of association similar to the values of less restrictive studies. In addition, mean half-weight indices may be calculated with or without the inclusion of zero values, often leading to confusion when comparing associations across study sites. For this reason, we draw comparisons between the mean top associations of males and females, as these are rather straight-forward.

When looking at the associations of females, the pattern of loose, ephemeral female bonds described across study sites held true within the SJR population. Most female top associations fell within 0.20 to 0.40, indicating a very fluid social sphere, in which all individuals were likely to indirectly interact. This pattern of intermediate female bonds echoes other studies in Sarasota, Florida (Wells et al. 1987), Port Stephens, Australia (Möller et al. 2006), and Shark Bay, Australia (Smolker et al. 1992). In my study, 69 % of known females' top associates were also females, similar to 64 % of female-female top associations noted in Shark Bay, Australia (Tsai and Mann 2013). However, maximum female-female bonds in the SJR ($\bar{x} = 0.27 \pm 0.11$) were reduced compared to other populations (Table 2). While this observation could be an artefact of non-reproductive females remaining within the UNK category, it can be argued that known females were unlikely to form close bonds with miscategorized non-reproductive females, as female-female bonds are often a factor of similar reproductive state (Möller and Harcourt 2008). To date, the SJR community showed little evidence of female bands, or cliques, as seen in the majority of other field sites (Sarasota, Florida [Wells et al. 1987], Cedar Keys, Florida [Quintana-Rizzo and Wells 2001], Gulf de Guayaquil, Ecuador [Felix 1997], Port Stephens, Australia [Möller et al. 2006], and Shark Bay, Australia [Smolker et al. 1992]). This pattern of limited female grouping may reflect the development of foraging specializations, as seen in Shark Bay, Australia, and Sarasota, Florida (Mann and Sargeant 2003; Weiss 2006), though foraging techniques within the SJR have not yet been examined in detail. It may also indicate a reduced risk of predation, as females with young calves have been known to form larger groups than other individuals, presumably in predator defense (Wells 1987, 2000; Gibson and Mann 2008), or a lack of synchronous reproductive states within the community (Wells et al. 1987; Möller and Harcourt 2008).

Mean top associations among unknown sex individuals ($\bar{x} = 0.60 \pm 0.27$) within the St. Johns River are similar to those of males in Panama City, Florida (Beauveroux and Mallefet 2010), Little Bahama Bank, Bahamas (Parsons et al. 2003), and Doubtful Sound, New Zealand (Lusseau et al. 2003), though still lower than those cited in Shark Bay, Australia (Smolker et al. 1992). However, this observation may be explained by the dilution of the UNK category by non-reproductive females. In addition, 91% of unknown individuals had another unknown individual as their top associate, comparable to Tsai and Mann (2013)'s observation of 86% of males forming top associations with other males in Shark Bay, Australia.

Allied and unallied individuals showed a similar pattern in bond strength to the observations of Owen et al. (2002) in Sarasota, Florida, in that the strongest bonds were within allied individuals, then within unallied individuals, and weakest between the two categories. However, based on a mean non-zero HWI of 0.13 ± 0.10 , allied and unallied individuals within the SJR appeared to interact at approximately base-line levels. In addition, similar to the findings of Owen et al (2002), allied and unallied individuals appear to interact equally with females.

In addition, the SJR is different from other study sites in that a reduced proportion (33 %) of males seem to utilize alliances as a mating strategy. The proportion of allied males in other populations range from 57 % in Sarasota, Florida (Owen et al. 2002), to 85 % in Shark Bay, Australia (Smolker et al. 1992), with other study sites supporting male alliances falling intermediate (Parsons et al. 2003; Wiszniewski et al. 2012). The reduced number of alliances within the SJR might be explained by the presence of several non-reproductive females within the male category, but may also be a factor of my stringent group definition and male alliance criteria. Most studies require partial fulfillment of the following criteria for alliance status:

above random associations, preferred associates, top reciprocal associates. This study utilizes all of the above but also incorporates a conservative HWI cut-off of 0.80 between putative allied males, which effectively excludes females from being assigned allied status (maximum female HWI $\bar{x} = 0.29 \pm 0.10$). Inevitably, this reduces the number of dyads that meet my criteria.

As only a portion of the community is allied, the strategies of males in the SJR most closely resemble those of Port Stephens, Australia, where males range from unallied to loosely allied and tightly allied (Wiszniewski et al. 2012). If a similar criteria were used in this study, many additional males would probably be categorized as loosely allied as well. In addition, the coexistence of allied and unallied males within the SJR suggests the presence of two alternative mating strategies within this community. Gross (1996) delineates alternative mating strategies into those which are fixed early in life, often through a polymorphism (Lank et al. 1995) and those which are sequential or condition-dependent and change with individual status (Duval 2007). A polymorphism is an unlikely cause of the variation we see in alliance status, particularly given the behavioral flexibility seen in bottlenose dolphins. Rather, forging and maintaining alliances is probably an extremely complex process and dependent upon a combination of many variables, including individual age, size, or competitive ability. Alternatively, as suggested by Owen et al. (2002), some males within the SJR may be in a transitional stage between alliances or prior to alliance crystallization. Male-male bonds may not solidify until up to twenty years of age, based upon the work of Owen et al. (2002), and subadult males may be responsible for the low proportion of allied males within the SJR.

Most importantly, some males in the SJR form second-order alliances, a level of bottlenose dolphin complexity previously described only in Shark Bay, Australia (Connor et al. 1992*a,b*), though recent evidence of second-order bonds have been described in Atlantic spotted

dolphins (*Stenella frontalis*) (Elliser and Herzing 2014). In fact, the bonds found within SJR second-order alliances ($\bar{x} = 0.52 \pm 0.12$) are extremely similar in strength to those identified in Shark Bay ($\bar{x} = 0.42 \pm 0.12$ within second-order alliances, $\bar{x} = 0.58$ within the super-alliance) (Smolker et al. 1992; Connor et al. 1999). In this sense, complex hierarchal male relationships are not unique to Shark Bay, Australia, but the outcome of a complex suite of ecological and demographic variables encouraging male cooperation. Continued research as to the shared ecological pressures between field sites supporting first and second-order alliances is needed to better understand what mechanisms govern the need for complex, multi-tiered social relationships.

Acknowledgements

None of this would have been possible without the funding of the Elizabeth Ordway Dunn Foundation, the UNF Coastal Biology Flagship Program, the UNF Environmental Center, and the San Marco Rotary Club. In addition, the work of our volunteers and undergraduates has been invaluable to this research.

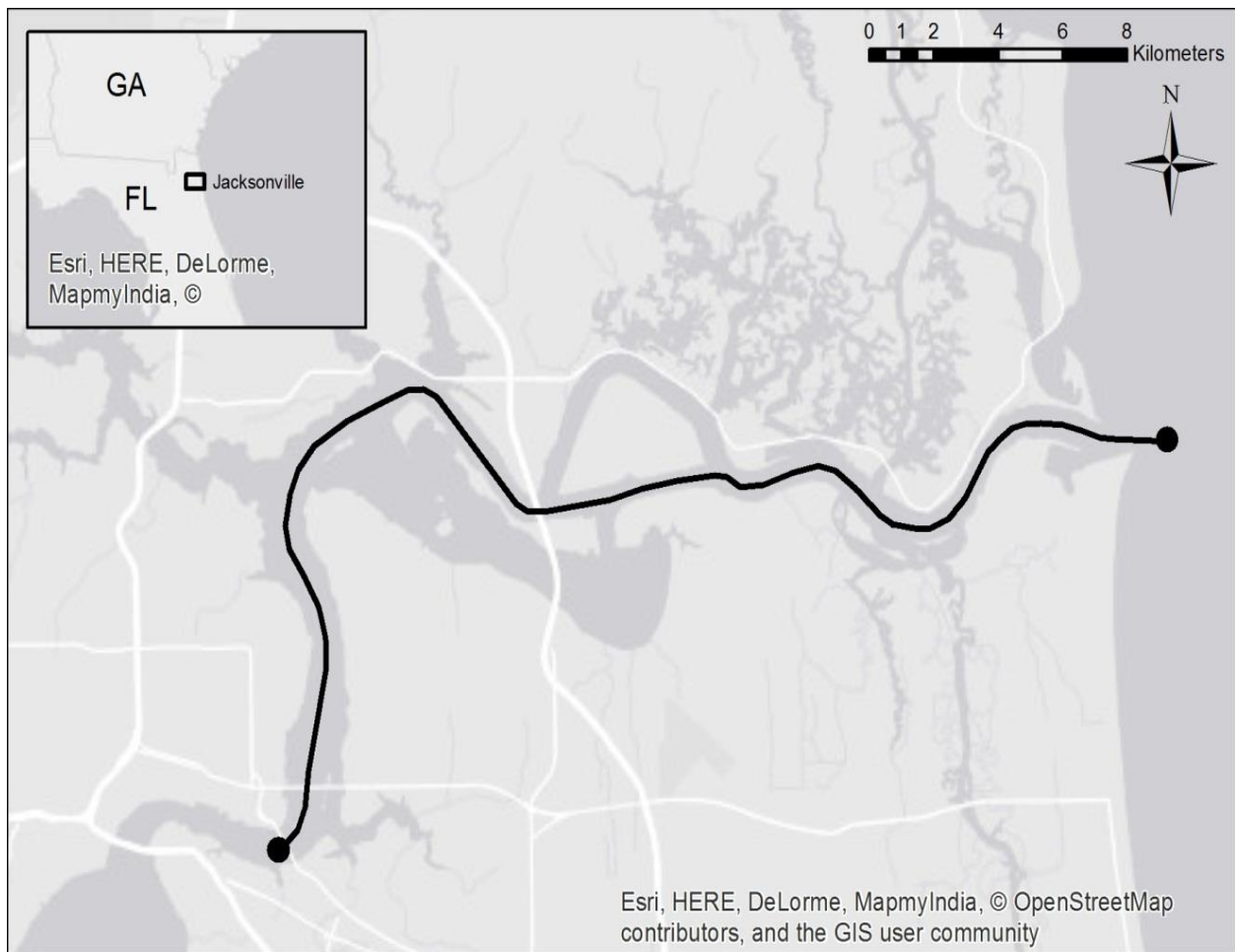


Figure 1. Data was collected through weekly photo-identification surveys from the mouth of the St. Johns River to downtown Jacksonville, with the direction of travel alternating weekly.

Table 1. Mean zero, non-zero, and maximum half-weight indices (HWI) within and between the sexes. A Mantel test revealed that within-sex bonds were significantly greater than between-sex bonds ($p = 1.000$).

	Mean HWI	Mean Non-zero HWI	Mean Top Association
Overall	0.05±0.02	0.13±0.11	0.51±0.27
FEM	0.04±0.01	0.11±0.06	0.29±0.10
UNK	0.05±0.02	0.14±0.13	0.61±0.26
FEM-FEM	0.06±0.02	0.12±0.07	0.27±0.11
UNK-UNK	0.05±0.02	0.16±0.15	0.60±0.27
Between sexes	0.04±0.02	0.10±0.05	0.18±0.09
Allied-Allied	0.11±0.04	0.27±0.30	0.91±0.08
Unallied-Unallied	0.06±0.03	0.16±0.12	0.43±0.20
Allied-Unallied	0.04±0.02	0.13±0.10	0.26±0.15
Allied-FEM	0.05±0.03	0.11±0.05	0.19±0.08
Unallied-FEM	0.03±0.02	0.12±0.09	0.17±0.08

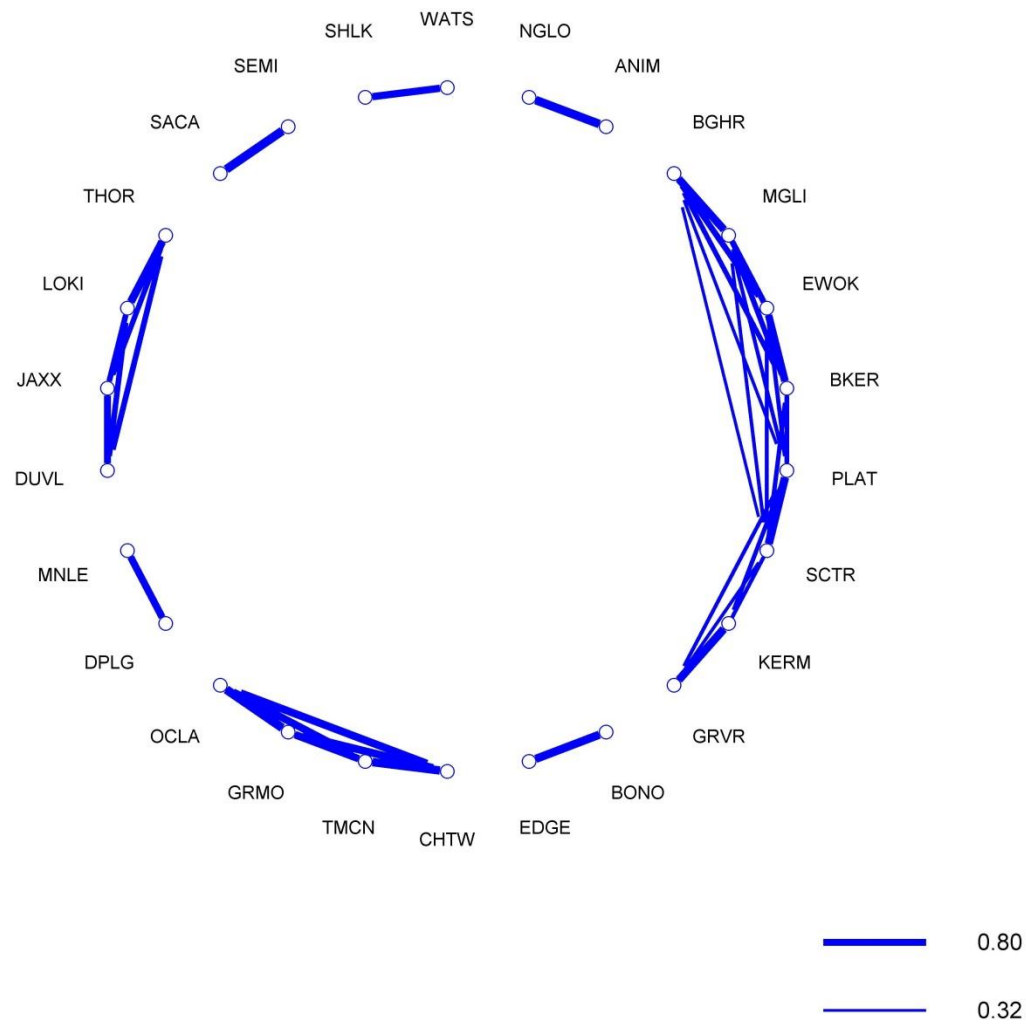


Figure 2. Sociogram of all allied males. First-order alliances ($HWI \geq 0.80$) are represented by thick lines while intermediate bonds between alliances ($HWI \geq 0.32$) are represented by thin lines.

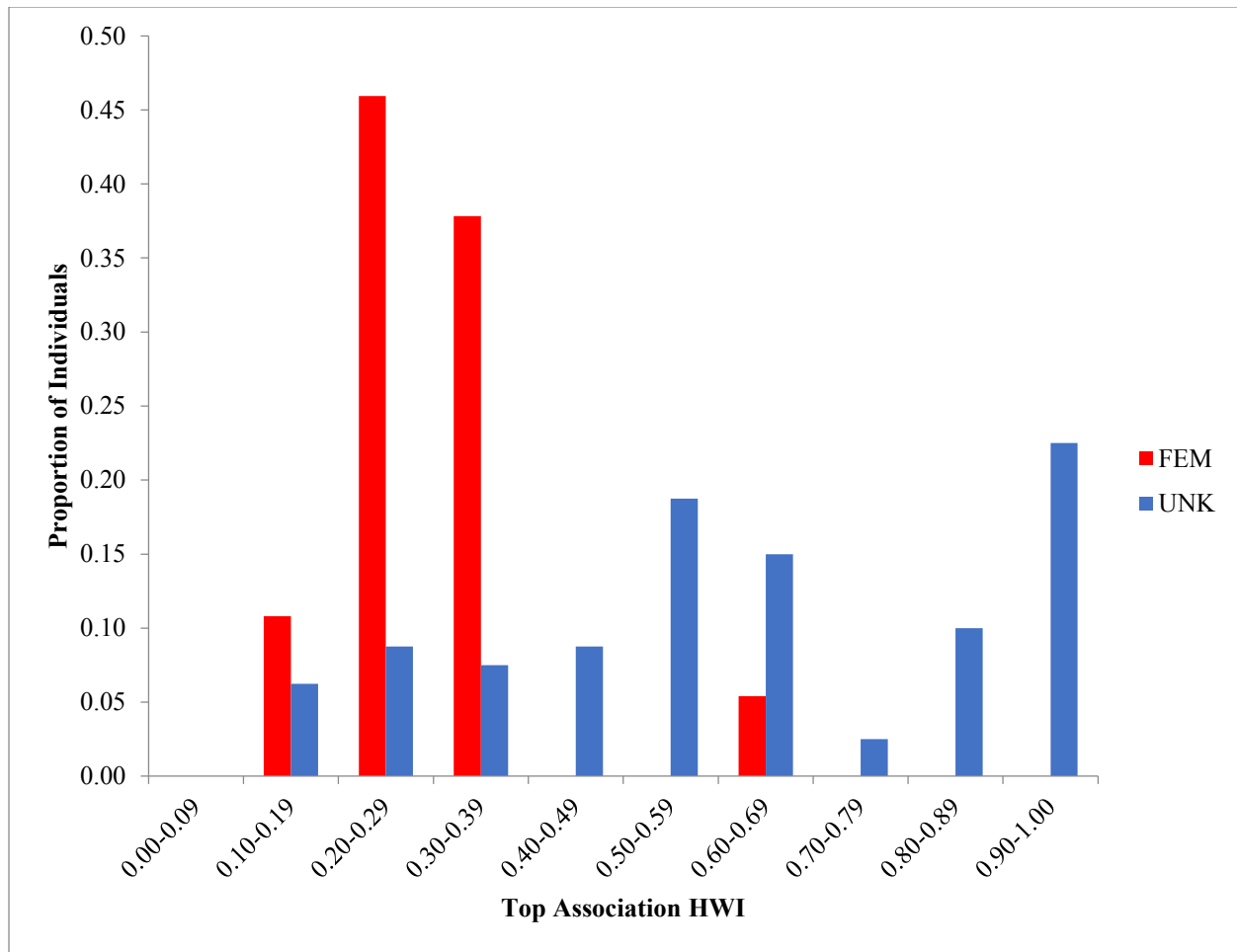


Figure 3. Mean top associations of females and unknown sex individuals. Female top associations ranged from HWI of 0.13 to 0.62 but fell primarily within HWI of 0.20 to 0.30. Unknown sex top associations ranged from HWI of 0.15 to 1.00 but were more variable than those of females.

Table 2. A comparison of bottlenose dolphin social structure studies world-wide.

Study Site	Mean Population HWI	Max Population HWI	Mean Male-Male HWI	Max Male-Male HWI	Mean Female-Female HWI	Max Female-Female HWI	Male Top HWI	Female Top HWI	Mean Mixed-sex HWI	Max Mixed-sex HWI	HWI of Second-order Alliances
St. Johns River, FL _A	0.05±0.02	0.51±0.27	0.05±0.02	0.60±0.27	0.06±0.02	0.27±0.11	1	0.62	0.04±0.02	0.18±0.09	0.52±0.12
Sarasota, FL			Paired _B 0.03-0.04 Unpaired _B 0.01-0.02	Paired _B 0.71-0.75 Unpaired _B 0.13-0.18	0.11-0.51 depending on reproductive state _C		Paired _B 0.927	0.80 _C			
Panama City, FL _D	0.11±0.04	0.49±0.27	0.19±0.07	0.67±0.26	0.06±0.02	0.29±0.10	0.97	0.45	0.07±0.04	0.21±0.09	
Cedar Keys, FL _E							0.92	0.57			
Bahamas			0.30±0.17 _F 0.08±0.16 _G	0.68±0.27 _G 0.76±0.15 _H	0.31±0.18 _F	0.68±0.22 _H	0.93 _F 1.0 _G	1 _F	0.26±0.14 _F		
Ecuador _I	0.32±0.18				0.39±0.19		0.96	0.83			
Doubtful Sound, New Zealand _J	0.47±0.04	0.63±0.08	0.49±0.04	0.65±0.07	0.47±0.05	0.60±0.08	0.74 _I	0.73 _I	0.45±0.04	0.57±0.07	
Moray Firth, Scotland _K	0.11±0.04	0.48±0.13	0.12±0.05	0.39±0.17	0.10±0.03	0.40±0.11	0.73 _E	0.67 _E	0.12±0.15	0.40±0.13	
Sado Estuary, Portugal _L	0.45±0.15										
Port Stephens, Australia	0.15±0.05 _M 0.09±0.02 _M	0.56±0.21 0.50±0.20	0.08±0.02 _Y 0.22±0.06 _Y 0.12±0.17 _O	0.39±0.16 _Y 0.45±0.10 _Y	0.11±0.05 _Y 0.25±0.15 _Y 0.12±0.16 _N	0.55±0.27 _Y 0.78±0.17 _Y 0.53±0.17 _P		0.81 _P			
Shark Bay, Australia				0.83±0.17 _R	0.02±0.06 _Q	0.51±0.18 _R	1.0 _R 0.97 _E	0.84 _R			0.42±0.12 _R
Bay of Islands, New Zealand _S	0.14±0.05	0.65±0.14	0.18±0.10	0.42±0.18	0.16±0.07	0.60±0.17	0.61	0.67	0.14±0.05	0.63±0.14	
Lampedusa Island, Italy _R	0.06±0.30										
Patagonia, Argentina _U	0.21±0.07										
São Tomé Island, Gulf of Guinea _V	0.17±0.09										

^ACOAs [‡]Presumed males
^B Simple-ratio indices from Owen et al. 2002
^C Wells et al. 1987
^D Bouveroux and Mallefet 2010
^E Quintana-Rizzo and Wells 2001
^F Non-zero annual COAs from Rogers et al. 2004
^G Parsons et al. 2003
^H Simple-ratio indices from Rossbach and Herzing 1999
^I Felix 1997
^J Lusseau et al. 2003
[†] Estimated from Fig. 4 in Lusseau et al. 2003
^K Eisfeld and Robinson 2004
[£] Estimated from Figure 3 in Eisfeld and Robinson 2004
^L Simple-ratio indices from Augusto et al. 2012
^M Data from East and West communities, respectively, in Wiszniewski et al. 2009
[¥] Interpreted from Fig. 3 in Wiszniewski et al. 2009
^N Möller et al. 2006
^O Möller et al. 2001
^P Calculations performed from data from Möller and Harcourt 2008
^Q Frère et al. 2010
^R Smolker et al. 1992
[€] Estimated from Fig. 2 in Connor et al. 2011
^S Mourão 2006
^T Pace et al. 2011
^U Vermeulen and Cammareri 2009
^V Pereira et al. 2014

Groups were defined using a 100-m chain rule in Wells et al. (1987), Quintana-Rizzo and Wells (2001), Owen et al. (2002), Wiszniewski et al. (2009), Möller et al. (2001), Möller et al. (2006), Möller and Harcourt (2008), Bouveroux and Mallefet (2010), and Vermeulen and Cammareri (2009). Groups were defined using a 10-m chain rule by Smolker et al. (1992), Lusseau et al. (2003), Connor et al. (2011), and within this study. Group extent was otherwise defined in the remaining publications

Chapter 2

The use of ecological and demographic variables to predict alliance formation

Abstract

Across study sites, male bottlenose dolphins fall within a continuum of social complexity, though two strategies predominate; males may be primarily solitary or allied within a first-order alliance to cooperatively herd females for access to breeding. Multi-tiered alliances in which first-order alliances cooperate to defend or assist in the theft of females are limited to Shark Bay, Australia, and Northeast Florida. However, not all study sites report male alliances and the factors behind variability in male mating strategies have not yet been examined. As such, the goal of this study was to quantify important ecological variables across study sites that differ in alliance presence and complexity to reveal possible correlation of these factors with alliance status. The variables included: predation (via shark bites), home range, sexual dimorphism, the rate of male-male encounter (via population density), and the operational sex ratio (via inter-birth intervals [IBIs]). No support was found linking predation, increased home range, or sexual dimorphism to patterns in alliance status. However, results indicated that alliance status is closely related to the rate of male-male encounter, in that populations with above average population density (1.32 dolphins/km²) have all documented male alliances. The two most dense study sites have documented second-order alliances, as well. In addition, the use of IBIs as a predictor of male alliance formation is promising, though care must be taken that IBIs correlate with male-male competition, as several study sites report long IBIs that do not result in increased

mate competition. As such, direct measurements of male-male competition may best indicate the need for male alliance formation. Future suggestions include examination of the temporal and spatial distribution of receptive females within populations as well as direct quantification of male aggression within and across study sites.

Introduction

Across populations male bottlenose dolphins (*Tursiops* sp.) fall within a continuum of social complexity, though they typically employ one of two strategies. Some males are solitary and encounter and herd females individually, while others operate within first-order alliances by forming strong bonds with two to three other males and herding females cooperatively (Connor et al. 1992*a,b*). Alliances of increased social complexity are largely limited to Shark Bay, Australia, where males exhibit second-order alliances in the shape of moderate bonds between members of first-order alliances (Connor et al. 1992*a,b*). In addition, Shark Bay is home to a super-alliance, fourteen males that form flexible bonds within a large group, while still showing preferences for specific partners (Connor et al. 2001). Finally, a further level of complexity is suspected in Shark Bay in the way of third-order alliances, as agonistic interactions have been observed between multiple second-order alliances (Connor et al. 2011). Recent evidence, however, suggest the presence of second-order alliances in Jacksonville, Florida, as well (Chapter 1), suggesting that complex mating strategies are not unique to Shark Bay, but perhaps a product of shared socio-ecological pressures.

When examining the distribution of these male mating strategies spatially, lower latitude sites, such as Doubtful Sound, New Zealand (Lusseau et al. 2003), Bay of Islands, New Zealand (Mourão 2006), and Moray Firth, Scotland (Eisfeld and Robinson 2004), lack evidence of male

alliances. In contrast, Sarasota, Florida (Owen et al. 2002), the Bahamas (Parsons et al. 2003), and Port Stephens, Australia (Wiszniewski et al. 2012), all support first-order alliances, and Shark Bay, Australia (Connor et al. 1992*a,b*), as well as Jacksonville, Florida, exhibit second-order alliances. This variability leads to the question, “What factors drive the patterns we see in alliance variation across study sites?”

To better understand the distribution of alliance variation, the aim of this study was to quantify the presence and extent of important ecological, demographic, and morphological variables across study sites that vary in alliance status. Variables potentially correlated with alliance formation were selected from the literature and chosen based upon availability and how quantifiable they were to facilitate comparison across study sites. When possible, data were included from the St. Johns River, Jacksonville, Florida, where first and second-order alliances have recently been documented (Chapter 1).

Rate of Encounter

One factor expected to affect male alliance formation is the extent of male-male and male-female interactions, as alliances are unlikely to form in populations in which males rarely interact (Connor et al. 2000) or in which there is little competition for females (Whitehead and Connor 2005). As first suggested by Connor et al. (2000), if there is a low probability of encountering a rival male, the best strategy is solitary travel. In contrast, if males encounter many rivals, sharing copulations may have a greater payoff than constantly competing. Similarly, if many females are present in a population, males would be better off pursuing females individually, while sharing the opportunity to mate might be more beneficial in a competitive population skewed towards males (Whitehead and Connor 2005). Rate of male-male encounter is here measured through population density and male-female encounters is

measured through female inter-birth intervals, as a proxy for the operational sex ratio (OSR) or number of males per reproductive female.

Population Density

Assuming sex ratios are approximately 1:1, encounter rate is largely a factor of population density. Within the literature, population density has variable effects on mating systems (see Kokko and Rankin 2006), though it has been positively correlated with male-male competition for mates (Jirotkul 1999). At some point, increased competition at high densities may become detrimental to fitness and the selection pressure for alternative strategies may shift (Cade 1980; Eadie and Fryxell 1992; Gage 1995; Tomkins and Brown 2004). As such, if male alliance formation is viewed as an alternative mating strategy, we might expect particularly dense dolphin populations to support alliances as a mechanism to reduce male-male competition. To calculate population density, population estimates from the literature were divided by the study site area to give an estimated number of dolphins per km². Whenever possible, both population estimates and study site size were taken from the same publication to reduce bias. If this was not possible, care was taken to use the most recent estimates of both parameters available. If only seasonal, as opposed to annual, abundance was available, breeding season (summer) abundance was utilized, as this is when male competition for mates takes place.

Hypothesis 1: Alliance formation will occur in bottlenose dolphin populations with above average population density.

Operational Sex Ratio

Classical sexual selectionist theory suggests that when the operational sex ratio (OSR) is skewed towards one sex, competition for mates and in turn sexual selection within that sex is heightened (Emlen and Oring 1977). As females typically invest more time into each offspring

(Trivers 1972), we can expect males to have a high potential reproductive rate and be the limited, and thus more competitive, sex. This is supported by a meta-analysis performed by Clutton-Brock and Vincent (1991), who found a strong link between potential reproductive rate and which sex was more competitive. If alliances are indeed a mechanism to reduce male competition, alliances are only expected to form when there are multiple males competing for each female, with alliance size ultimately dictated by the ratio of competitive males to available females (Whitehead and Connor 2005). Although many factors impact the number of reproductive females within a population, to a large degree this is determined by how long a female provides parental care to her young before returning to cycling. For this reason we use inter-birth intervals (IBIs) as a simplified proxy for the OSR.

Hypothesis 2: Populations with elevated IBIs will exhibit alliances, with the skew of the IBIs proportional to alliance complexity.

Benefits of Alliance Formation

Alternatively, alliance formation may be a factor of the benefits gained from group living. The most commonly cited advantage to group living is that of increased predator protection. For example, both elk and a handful of primates are thought to seek out large groups to decrease predation risks through the dilution effect or increased vigilance (Hebblewhite and Pletscher 2002; Hill and Lee 1998). This idea was expanded upon by Wells (1991a), who suggested allied males may experience increased predator protection compared to their unallied peers. Owen (2003) later expanded upon this hypothesis by suggesting the increased predator protection of allied males allowed them to maintain larger home ranges, which in turn may allow them to encounter a greater number of females (Wells 1991b). To quantify predation, the proportion of the population exhibiting scars from shark attacks is compared across populations.

Hypothesis 3: Alliance complexity will be correlated with increased predation.

In addition, a disadvantage to group living, an increase in travel and home range size to find adequate resources (van Schaik et al. 1983; Chapman and Chapman 2000), might actually be a benefit to males seeking mating opportunities. Not only are travel costs reduced via aquatic locomotion (Williams 1999), but as noted above, an increase in home range may expose allied males to a greater number of females, allowing for greater mating opportunities (Wells 1991b).

Hypothesis 4: Allied males will maintain larger home ranges than unallied males.

Sexual Dimorphism

Secondary sex traits, such as increased male body size, are often a result of intrasexual selection in competition for mates (Darwin 1871; Andersson 1994). Across polygynous primate species, for example, the degree of sexual dimorphism typically correlates to the level of male competition, even after controlling for body weight and phylogeny (Mitani et al. 1996).

Intrasexual selection on male size is, in particular, the primary force behind sexual dimorphism (Gaulin and Sailer 1984; Mitani et al. 1996), with monogamous anthropoids experiencing less weight dimorphism than polygamous ones (Plavcan and van Schaik 1997). If dimorphism, a variable typically associated with increased male competitive ability, is constrained within a population, perhaps individuals will seek out alternative mating strategies to increase reproductive success. Length and/or mass of male and female bottlenose dolphins were compared within and between study sites to test this hypothesis.

Hypothesis 5: Alliances will occur in populations in which sexual dimorphism is minimal.

Other Factors

Other factors include any potential costs of male alliances, such as feeding competition, which could limit their use in particular populations (Whitehead and Connor 2005) or habitat

complexity that limits male-male encounter rates (Smolker et al. 1992). Another explanation is that female choice may be at work and that alliances may not be favored over solitary males in all populations (Whitehead and Connor 2005). However, these factors are much more difficult to document and quantify in the field.

Results and Discussion

Population density was extremely variable across study sites, ranging from 0.02 dolphins/km² in Moray Firth, Scotland (Wilson et al. 1997; 1999), to 6.76 dolphins/km² in the St. Johns River (\bar{x} =1.32 dolphin/km²). Most study sites with first-order alliances, such as Sarasota, Florida (1.30 dolphins/km²; Wells 2013), and Port Stephens, Australia (1.40 dolphins/km²; Möller et al. 2002), approached or exceeded the average population density across all study sites. In addition, second-order alliances were limited to sites with elevated dolphin density; Shark Bay has a reported dolphin density of 2.40 dolphins/km² (Watson-Capps 2005) and the St. Johns River supports 6.76 dolphins/km². Refer to Table 1 for a summary of dolphin density and social complexity. Overall, this pattern of increased male social complexity at higher dolphin densities supports the hypothesis that alliances are an outcome of increased male-male encounters and subsequent competition for mates.

Inter-birth intervals ranged from 2.9 years (Thayer 2008) to 4.55 years (Mann et al. 2000) and possibly upwards of five years, as measured by the age of separation in Sarasota, Florida (Wells 1993). The majority of study sites that have not documented male alliances reported interbirth intervals of 3-4 years, with the exceptions of the Bay of Islands and Doubtful Sound in New Zealand, where females typically give birth at 4.25 and 4.37 year intervals, respectively (Tezanos-Pinto 2009; Henderson et al. 2014). Only the two study sites with the longest inter-

birth intervals, Shark Bay, Australia (Mann et al. 2000), and Sarasota, Florida (Wells 1993), support male alliances. Overall, there is a tendency of study sites with presumably fewer cycling females to support male alliances. This suggests that alliances are a cooperative solution to increased male competition for mates.

However, the inter-birth intervals reported for the Bay of Islands and Doubtful Sound in New Zealand are anomalous given that alliances have not been documented (Lusseau et al. 2003; Mourão 2006). It should be noted that calving intervals from the Bay of Islands were calculated from a small sample size of six females, and may not be overly representative of the population as a whole (Tezanos-Pinto 2009). In addition, data collection from Doubtful Sound took place seasonally over 2-6 week periods, with the potential to miss calves that died soon after birth, subsequently biasing their calving ratio high (Henderson et al. 2014). However, if this trend holds true, the lack of male alliances in a population in which there are few reproductive females at any given time is puzzling. Lusseau et al. (2007) noted an apparent lack of female consortship, intense male competition for female access, or infanticide within the Doubtful Sound population. Rather, affiliative relationships with females may play a larger role in securing breeding opportunities within fjord systems, where food resources are extremely variable in space and time (Lusseau et al. 2003).

There was no clear pattern in predation rate and alliance formation across study sites. Predation was highest (74.2% of adults) in Shark Bay, Australia, (Heithaus 2001) and nearly lowest (1.76% of the population) in Little Bank, Bahamas (Fearnbach et al. 2011), both of which possess male alliances. Sites that lacked alliances and also Sarasota, Florida, had low to intermediate levels of shark predation. In locations where predation was absent (Adriatic Sea [Bearzi et al. 1997], Moray Firth, Scotland [Wilson 1995]), no male alliances have been

recorded. Together, these observations suggest that male alliance formation is not primarily a solution to predation. This contrasts with Wells (1991*a*) observation that while paired males had a greater number of shark bites, they typically lived longer, suggesting they less often suffered fatal attacks due to the protection of an ally. Though the addition of one to two allies may not offer increased predator protection, this hypothesis could be extended to see if group size varied predictably according to predation risk. Alternatively, allied males may live longer than unallied males for reasons unrelated to predation.

Analysis of home range size across study sites was limited in that information regarding allied and unallied home ranges was only available for two study sites. However, within both study sites, allied males maintained larger home ranges than unallied males. Allied males in Sarasota used home ranges of $162.58 \pm 24.21 \text{ km}^2$, double that of unallied males ($72.11 \pm 24.37 \text{ km}^2$) within the same study area (Owen et al. 2002). In addition, males in first or second-order alliances in Shark Bay also maintained extensively larger home ranges ($92.31 \pm 6.78 \text{ km}^2$; Randić et al. 2012) than the male category in general ($59 \pm 11 \text{ km}^2$; Tsai and Mann 2013). No data were yet available regarding the home ranges of allied vs. unallied males within the Bahamas, Port Stephens, Australia, or the St. Johns River, Florida. Though preliminary, this suggests allied males may maintain larger home ranges than unallied conspecifics. While this is in accordance with the hypotheses of Wells (1991*a*), as noted above, there is little support for increased predator protection as the ultimate cause of increased home range size in allied males. Rather, perhaps allied males must range farther to profit from shared copulations or increased foraging competition with one another. If so, an increase in home range is merely a product of alliance formation, not the purpose.

When examining sexual dimorphism, female length varied from 92 % of male length (Fernandez and Hohn 1998; McFee et al. 2012) to 100 % of male length (Mead and Potter 1990; Hale et al. 2000). However, there was no pattern in the presence of sexual dimorphism between sites that had and had not documented male alliances. For example, similar levels of sexual dimorphism (92 to 94% of male length) were found between the Indian River Lagoon, Florida (McFee et al. 2012), the Texas coast (Fernandez and Hohn 1998), and Sarasota, Florida (Tolley et al. 1995), only the latter of which have male alliances (Owen et al. 2002). Similarly, no sexual dimorphism was found off the coast of North Carolina (Mead and Potter 1990) where no alliances have been noted or in *Tursiops aduncus* off the Eastern coast of Australia (Hale et al. 2000), where stable male alliances exist (Wiszniewski et al. 2012). Body mass was only available for three study sites (Indian River Lagoon, Natal, South Africa, and Sarasota, Florida), and as such, these three locations were compared separately. Reduced sexual dimorphism (89 % of male mass) was found in dolphins off the coast of Natal, Africa (Cockcroft and Ross 1990), but more extreme dimorphism was found in both the Indian River Lagoon, Florida (68% of male mass; McFee et al. 2012), which lacks alliances, and in Sarasota, Florida (75 % of male mass; Read et al. 1993), where males are typically allied (Owen et al. 2002). See Table 3 for a full description of sexual dimorphism by study sites. Though more current documentation is needed, particularly regarding intersexual differences in body mass, the amount of variation in sexual dimorphism across sites that lack and possess male alliances suggest that sexual dimorphism is not a driving force behind alliance formation.

Conclusion

Of those variables analyzed, population density was most predictive of male alliance formation, with most study sites supporting male alliances skewed towards high dolphin

densities and those without alliances with densities typically less than 1.30 dolphins/km². The one exception to this trend, Bahama Bank, Bahamas, experienced a recent decline in the population; using the best prior estimate resulted in a density of 1.20 dolphins/km², a statistic in line with other allied field sites (Fearnbach et al. 2012). In addition, though summer abundance was used to calculate population density within the Indian River Lagoon, extreme seasonal variation exists within the population (0.39-1.41 dolphins/km²; Durden et al. 2011). As such, greater insight as to the social structure of those individuals is warranted. Presumably, as population density exceeds 1 dolphin/km² male-male encounters become frequent enough to warrant alliance formation, though focal follows quantifying male encounter rates should be used to verify this. The rate at which males encounter cycling females also appear to play a role in whether males form alliances, as the two populations with documented alliances also maintained the highest inter-birth intervals. However, females endemic to New Zealand also appear to have long inter-birth intervals that do not result in increased male competition. In this sense, male competition and the operational sex ratio may not always correlate with one another. Instead, direct measurements, such as the level of male-male aggression, may be more useful in predicting alliance formation.

No support was found for the predation-protection hypothesis, though allied males appear to maintain larger home ranges than unallied conspecifics. However, if predation is not limiting unallied males from also extending their home ranges in search of available females, perhaps larger home ranges are necessary for allied males to benefit from sharing consortships or increased food competition. The use of sexual dimorphism to predict alliance formation also lacked support, as both study sites that possessed and lacked male alliances showed similar variation in sexual dimorphism.

Future Considerations

Overall, increased documentation of morphology, demography, and life history parameters are needed to make meaningful comparisons between populations. Increased male-male competition seems to best predict alliance formation. As such, greater research is needed to define what parameters drive male-male competition. Suggestions include examining the temporal and spatial distribution of receptive females within populations as an indirect measure of male competition, as well as direct quantification of male aggression within and across study sites.

Acknowledgements

I would like to thank the Elizabeth Ordway Dunn Foundation, the UNF Coastal Biology Flagship Program, the UNF Environmental Center, and the San Marco Rotary Club for their financial support.

Table 1. Comparison of the population density and male social complexity across study sites world-wide. Study sites in which alliances are present are shaded.

Study Location	Population Density (km ²)	Male Social Complexity
Moray Firth, Scotland _A	0.02	No male alliances
Adriatic Sea _B	0.17	No recorded male alliances*
Marlborough Sound, New Zealand _C	0.24	No recorded male alliances*
Indian River Lagoon _D	0.39	No recorded male alliances*
Bay of Islands, New Zealand _E	0.52	No male alliances
Bahama Bank, Bahamas _F	0.60	First-order alliances
Shannon Estuary, Ireland _G	0.93	No recorded male alliances*
Doubtful Sound, New Zealand _H	0.78	No male alliances
Sarasota, Florida _I	1.30	First-order alliances
Port Stephens, Australia _J	1.40	First-order alliances
Shark Bay, Australia _K	2.40	Second-order alliances
St. Johns River, Jacksonville, Florida _L	6.76	Second-order alliances

* Indicates populations that lack social structure analysis

_AWilson et al.1997, 1999; _BBearzi et al. 1997; _CMerriman et al. 2009; _DSummer abundance from Durden et al. 2011; _ETezanos-Pinto 2009; _FFearnbach et al. 2012; _GIngram and Rogan 2002; Englund et al. 2007; _HLusseau et al. 2003; _IWells 2013; _JSummer abundance from Möller et al. 2002; _KWatson-Capps 2005; _LPresent study (Summer abundance of 250 dolphins over an approximately 37 km² field site)

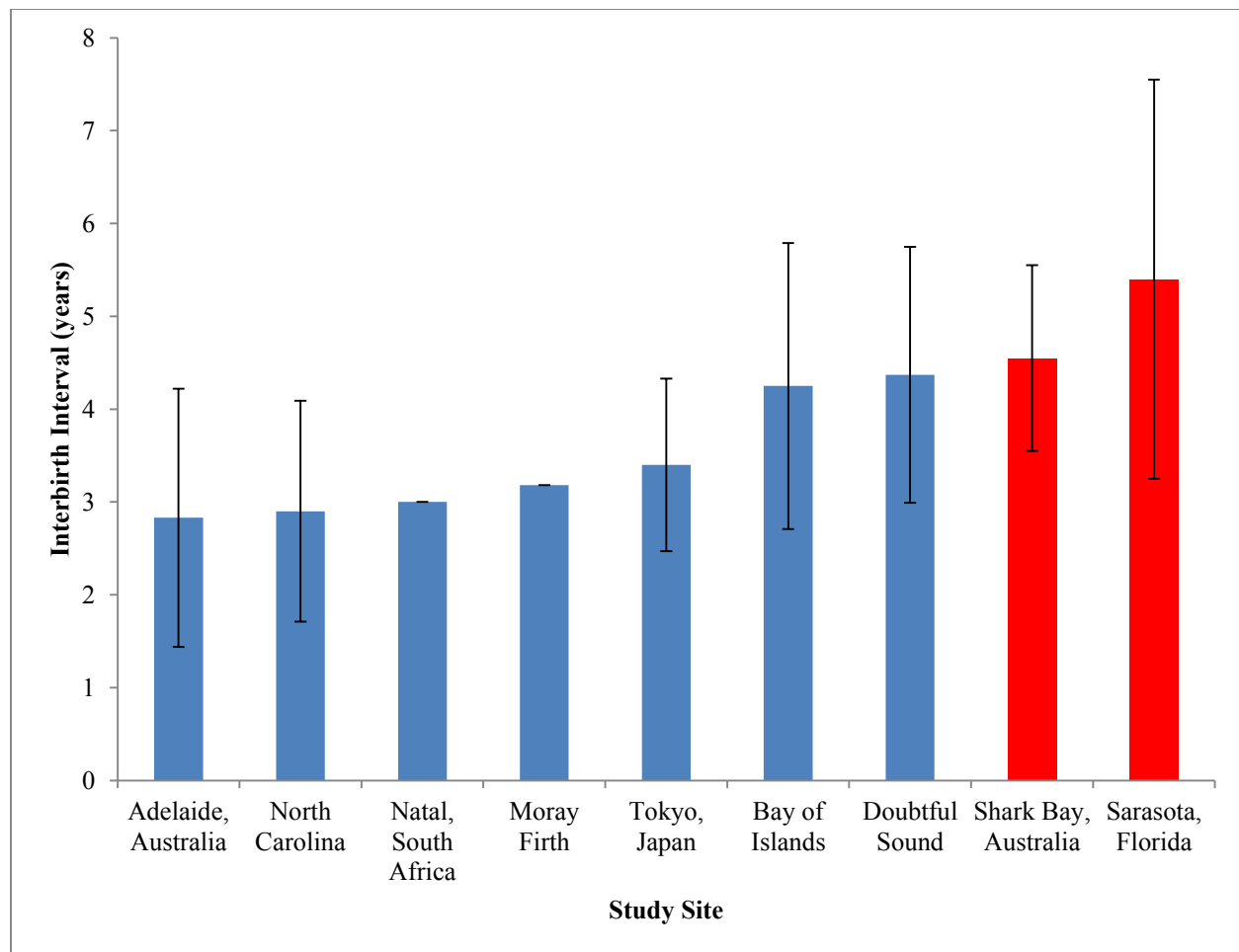


Figure 1. Mean and standard deviation of inter-birth intervals for available study sites. Study sites that support male alliances are noted in red. Data presented from: Adelaide, Australia (Steiner and Bossley 2008), North Carolina (Thayer 2008), Natal, South Africa (Cockcroft and Ross 1990), Moray Firth, Scotland (Mitcheson 2008), Tokyo, Japan (Kogi et al. 2004), Bay of Islands, New Zealand (Tezanos-Pinto 2009), Doubtful Sound, New Zealand (weighted IBI from the work of Henderson et al. 2014), Shark Bay, Australia (Mann et al. 2000), and Sarasota, Florida (Wells 1993).

Table 2. Predation rate as measured by the proportion of shark bites across populations. Study sites that support male alliances are highlighted.

Study Location	Predation (Proportion of population with shark bites)	Male Social Complexity
Moray Firth, Scotland _A	0.00%	No male alliances
Adriatic Sea _B	0.00%	No recorded male alliances*
Adelaide, Australia _C	0.50%	No recorded male alliances*
Bahama Bank, Bahamas _D	1.76%	First-order alliances
Texas Coast _E	2.00%	No recorded male alliances*
Natal, South Africa _F	10.34%	No recorded male alliances*
Sarasota, Florida _H	21.90% _I	First-order alliances
Marineland, Florida _G	22.73%	Possibly Indian River Lagoon individuals, whom have no recorded male alliances*
Moreton Bay, Australia _I	36.60%	No recorded male alliances*
Shark Bay, Australia _J	74.20% _I	Second-order alliances

*Indicates populations that lack social structure analysis

_IDenotes statistics refer to the adult population only

_AWilson 1995; _BBearzi et al. 1997; _CSteiner and Bossley 2008; _DFearnbach et al. 2011; _EFertl 1994; _FCockcroft et al. 1989; _GWood et al. 1970; _HWells et al. 1987; _ICorkeron et al. 1987; _JHeithaus 2001

Table 3. Length and mass measurements of male and female bottlenose dolphins across study sites, with the proportion of female to male length/mass noted. Study sites at which male alliances have been recorded are highlighted.

Study Location	Length (cm)	Percentage of Male	Mass (kg)	Percentage of Male
Texas Coast ^{A*}	Male: 268 Female: 247	92		
Indian River Lagoon, Florida ^{B*}	Male: 258 Female: 240	93	Male: 277 Female: 188	68
Sarasota, Florida	Male: 266 Female: 250 ^C	94	Male: 259 Female: 194 ^D	75
Natal, South Africa ^{E*}	Male: 246 Female: 240	98	Male: 187 Female: 167	89
Gulf of Mexico ^{F*}	Male: 255 Female: 250	98		
Eastern Australia ^G	<i>T. truncatus</i> Male: 283 Female: 279 (0.99) <i>T. aduncus</i> Male: 230 Female: 229	99 100		
North Carolina ^{H*}	Male: 250 Female: 250	100		

*Indicates populations that lack social structure analysis

^AFernandez and Hohn 1998; ^BMcFee et al. 2012; ^CTolley et al. 1995; ^DRead et al. 1993;

^ECockcroft and Ross 1990; ^FMattson et al. 2006; ^GHale et al. 2000; ^HMead and Potter 1990

Chapter 3

Quantification of seasonal aggression in bottlenose dolphins (*Tursiops truncatus*) through the use of tooth rakes

Abstract

Intraspecific competition is prominent within group-living species in a variety of contexts, particularly in competition for mates and between potential mates, and is often expressed as aggression. Here we use tooth rake marks as a proxy for conspecific aggression in bottlenose dolphins (*Tursiops truncatus*) to document seasonal trends in aggression across the sexes (female [n=96] vs. unknown sex [n=177, including 10 known males]) and males of differing mating strategies (allied [n=28] vs. unallied [n=149]). A larger proportion of both sexes were predicted to have new rake marks in the breeding season, consistent with intra-sexual male competition and coercive mating. Additionally, a greater proportion of allied males were predicted to have new rake marks outside the breeding due to intra-alliance aggression. Data was collected in the St. Johns River, Jacksonville, Florida, through weekly boat-based photo-identification surveys. High quality photographs (n=2351) from March 2011-February 2012 were analyzed for the presence and extent of rakes. Rake marks were categorized as new, obvious, or faint and ranked for extensive coverage (> 50% of a body part) for each of seven body parts. A condensed score was assigned to each individual within each season (spring, summer, autumn, winter, breeding season, non-breeding season) and comparisons were made using Chi Square goodness of fit tests. Contrary to my predictions, both unknown sex and female new rake mark presence peaked in the non-breeding season (p=0.007). A significantly

greater proportion of unknown sex individuals had new rake marks relative to females across all seasons ($p < 0.05$). No differences were found in rake mark attributes between allied and unallied individuals. Together, this suggests male-male competition is a driving force behind conspecific aggression in bottlenose dolphins and that male-delivered aggression may occur outside the context of breeding. Explanations include the possibility of increased socio-sexual behavior and/or anovulatory cycling within the winter.

Introduction

Intraspecific conflict can arise in many contexts: between possible mates (Smuts and Smuts 1993), between competitors for mates (Darwin 1871; Trivers 1972; Clutton-Brock and Vincent 1991), between parents and offspring (Trivers 1974), or between conspecifics in competition for resources, such as food, territory, or rank (Huntingford and Turner 1987). Group-living species, in particular, face increased potential for conflict when making decisions regarding activity choice, travel direction, and group composition (Conradt and Roper 2000; King and Cowlishaw 2009). Several energetically inexpensive mechanisms serve to avoid conflict, including the use of sensory cues (Arnott and Elwood 2009), stable dominance hierarchies (Heitor et al. 2006), or sociosexual contact (Palagi et al. 2006). However, when these measures fail, aggression often results from conflict between conspecifics, with the players governed by who competes most heavily for resources, including mates. In this way, the mating system plays a large role in dictating whether aggression occurs between the sexes or within one sex.

Intrasexual competition

Intrasexual competition for mates is typically strongest within the sex that makes less parental investment (Trivers 1972; Clutton-Brock and Vincent 1991), which in the vast majority of mammalian species, is the male sex (Clutton-Brock 1991). Reduced investment in parental care allows males to attain greater potential rates of reproduction than females (Clutton-Brock and Vincent 1991). This, in turn, results in an operational sex ratio skewed towards breeding males (Emlen and Oring 1977), which only increases breeding competition and results in greater male variance in reproductive success (Trivers 1972; Emlen and Oring 1977). The predominance of male-male competition and male sexual selection implies that male-male aggression might be a more common occurrence than intersexual or female-female aggression. Male competition may be direct, such as male-male combat, or indirect, via sperm competition or infanticide.

However, the competitive sex is not always male. Recent work suggests that females of some species regularly compete for resources critical to reproduction (Clutton-Brock et al. 2006; Stockley and Bro-Jørgensen 2011; Rosvall 2011), particularly food resources (Wrangham 1980; Sterck et al. 1997). For example, female meerkats compete for high rank and the associated breeding opportunities and are considered the more aggressive sex (Clutton-Brock et al. 2006). Female-female competition is also seen in female chimpanzees and spotted hyenas, where high social rank is associated with improved diet and increased reproductive success (Holekamp et al. 1996; Pusey et al. 1997; Murray et al. 2006).

Intersexual competition

Because females and males are governed by different socioecological pressures, they often pursue different reproductive strategies that result in conflict. For example, while males typically benefit by mating with many females, females might benefit by exercising mate choice

in favor of a superior male (Clutton-Brock and McAuliffe 2009) or delaying mating until ecological conditions are best, as reproduction is often timed around environmental cues (Loe et al. 2005) or the mothers' body condition (Bêty et al. 2003). Sometimes this conflict can be resolved when males offer material benefits to females, such as food or protection (Gray 1997; Cothran et al. 2012). However, because these concessions are costly to males, they may overcome them through mate coercion (Smuts and Smuts 1993). Male sexual aggression is thought to be most common in gregarious and polygynous species in which females do not form long-term bonds with males (Smuts and Smuts 1993). Smuts and Smuts (1993) define sexual coercion by three criteria: 1) Aggression intensifies in reproductive contexts, 2) Increased aggression should result in increased reproductive success, and 3) Coercion must come at a cost to females. Mate coercion is observed across a wide variety of taxa, from the fruit fly (Seeley and Dukas 2011) to the great apes (Muller et al. 2009), but often lacks empirical evidence. However, recent work suggests mate coercion can be quantified. Muller (2007) found that male chimpanzees at Kanyawara have greater mating success with females to whom they direct aggression and they specifically direct their aggression towards parous females, whom experience increased cortisol levels in response. Similarly, after aggressive herding during male takeovers in hamadryas baboons, female inter-birth intervals increased by more than three months, demonstrating a clear cost to female fitness (Polo et al. 2014).

Aggression in bottlenose dolphins

Bottlenose dolphins live within a fission-fusion society in which group size and composition change fluidly across time. Social bonds are typically strongest within the sexes (Tsai and Mann 2013), with females forming loose bonds based around reproductive status (Wells et al. 1987; Smolker et al. 1992; Möller et al. 2006; Möller and Harcourt 2008).

However, males typically utilize one of two strategies. Male dolphins may take a solitary strategy and individually consort females for breeding opportunities or they may form strong bonds with one or two other males in the shape of an alliance to cooperatively herd females for breeding (Connor et al. 1992*a,b*). Increased male-male competition, measured via population density and/or the operational sex ratio, is hypothesized to be predictive of alliance formation (Connor et al. 2000; Whitehead and Connor 2005; Chapter 2). However, significant variation in social structure exists, in that not all populations of bottlenose dolphins utilize alliances (Lusseau et al. 2003; Eisfeld and Robinson 2004), alliances may or may not form multiple levels (Connor et al. 1992*a,b*; Chapter 1), and males within a population may utilize different strategies (Wiszniewski et al. 2012).

The distribution of aggression among male and female bottlenose dolphins has not been thoroughly explored across study sites or among populations with different mating strategies. Previous studies suggest that males are the more agonistic sex (Samuels and Gifford 1997; Scott et al. 2005), while females have been found to be extremely tolerant, both in and out of the wild (Samuels and Gifford 1997; Scott et al. 2005). However, the proportion of male aggression directed towards males versus females is likely variable across time and space as a factor of community social structure and population demographics.

Though bottlenose dolphins express aggression through various means, tooth rake marks, thin, parallel marks on the surface of the skin (Samuels and Gifford 1997), are perhaps the most easily quantified. However, only two studies to date have used rake marks as a proxy for aggressive interactions in bottlenose dolphins (Scott et al. 2005; Marley et al. 2013). Both studies found support for male-male aggression through significantly greater male rake mark presence and/or coverage (Scott et al. 2005; Marley et al. 2013), and Scott et al. (2005) found

support for aggression via coercive mating, as cycling females had significantly more new rake marks than their non-cycling counterparts (Scott et al. 2005). However, neither study examined the effect of seasonality or the effect of differing male mating strategies, such as alliance formation, on aggression.

Here, we examine the distribution of aggression across seasons, sexes, and mating strategies in a resident community of bottlenose dolphins in Jacksonville, Florida, U.S.A., using rake marks as a proxy for agonistic interactions. We delineate between several working hypotheses presented in Table 1. For example, if the majority of male-female aggressive interactions occur as a result of coercive mating, we would expect the proportion of females with rake marks to peak during the summer breeding season. We also may expect elevated male-male aggression to occur at this time in conflict over females. However, the hypothesis that male competition is a result of intra-alliance conflict, as suggested by Connor and Smolker (1995), would yield greater male-male aggression within allied males outside of the breeding season, when alliance members may compete for herding partners. In this sense, peaks of aggression outside of the breeding season could either represent year-round cycling or intra-alliance competition, while peaks of aggression within the breeding season might represent male-male conflict and coercive mating (see Table 1). Documentation of seasonal aggression is the first step in distinguishing between these scenarios.

Methods

Field Methods

The St. Johns River (SJR) is a large blackwater river that drains into the Atlantic Ocean at Mayport Inlet (N30.39904, W-81.39396) approximately 40 km east of downtown Jacksonville

(N30.31479, W-81.62987). It is characterized by brackish water, depths of up to 18m within dredging zones, and extensive boat traffic (DeMort 1991; Benke and Cushing 2005). Little is known about the prevalence of agonistic behavior in wild bottlenose dolphins in general, but the collection of baseline aggression data within the SJR, a rapidly expanding port of trade, will be useful in gauging the anthropogenic impact development has upon these estuarine dolphins. Data collection has taken place through weekly photo-identification surveys from March 2011-present along a fixed 40 km transect from Mayport Inlet to downtown Jacksonville, with the direction of travel alternating each week. Researchers conducted surveys from either a 6.4m Carolina Skiff or a 7.9 Twin Vee Catamaran and traveled at a consistent speed of 10-12 km/hr until dolphins were sighted, at which time the vessel approached and maintained proximity to the group until all individuals were photographed, typically over a span of 5-30 minutes. The dorsal fins of all dolphins within the group (defined using a conservative 10m-chain rule as in Smolker et al. 1992) were photographed using a professional grade digital camera with 400 mm telephoto lens. Behavioral and environmental variables were recorded in addition to group composition for each sighting. All data were collected under the authorization of NOAA Fisheries GA LOC 14157 and UNF IACUC 10-013.

Data Analysis

Photographs were processed using standard photo-identification techniques (Mazzoil et al. 2004). The best photograph of each individual within each sighting was chosen and compared to a master catalogue for identification, which was based upon the unique shape and notch pattern of the leading and trailing edge of each dolphin's dorsal fin. Distinctive individuals for which matches were not found were added to the catalogue as new individuals. Good quality photographs of non-calf bottlenose dolphins over the period of March 2011-

February 2012 were then examined for dorsal surface rake marks. For each photo processed, the dolphin body was divided into seven sections: head, anterior body, dorsal fin, mid flank, anterior peduncle, posterior peduncle, and fluke. Each body section was then scored for visibility as either greater than or less than seventy-five percent visible. For example, a fully visible ($> 75\%$ visible) dorsal fin would score as a 1, while a partially visible fin ($< 75\%$) would score as 0.5. Next, each body section was scored for the presence (1) or absence (0) of rake marks. Rake marks were further classified into three categories of recency: faint (faded white parallel rake marks), obvious (gray clearly visible rake marks), and new (broken skin) (See Figure 1). In addition, the coverage of rake marks for each visible body section was also scored as greater than fifty percent (1) or less than fifty percent (0). Photos were then divided into seasons as follows: Spring (March-May), Summer (June-August), Autumn (September-November), Winter (December-February). The sample size of individuals varied across seasons due to local emigration patterns (Spring: $n = 121$, Summer: $n = 253$, Fall: $n = 137$, Winter: $n = 125$, Non-breeding Season: $n = 167$, Breeding Season: $n = 268$). For analyses regarding the timing of aggression relative to breeding, the breeding season was defined as April-September based on the timing of local births (Urian et al. 1996), which due to an 11.5-12 month gestation period, coincide with the breeding season. Within each season all photos of each individual were consolidated into a single score for each body part using the most recent rake mark type and the most extensive coverage noted within the time period, as seen in Scott et al. (2005).

Although the current study was focused on one year of data, sex determination was based on all available sighting data collected from March 2011 – August 2014. Each individual dolphin ($n = 273$) was categorized as a female or unknown sex. Poor water clarity inhibits frequent direct observation of the genitals within the SJR. Instead, individuals were categorized as female if

they had been sighted with a calf in infant position (Mann et al. 2000) on at least two sightings ($n = 96$). In addition, to examine patterns of male aggression towards estrous females, females were retrospectively divided into cycling vs. non-cycling based upon the birth of a calf the following year ($n = 21$ cycling females). All other individuals were categorized within the unknown sex category ($n = 177$), which included several known males ($n=10$), behaviorally-presumed males, and non-reproductive females. Known males were included in the unknown sex category with presumed males to increase sample size. Due to our inability to sex non-reproductive females, the unknown category is probably confounded by approximately 40 true females, given the assumption that the sex ratio of our sample is 1:1. Unknown sex individuals were further divided into allied vs. unallied based on two years' of association data (March 2011-March 2013; Chapter 1). Associations were defined using the half-weight index, where $HWI = 2N_T/(N_A+N_B)$, where N_T is the total number of joint sightings of individuals A and B and N_A and N_B are the total number of sightings for each individual, respectively. Allied "males" ($n = 28$) fit the following criteria: 1) Were reciprocal top associates (or second top associates with a half weight index within 20% of the top association, and 2) Maintained above random associations, greater than a conservative half-weight index of 0.80, criteria adapted from the methods of Connor et al. (1992b, 1999), Möller et al. (2001), Parsons et al. (2003), and Wiszniewski et al. (2012). These criteria exclude all known females (female maximum HWI in the SJR: $\bar{x} = 0.29 \pm 0.10$), as well as the lower proportion of unknown sex individuals, which may be non-reproductive females or immature males (unknown sex maximum HWI: $\bar{x} = 0.61 \pm 0.26$). Seasonal, sex, and alliance status comparisons of rake mark attributes were then calculated using Chi Square goodness of fit tests. Statistical significance was defined as $p \leq 0.050$ while trends were defined as $p < 0.110$.

Results

In total, 2,351 photos were analyzed for the presence and extent of rake marks, with an average of three body parts visible ($\bar{x} = 3.050 \pm 1.014$) across 273 unique individuals. Over the course of one year an overwhelming proportion of individuals (97.07 %) had one or more visible rake marks. There was no significant difference in rake mark presence across seasons, though there was a trend of rake mark presence increasing in the winter months ($p = 0.065$). There was, however, a significant seasonal difference in the presence of new rake marks ($p = 0.026$), with peaks in the proportion of individuals with new rake marks in winter and spring (Figure 2). New rakes were also observed on a significantly greater proportion of individuals in the non-breeding season than the breeding season ($p = 0.007$). Extensive coverage was also variable across the four seasons ($p = 0.003$), with a larger proportion of individuals exhibiting extensive coverage in the winter and summer relative to the spring (Figure 3). When consolidating the data into the breeding and non-breeding season, there was no seasonal difference in the proportion of individuals with extensive rake mark coverage.

Females

Female rake mark presence in general was constant across seasons. New rake mark presence was also stable across the four seasons. However, when the seasons were condensed into the breeding and non-breeding season, twice the proportion of females had new rake marks in the non-breeding season compared to the breeding season ($p = 0.012$; Table 2). In addition, females exhibited significantly different coverage across the four seasons, with peaks in summer and winter ($p = 0.037$; Figure 4); this pattern was lost when the seasons were condensed. There was no difference in the proportion of cycling females vs. non-cycling females that had rake marks or new rake marks in the breeding season. However, there was a trend towards a smaller

proportion of cycling females having extensive coverage in the summer ($p = 0.055$) and within the breeding season ($p = 0.078$).

Unknown Sex Individuals

The proportion of individuals with rake marks (all categories combined) was consistent across seasons. There was, however, a trend towards a larger proportion of unknown sex individuals having new rake marks ($p = 0.108$) within the winter, though this pattern was lost when the seasons were combined into breeding and non-breeding seasons. In addition, there was a trend towards reduced extensive coverage in the spring ($p = 0.052$; Figure 4), though no difference was seen in extensive coverage between the breeding and non-breeding season.

Sex Comparisons

When examining sex differences, fewer females than unknown sex individuals had rake marks within the summer and fall, as well as within both the breeding and non-breeding seasons (Table 2). Across all seasons significantly fewer females than unknown sex individuals had new rake marks (Figure 5). In addition, significantly fewer females had extensive coverage compared to unknowns in all seasons ($p < 0.05$) except winter, where there were no sex differences (Figure 4).

Alliance Comparisons

Allied males had no variation in rake mark presence, recency, or coverage across seasons. Unallied males experienced no variation in rake mark presence or recency, but significant differences in extensive coverage ($p = 0.018$), with reduced extensive coverage in the spring, though this pattern did not hold when seasons were combined. Seasonal comparison of allied to unallied males failed to reveal any differences in rake mark attributes.

Discussion

Overall, our intra-sexual competition hypothesis was partially supported, as a greater proportion of unknown sex individuals had rake marks relative to females, though our seasonal predictions were not upheld. The remaining hypotheses (intra-alliance aggression and sexual coercion) lacked support.

Intra-sexual Competition

True to our first prediction for the intra-sexual male competition hypothesis, a greater proportion of unknown sex individuals in comparison to females had new rake marks across all seasons, as well as greater rake mark prevalence and coverage within some seasons. This aligns with the work of Scott et al. (2005) and Marley et al. (2013) in which males had greater prevalence of rake marks and/or greater body coverage. In addition, Scott et al. (2005) found that 89 % of all males and 82 % of adult females had rake marks. Relative to this work, the SJR community has an elevated proportion of both unknown sex individuals (99 %) and adult females (95 %) with rake marks. Across study sites, the greater prevalence of rake marks within unknown sex individuals/males relative to females implies the importance of intra-sexual competition and increased male-male aggression. In addition, increased rake mark presence relative to Shark Bay indicates that SJR males may have heightened aggression levels, perhaps due to elevated stress levels and altered behavioral patterns as a factor of increased anthropogenic impact within the SJR (Constantine et al. 2004; Romano et al. 2004; Rolland et al. 2012).

However, there was no clear temporal pattern in rake mark presence, recency, or coverage of unknown sex individuals, despite our prediction that male-male aggression would

peak during the summer breeding season. Rake mark presence was constant across seasons, while there was a trend towards new rake mark presence ($p = 0.108$) and coverage ($p = 0.053$) being greatest in winter. These observations reject the possibility of breeding related aggression and lack an obvious explanation. It cannot be ruled out that females are cycling outside of the breeding season, though this cycling is unlikely conceptive, given the diffuse summer timing of births in the SJR. Rather, females may be anovulatory cycling to assess male quality prior to the breeding season, as suggested by Connor et al. (1996). In addition, similar instances of non-conceptive mating have been noted in several species including blue monkeys (Pazol 2003), hamadryas baboons (Zinner and Deschner 2000), and lions (Packer and Pusey 1983) as a mechanism to reduce male infanticide. A more likely possibility is that greater social-sexual behavior occurs in the winter months and males are accumulating rake marks by these means, rather than in a reproductive context. This was supported by our observation that groups comprised of only unknown sex individuals were documented to socialize more in the winter than all other seasons (Gibson, unpublished data), as well as by preliminary analysis of seasonal associations between the sexes, as male-female maximum bonds peak during the summer (HWI $\bar{x} = 0.45 \pm 0.22$) and male-male maximum bonds peak during the winter (HWI $\bar{x} = 0.76 \pm 0.29$) (Gibson, unpublished data), suggesting male-male socio-sexual behavior is responsible for the observed winter peak in new rake marks.

Intra-alliance Conflict

We found no evidence for increased aggression within allied males relative to unallied males outside of the breeding season. Previous explanations of intra-alliance conflict included a testosterone spike prior to the breeding season, as seen in one captive dolphin (Schroeder and Keller 1989) or competition fueled by partner switching (Connor and Smolker 1995). However,

if females cycle continuously within the SJR population, there may not be a sufficient decrease in competition between alliances throughout the course of the year to allow males to test bonds within their alliances. In addition, only a portion (33%) of the SJR unknown sex population is known to form alliances, which may reduce the likelihood of partner switching. Alternatively, alliances within the SJR may be stable across years, as seen in Shark Bay, Australia, and Sarasota, Florida, where males are allied for decades or even lifetimes (Wells 1991*b*; Connor and Mann 2006).

Coercive Mating

Females did show a seasonal pattern in rake accumulation; however, it was not centered in the breeding season. Instead, twice the proportion of females received new rakes outside of the summer breeding season, with the highest proportion of new rakes within the winter and spring. In addition, cycling females were not found to receive greater aggression than non-cycling females within the breeding season. This suggests that male-female aggression is not directed towards females in the context of breeding but prior to the breeding season. In addition to the possibility of anovulatory cycling, this introduces the possibility that males may be intimidating females prior to entering oestrus in an effort to increase female cooperation in the future, as suggested by Goodall (1986) of chimpanzees. However, in a study by Stumpf and Boesch (2010), male chimpanzees' aggression prior to oestrus was not linked to future female cooperation. This suggests male aggression may serve other functions, such as maintaining dominance (Campbell 2003).

In addition, direct coercion in chimpanzees has been noted as the strategy of unpreferred males (Muller et al. 2009; Stumpf and Boesch 2010), while high ranking males typically herded

and mate-guarded females (Watts 1998; Muller et al. 2009). Though no differences were found in rake mark accumulation between allied and unallied males, they may be delivering aggression towards females differently. Focal follow data documenting the consortships of allied males in the SJR may reveal whether males of different strategies utilize aggression towards females differently. Finally, increased male-female aggression may be a byproduct of increased male overall aggression centered around the non-breeding season, perhaps due to an increase in testosterone, as seen in Schroeder and Keller (1989).

Conclusions

Overall, bottlenose dolphin aggression within the SJR was elevated outside of the breeding season and directed towards both sexes. Increased aggression at this time could be a result of increased male testosterone and resultant socio-sexual behavior directed towards males and females, as well as an indicator of anovulatory cycling within SJR females. Increased behavioral observations of male-male and mixed sex groups outside of the breeding season are necessary to determine the contexts in which aggression is used and its implications on male-male competition and bottlenose dolphin mating strategies.

Acknowledgements

I would like to acknowledge the Elizabeth Ordway Dunn Foundation, the UNF Coastal Biology Flagship Program, the UNF Environmental Center, and the San Marco Rotary Club for their financial support. Also, special thanks to Drs. Eric Johnson and Julie Avery for statistical assistance.

Table 1. Hypotheses regarding sex and seasonal patterns in rake mark presence. Note that hypotheses are non-mutually exclusive in nature.

Hypotheses	Predictions
Intra-sexual Male Competition	If male-male competition for mates is a driving factor in intraspecific aggression, we would expect a greater proportion of males to have a rake marks than females, with a peak in new rake marks within the breeding season.
Intra-alliance Conflict	If conflict between alliance partners is a source of aggression, we would expect a greater proportion of allied males than their unallied peers to exhibit new rake marks outside of the breeding season, when competition for herding partner is expected.
Coercive Mating	If coercive mating is a strategy utilized by this community, we would expect a larger proportion of females to have new rake marks in the summer breeding season compared to other months.

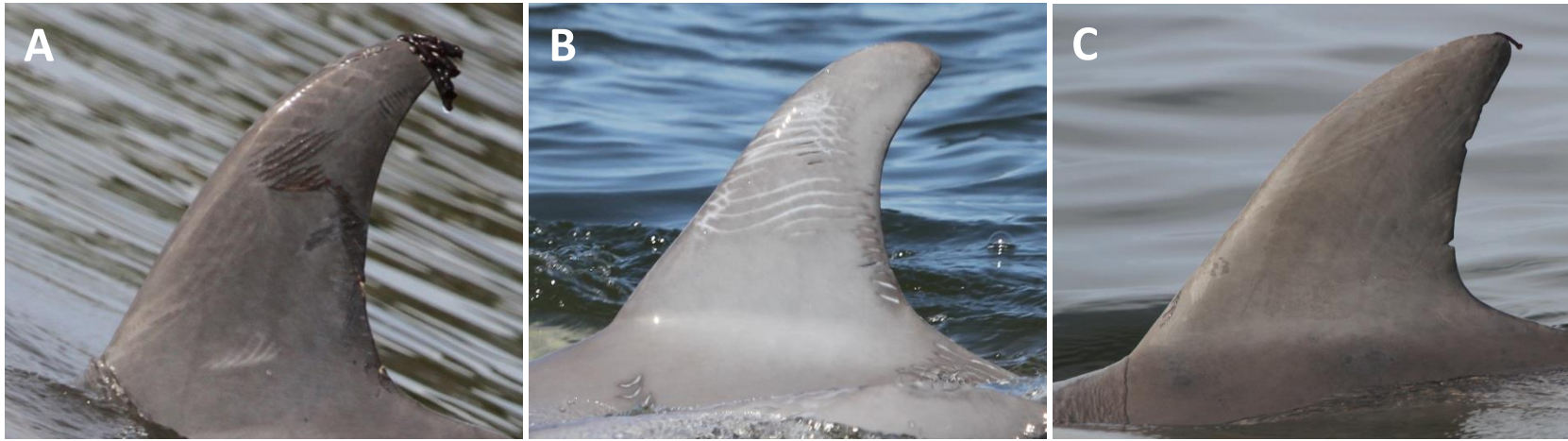


Figure 1. Rake marks were categorized by recency as A) new, B) obvious, and C) faint.

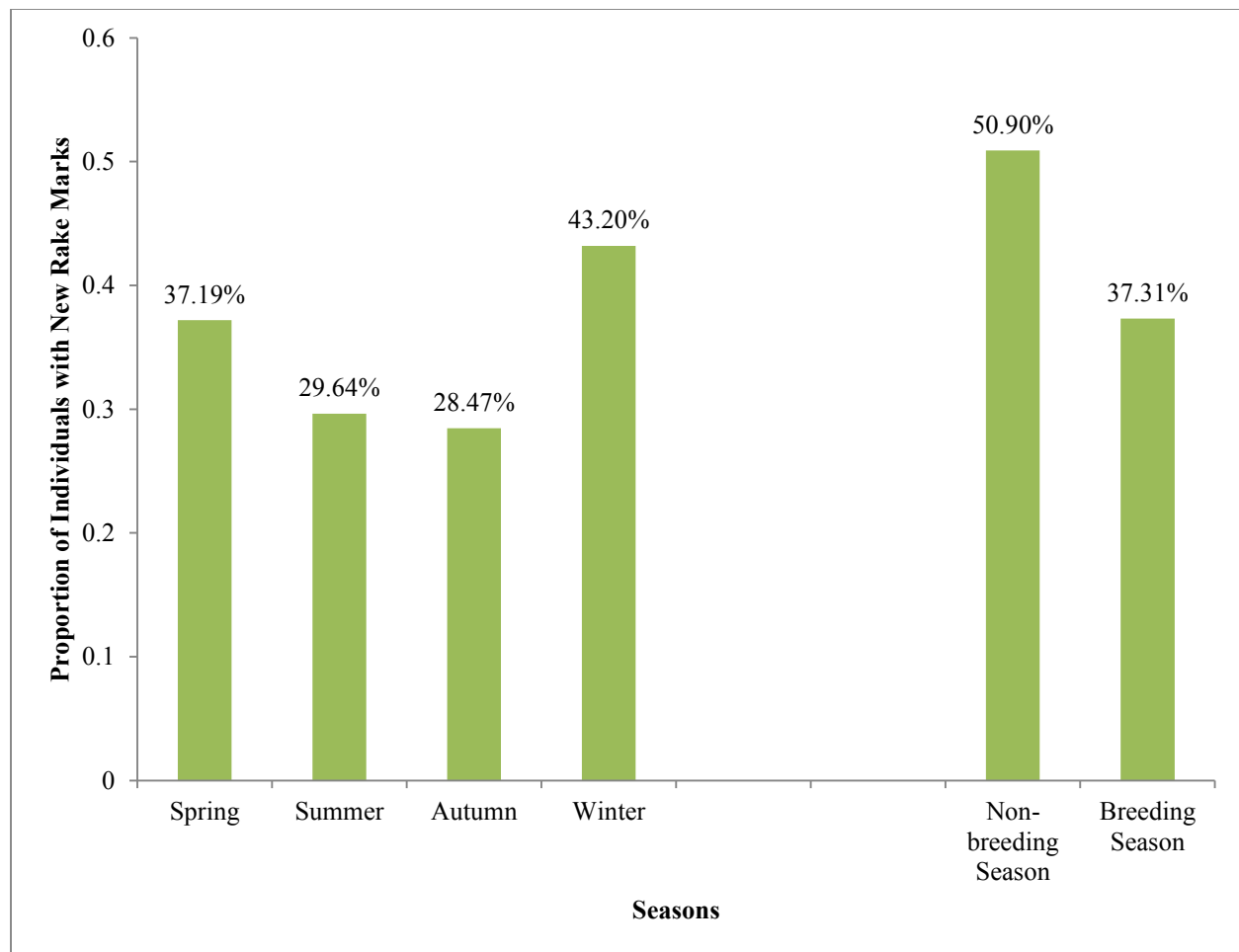


Figure 2. There was a significant difference in the presence of new rake marks both across the four seasons ($p = 0.026$) and between the breeding and non-breeding season ($p = 0.007$). The greatest proportion of new rake marks occurred in the non-breeding season, and more specifically in the winter and spring.

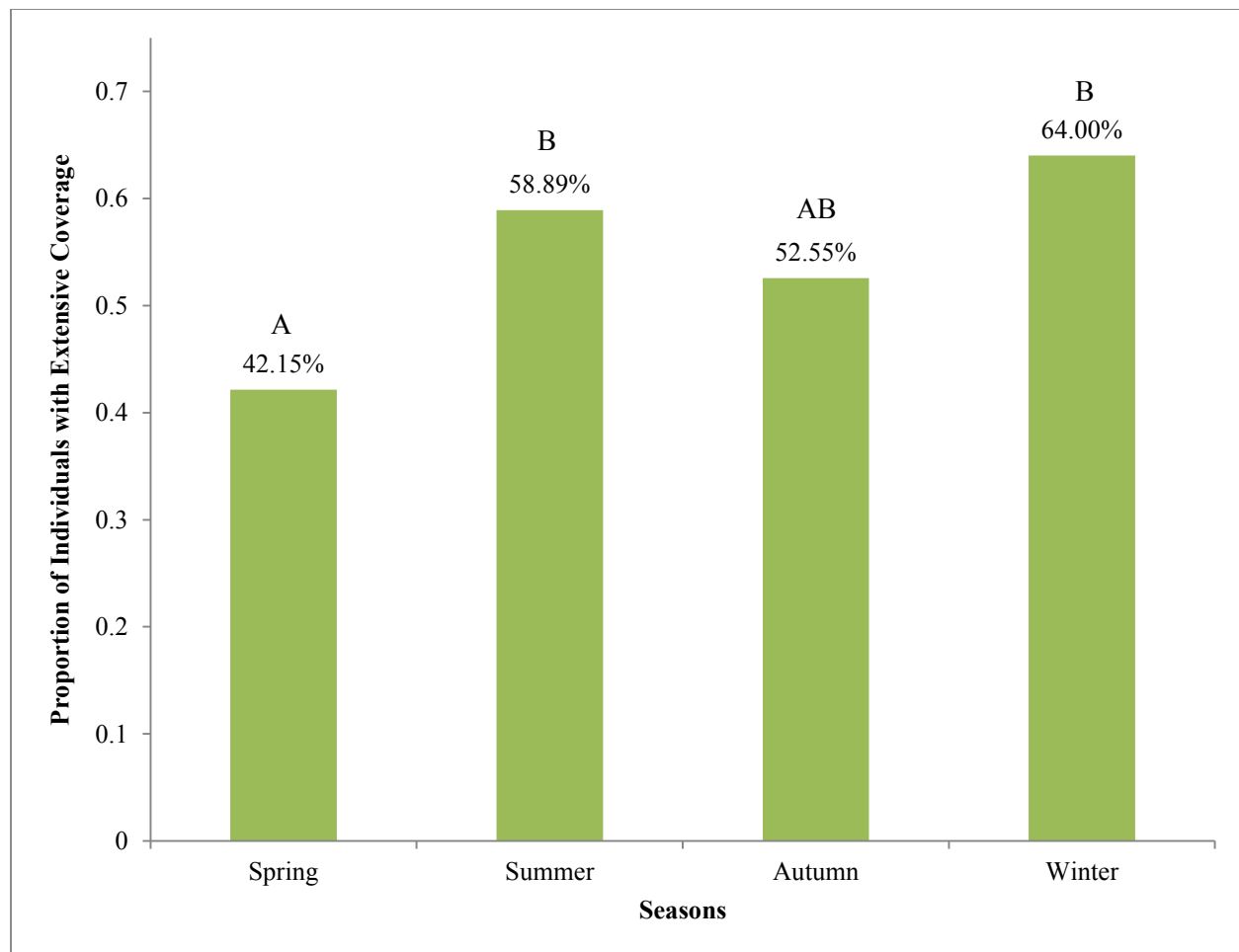


Figure 3. Extensive coverage, defined as rake mark coverage $\geq 50\%$ within a body section, was significantly different across seasons ($p = 0.003$), with winter and summer coverage significantly greater than in spring.

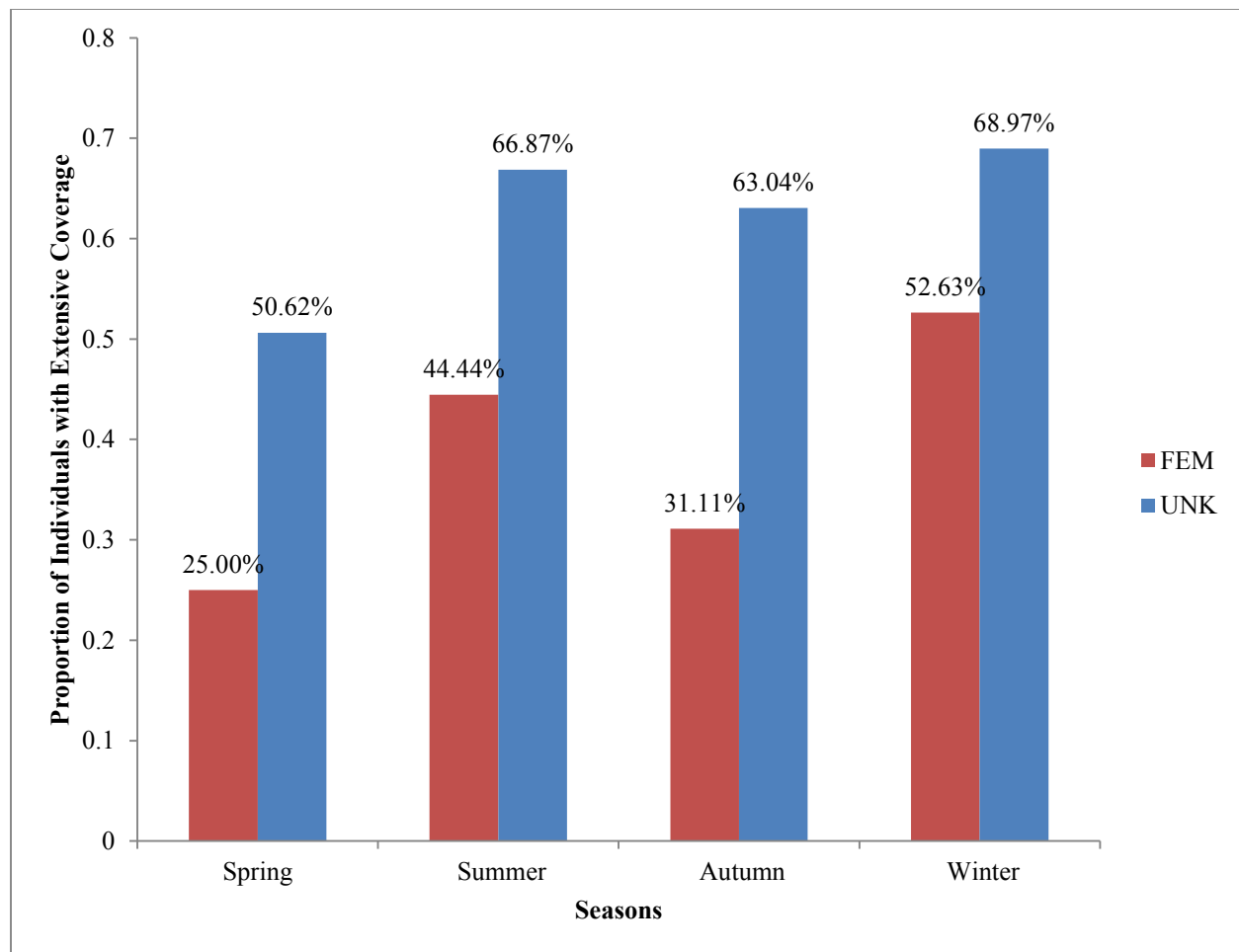


Figure 4. Female extensive coverage was significantly different across seasons ($p = 0.037$), with peaks in winter and summer, while unknown sex extensive coverage exhibited a trend ($p = 0.052$) towards decreased extensive coverage in the spring. A greater proportion of unknown sex individuals had extensive coverage in comparison to females in spring, summer, and fall ($p < 0.050$).

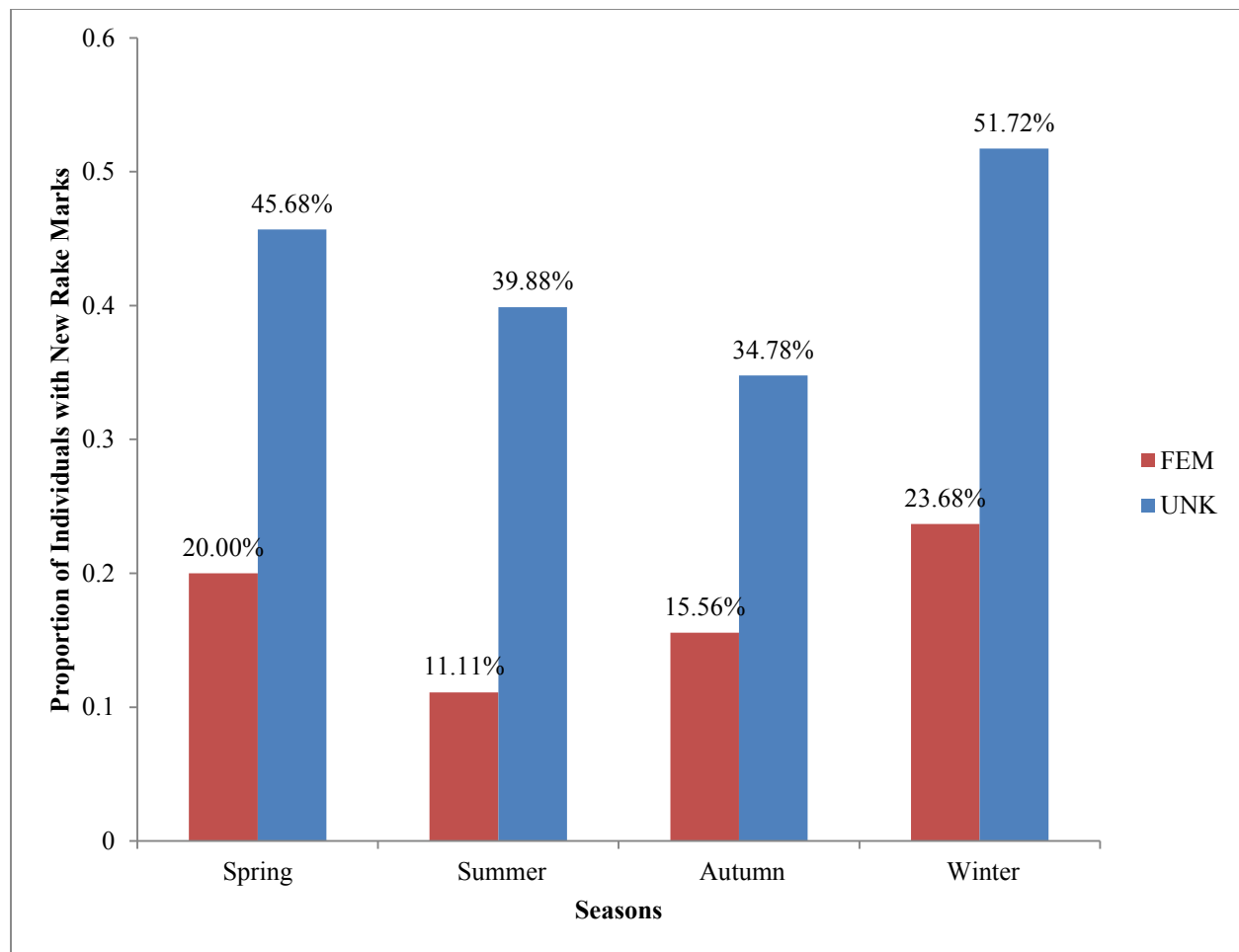


Figure 5. Across all seasons, a significantly greater proportion of unknown sex individuals had new rake marks compared to females ($p < 0.050$).

Table 2. A significantly smaller proportion of females had rake marks and new rake marks, as well as extensive coverage in comparison to unknown individuals in both the breeding and non-breeding seasons ($p < 0.050$).

	Breeding Season		Non-breeding Season	
	Females	Unknown sex	Females	Unknown sex
Rake Mark Presence	90.4%	97.1%	92.6%	100.0%
New Rake Marks	17.0%	48.3%	35.2%	58.4%
Extensive Coverage	47.9%	73.0%	51.9%	77.0%

References

- ALEXANDER, R.D. 1974. The evolution of social behavior. *Annual review of ecology and systematics*: 325-383.
- ANDERSSON, M. 1994. *Sexual selection*. Princeton University Press: Princeton, New Jersey.
- ARNOTT, G. AND R.W. ELWOOD. 2009. Assessment of fighting ability in animal contests. *Animal Behaviour* 77: 991-1004.
- AUGUSTO, J.F., P. RACHINAS-LOPES, AND M.E. DOS SANTOS. 2012. Social structure of the declining community of common bottlenose dolphins in the Sade Estuary, Portugal. *Journal of the Marine Biological Association of the United Kingdom* 92: 1773-1782.
- AURELI, F. ET AL. 2008. Fission-fusion dynamics. *Current Anthropology* 49: 627-654.
- BEARZI, G., G. NOTARBARTOLO-DI-SCIARA, AND E. POLITI. 1997. Social ecology of bottlenose dolphin in the Kvarneric (Northern Adriatic Sea). *Marine Mammal Science* 13: 650-668.
- BEJDER, L. D. FLETCHER, AND S. BRÄGER. 1998. A method for testing association patterns of social animals. *Animal Behaviour* 56: 719-725.
- BENKE, A. AND C. CUSHING. 2005. *Rivers of North America*. Elsevier/Academic Press, Boston, Massachusetts.
- BÊTY, J., G. GAUTHIER, AND J. GIROUX. 2003. Body condition, migration, and timing of reproduction in snow geese: a test of the condition-dependent model of optimal clutch size. *The American Naturalist* 162: 110-121.
- BOUVEROUX, T.H., AND J. MALLEFET. 2010. Social structure of bottlenose dolphins, *Tursiops truncatus*, in Panama City, Florida. *Journal of the Marine Biological Association of the United Kingdom* 90: 1685-1692.
- CADE, W. 1980. Alternative male reproductive behaviors. *Florida Entomologist* 63:30-45.
- CAIRNS, S. J. AND S. J. SCHWAGER. 1987. A comparison of association indices. *Animal Behaviour* 35: 1454-1469.
- CALDWELL, M. 2001. Social and genetic structure of bottlenose dolphin (*Tursiops truncatus*) in Jacksonville, Florida. PhD thesis, University of Miami, Coral Gables, Florida.
- CAMPBELL, C.J. 2003. Female-directed aggression in free-ranging *Ateles geoffroyi*. *International Journal of Primatology* 24: 223-237.
- CHAPMAN, C.A., AND L.J. CHAPMAN. 2000. Determinants of group size in primates: the importance of travel costs. Pages 24-41 *in* *On the move: how and why animals travel in groups* (S. Boinski and P.A. Garber, eds.). University of Chicago Press, Chicago.
- CLUTTON-BROCK ET AL. 2006. Intrasexual competition and sexual selection in cooperative mammals. *Nature* 444: 1065-1068.
- CLUTTON-BROCK, T.H. 1991. *The Evolution of Parental Care*. Princeton University Press, Princeton, New Jersey.
- CLUTTON-BROCK, T.H. AND A.C.J. VINCENT. 1991. Sexual selection and the potential reproductive rates of males and females. *Nature* 351: 58-60.
- CLUTTON-BROCK, T.H. AND K. MCAULIFFE. 2009. Female mate choice in mammals. *The Quarterly Review of Biology* 84: 3-27.
- COCKCROFT, V.G., G. CLIFF, AND G.J.B. ROSS. 1989. Shark predation on Indian Ocean bottlenose dolphins *Tursiops truncatus* off Natal, South Africa. *South African Journal of Zoology* 24: 305-310.

- COCKCROFT, V.G. AND G.B. ROSS. 1990. Age, growth, and reproduction of bottlenose dolphins *Tursiops truncatus* from the east coast of southern Africa. *Fishery Bulletin* 88: 289-302.
- CONNOR, R. AND N. VOLLMER. 2009. Sexual coercion in dolphin consortships: a comparison with chimpanzees. Pages 218-243 *in* sexual coercion in primates and humans: an evolutionary perspective on male aggression against females (M. Martin, and R.W. Wrangham, eds.). Harvard University Press, U.S.A.
- CONNOR, R., J.J. WATSON-CAPPS, W.B. SHERWIN, AND M. KRÜTZEN. 2011. A new level of complexity in the male alliance networks of Indian Ocean bottlenose dolphins (*Tursiops* sp.). *Biology Letters* 7: 623-626.
- CONNOR, R., R. SMOLKER, AND A. RICHARDS. 1992a. Dolphin alliances and coalitions. Pages 415-433 *in* Coalitions and alliances in humans and other animals (A. Harcourt and F. de Waal, eds.). Oxford University Press, New York, New York.
- CONNOR, R., R. SMOLKER, AND A. RICHARDS. 1992b. Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proceedings of the National Academy of Sciences of the United States of America* 89: 987-990.
- CONNOR, R., R. WELLS, J. MANN, AND A. READ. 2000. The bottlenose dolphin: social relationships in a fission-fusion society. Pages 91-124 *in* Cetacean societies: field studies of dolphins and whales (J. Mann, R. Connor, P. Tyack, and H. Whitehead, eds.). The University of Chicago Press, Chicago, Illinois.
- CONNOR, R.C. A.F. RICHARDS, R.A. SMOLKER, AND J. MANN. 1996. Patterns of female attractiveness in Indian Ocean bottlenose dolphins. *Behaviour* 133: 37-69.
- CONNOR, R.C. AND J. MANN. 2006. Social cognition in the wild: Machiavellian dolphins. Pages 329-367 *in* Rational Animals? (S. Hurley and M. Nudds, eds.) Oxford University Press, Oxford, New York.
- CONNOR, R.C. AND R.A. SMOLKER. 1995. Seasonal changes in the stability of male-male bonds in Indian Ocean bottlenose dolphins. *Aquatic Mammals* 21: 213-216.
- CONNOR, R.C., M.R. HEITHAUS, AND L.M. BARRE. 2001. Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance'. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 268: 263-267.
- CONNOR, R.C., M.R. HEITHAUS, AND L.M. BARRE. 1999. Superalliance of bottlenose dolphins. *Nature* 397: 571-572.
- CONRADT, L. AND T.J. ROPER. 2000. Activity synchrony and social cohesion: a fission-fusion model. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 267: 2213-2218.
- CONSTANTINE, R., D.H. BRUNTON, AND T. DENNIS. 2004. Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behavior. *Biological Conservation* 117: 299-307.
- CORKERON, P.J., R.J. MORRIS, AND M.M. BRYDEN. 1987. Interactions between bottlenose dolphins and sharks in Moreton Bay, Queensland. *Aquatic Mammals* 13: 109-113.
- COTHRAN, R.D., K. CHAPMAN, A.R. STIFF, AND R.A. RELYEA. 2012. "Cryptic" direct benefits of mate choice: choosy females experience reduced predation risk while in precopula. *Behavioral Ecology and Sociobiology* 66: 905-913.
- DARWIN, C. 1871. *The descent of man, and selection in relation to sex*. London: John Murray.

- DEMORT, C. 1991. The St. Johns River system. Pages 97-120. *in* The rivers of Florida (R. J. Livingston, ed.). Springer-Verlag, Ecological Series, No. 83, New York, New York.
- DESCIOLI, P. AND R. KURZBAN. 2009. The alliance hypothesis for human friendship. *PLoS One* 4: e5802.
- DURDEN, W.N., E.D. STOLEN, AND M.K. STOLEN. 2011. Abundance, distribution, and group composition of Indian River Lagoon bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals* 37: 175-186.
- DUVAL, E.H. 2007. Social organization and variation in cooperative alliances among male lance-tailed manakins. *Animal Behaviour* 73: 391-401.
- EADIE, J.M. AND J.M. FRYXELL. 1992. Density dependence, frequency dependence, and alternative nesting strategies in goldeneyes. *American Naturalist* 140: 621-641.
- EISFELD, S.M. AND K.P. ROBINSON. 2004. The sociality of bottlenose dolphins in the outer southern Moray Firth, NE Scotland: implications for current management proposals. *European Research on Cetaceans* 18.
- ELLISER, C.R. AND D.L. HERZING. 2014. Long-term social structure of a resident community of Atlantic spotted dolphins, *Stenella Frontalis*, in the Bahamas 1991-2002. *Marine Mammal Science* 30: 308-328.
- EMLEN, S.T. AND L.W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. *Nature* 197: 215-223.
- ENGLUND, A., S. INGRAM, AND E. ROGAN. 2007. Population status report for bottlenose dolphins using the Lower River Shannon SAC, 2006-2007. Final report to the National Parks and Wildlife Service: 1-35.
- FEARNBACH, H., J. DURBAN, K. PARSONS, AND D. CLARIDGE. 2011. Seasonality of calving and predation risk in bottlenose dolphins on Little Bahama Bank. *Marine mammal Science* 28: 402-411.
- FEARNBACH, H., J. DURBAN, K. PARSONS, AND D. CLARIDGE. 2012. Photographic mark-recapture analysis of local dynamics within an open population of dolphins. *Ecological Applications* 22: 1689-1700.
- FELIX, F. 1997. Organization and social structure of the coastal bottlenose dolphin *Tursiops truncatus* in the Gulf de Guayaquil, Ecuador. *Aquatic Mammals* 23: 1-16.
- FERNANDEZ, S. AND A.A. HOHN. 1998. Age, growth, and calving season of bottlenose dolphins, *Tursiops truncatus*, off coastal Texas. *Fishery Bulletin* 96: 357-365.
- FERTL, D. 1994. Occurrence patterns and behavior of bottlenose dolphins (*Tursiops truncatus*) in the Galveston ship channel, Texas. *The Texas Journal of Science* 46: 299-317.
- FRÈRE ET AL. 2010. Home range overlap, matrilineal and biparental kinship drive female associations in bottlenose dolphins. *Animal Behaviour* 80: 481-486.
- FURY, C.A., K.E. RUCKSTUHL, AND P.L. HARRISON. 2013. Spatial and social sexual segregation patterns in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *PLoS one* 8: e52987.
- GAGE, M.J.G. 1995. Continuous variation in reproductive strategy as an adaptive response to population density in the moth *Plodia interpunctella*. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 261: 25-30.
- GAULIN, S.J.C. AND L.D. SAILER. 1984. Sexual dimorphism in weight among the primates: the relative impact of allometry and sexual selection. *International Journal of Primatology* 5: 515-535.

- GIBSON, Q.A. AND J. MANN. 2008. Early social development in wild bottlenose dolphins: sex differences, individual variation, and maternal influence. *Animal Behavior* 76: 375-387.
- GOODALL, J. 1986. The chimpanzees of gombe: patterns of behavior. Harvard University Press, Cambridge, Massachusetts.
- GRAY, E.M. 1997. Female red-winged blackbirds accrue material benefits from copulating with extra-pair males. *Animal Behaviour* 53: 625-639.
- GROSS, M.R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology and Evolution* 11: 92-98.
- HALE, P.T., A.S. BARRETO, AND G.J.B. ROSS. 2000. Comparative morphology and distribution of the *aduncus* and *truncatus* forms of bottlenose dolphin *Tursiops* in the Indian and Western Pacific Oceans. *Aquatic Mammals* 26: 101-110.
- HEBBLEWHITE, M. AND D.H. PLETSCHER. 2002. Effects of elk group size on predation by wolves. *Canadian Journal of Zoology* 80: 800-809.
- HEITHAUS, M.R. 2001. Shark attacks on bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia: attack rate, bite scare frequencies, and attack seasonality. *Marine Mammal Science* 17: 526-539.
- HEITOR, F., M. DO MAR OOM, AND L. VINCENTE. 2006. Social relationships in a herd of Sorraia horses: Part II. Factors affecting affiliative relationships and sexual behaviors. *Behavioural Processes* 73: 231-239.
- HENDERSON, S.D., S.M. DAWSON, R.J.C. CURREY, D. LUSSEAU, AND K. SCHNEIDER. 2014. Reproduction, birth seasonality, and calf survival of bottlenose dolphins in Doubtful Sound, New Zealand. *Marine Mammal Science* 30: 1067-1080.
- HILL, R.A. AND P.C. LEE. 1998. Predation risk as an influence on group size in cercopithecoid primates: implications for social structure. *Journal of Zoology, London* 245: 447-456.
- HOLEKAMP, K.E., L. SMALE, AND M. SZYKMAN. 1996. Rank and reproduction in the female spotted hyaena. *Journal of Reproduction and fertility* 108: 229-237.
- HUNTINGFORD, F.A., A.K. TURNER, AND L.M. DOWNIE. 1987. *Animal Conflict*. Chapman & Hall/CRC, Boca Raton, Florida.
- INGRAM, S.N. 2000. The ecology and conservation of bottlenose dolphins in the Shannon estuary, Ireland. PhD thesis, University of College Cork, Ireland.
- INGRAM, S.N. AND E. ROGAN. 2002. Identifying critical areas and habitat preferences of bottlenose dolphins *Tursiops truncatus*. *Marine Ecology Progress Series* 244: 247-255.
- JIROTKUL, M. 1999. Operational sex ratio influences female preference and male-male competition in guppies. *Animal Behaviour* 58: 287-294.
- KING, A.J. AND G. COWLISHAW. 2009. Leaders, followers and group decision-making. *Communicative & Integrative Biology* 2: 147-150.
- KOGI, K., T. HISHI, A. IMAMURA, T. IWATANI, AND K.M. DUDZINSKI. 2004. Demographic parameters of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around Mikura Island, Japan. *Marine Mammal Science* 20: 510-526.
- KOKKO, H. AND D.J. RANKIN. 2006. Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society, B Series: Biological Sciences* 361: 319-334.
- KRAUSE, J. AND G.D. RUXTON. 2002. *Living in groups*. Oxford University Press, Oxford, New York.

- KUMMER, H. 1968. Social organization of hamadryas baboons. Vol. 765. University of Chicago Press, Chicago, Illinois.
- KUMMER, H. 1971. Primate societies. Group Techniques of Ecological Adaptation. Aldine-Athertone, Chicago, Illinois.
- LANGERGRABER, K., J. MITANI, AND L. VIGILANT. 2009. Kinship and social bonds in female chimpanzees (*Pan troglodytes*). American Journal of Primatology 71: 840-851.
- LANK, D.B., C.M. SMITH, O. HANOTTE, T. BURKE, AND F. COOK. 1995. Genetic polymorphism for alternative mating behavior in lekking male ruff. Nature 378: 59-62.
- LEHMANN, J., A.H. KORSTJENS, AND R.I.M. DUNBAR. 2007. Fission-fusion social systems as a strategy for coping with ecological constraints: a primate case. Evolutionary Ecology 21: 613-634.
- LEHMANN, J. AND C. BOESCH. 2008. Sexual differences in chimpanzee sociality. International Journal of Primatology 29: 65-81.
- LOE, L.E. ET AL. 2005. Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France. Journal of Animal Ecology 74: 579-588.
- LUSSEAU, D. 2007. Why are male social relationships complex in the Doubtful Sound bottlenose dolphin population? PLoS One 2: e348.
- LUSSEAU, D., K. SCHNEIDER, O.J. BOISSEAU, P. HAASE, E. SLOOTEN, AND S.M. DAWSON. 2003. The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations. Behavioral Ecology and Sociobiology 54: 396-405.
- MANN, J. 2006. Establishing trust: socio-sexual behavior and the development of male-male bonds among Indian Ocean bottlenose dolphins. Pages 107-130 in Homosexual behavior in animals: an evolutionary perspective (S. Volker and L. Vasey, eds). Cambridge University Press, New York, New York.
- MANN, J. AND B. SARGEANT. 2003. Like mother, like calf: the ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (*Tursiops* sp.). Pages 236-266 in The biology of traditions: models and evidence (D. Frigaszy and S. Perry, eds.). Cambridge University Press, New York, New York.
- MANN, J., R. CONNOR, L. BARRE, AND M. HEITHAUS. 2000. Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. Behavioral Ecology 11: 210-219.
- MARLEY, S.A., B. CHENEY, AND P.M. THOMPSON. 2013. Using tooth rakes to monitor population and sex differences in aggressive behavior in bottlenose dolphins (*Tursiops truncatus*). Aquatic mammals 39: 107-115.
- MATTSON, M.C., K.D. MULLIN, G.W. INGRAM, AND W. HOGGARD. 2006. Age structure and growth of the bottlenose dolphin (*Tursiops truncatus*) from strandings in the Mississippi Sound region of the north-central Gulf of Mexico from 1986 to 2003. Marine Mammal Science 22: 654-666.
- MAZZOIL, M., S.D. MCCULLOCH, R.H. DEFRAN, AND M.E. MURDOCH. 2004. Use of digital photography and analysis of dorsal fins for photo-identification of bottlenose dolphins. Aquatic Mammals 30: 209-219.
- MCFEE, W.E., J.D. ADAMS, P.A. FAIR, AND G.D. BOSSART. 2012. Age distributions and population growth of two bottlenose dolphin (*Tursiops truncatus*) populations from capture-release studies in the Southeastern United States. Aquatic Mammals 38: 17-30.

- MEAD, J.G. AND C.W. POTTER. 1990. Natural history of bottlenose dolphins along the central Atlantic coast of the United States. Pages 165-195 in *The Bottlenose Dolphin* (S. Leatherwood and R.R. Reeves, eds.). Academic Press, Inc., San Diego, California.
- MERRIMAN, M.G., T.M. MARKOWITZ, A.D. HARLIN-COGNATO, AND K.A. STOCKIN. 2009. Bottlenose dolphin (*Tursiops truncatus*) abundance, site fidelity, and group dynamics in the Marlborough Sounds, New Zealand. *Aquatic Mammals* 35: 511-522.
- MITANI, J.C., J. GROS-LOUIS, AND A.F. RICHARDS. 1996. Sexual dimorphism, the operational sex ration, and the intensity of male competition in polygynous primates. *The American Naturalist* 147: 966-980.
- MITCHESON, H. 2008. Inter-birth interval estimation for a population of bottlenose dolphins (*Tursiops truncatus*): accounting for the effects of individual variation and changes over time. Master's thesis, University of St. Andrews, Scotland.
- MÖLLER, L.M. AND R.G. HARCOURT. 2008. Shared reproductive state enhances female associations in dolphins. *Research Letters in Ecology* 2008. Article ID 498390, 5 pages, 2008. doi:10.1155/2008/498390
- MÖLLER, L.M., L.B. BEHEREGARAY, R.G. HARCOURT, AND M. KRÜTZEN. 2001. Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 268: 1941-1947.
- MÖLLER, L.M., L.B. BEHEREGARAY, S.J. ALLEN, AND R.G. HARCOURT. 2006. Association patterns and kinship in female Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Behavioral Ecology and Sociobiology* 61: 109-117.
- MÖLLER, L.M., S.J. ALLEN, AND R.G. HARCOURT. 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: 11-22.
- MOURÃO, F. 2006. Patterns of association among bottlenose dolphins in the Bay of Islands, New Zealand. Master's thesis. University of Auckland, Auckland, New Zealand.
- MULLER, N.M. AND R.W. WRANGHAM. 2009. Sexual coercion in primates and humans: An evolutionary perspective on male aggression against females. Harvard University Press, Cambridge, Massachusetts.
- MULLER, N.M., S.M. KAHLENBERG, AND R.W. WRANGHAM. 2009. Male aggression and sexual coercion of females in primates. Pages 3-22 in *Sexual Coercion in Primates and Humans: An Evolutionary Perspective on Male Aggression* (M.N. Muller and R.W. Wrangham, eds.). Harvard University Press, Cambridge, Massachusetts.
- MULLER, N.M., S.M. KAHLENBERG, M.E. THOMPSON, AND R.W. WRANGHAM. 2007. Male coercion and the costs of promiscuous mating for female chimpanzees. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 274: 1009-1014.
- MURRAY, C.M., L.E. EBERLY, AND A.E. PUSEY. 2006. Foraging strategies as a function of season and rank among wild female chimpanzees (*Pan troglodytes*). *Behavioral Ecology* 17: 1020-1028.
- NISHIDA, T. 1983. Alpha status and agonistic alliance in wild chimpanzee (*Pan troglodytes schweinfurthii*). *Primates* 24: 318-336.
- OWEN, E.C.G. 2003. The reproductive and ecological functions of the pair-bond between allied, adult male bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. PhD thesis, University of California, Santa Cruz, California.

- OWEN, E., R. WELLS, AND S. HOFMANN. 2002. Ranging and association patterns of paired and unpaired adult male Atlantic bottlenose dolphins, *Tursiops truncatus*, in Sarasota, Florida, provide no evidence for alternative mating strategies. *Canadian Journal of Zoology* 80: 2072-2089.
- PACE, D.S., M. PULCINI, AND F. TRIOSI. 2011. Anthropogenic food patches and association patterns of *Tursiops truncatus* at Lampedusa island, Italy. *Behavioral Ecology* 180: arr180.
- PACKER, C. AND A.E. PUSEY. 1983. Adaptations of female lions to infanticide by incoming males. *American Naturalist* 121: 716-728.
- PACKER, C., D.A. GILBERT, A.E. PUSEY, AND S.J. O'BRIEN. 1991. A molecular genetic analysis of kinship and cooperation in African lions. *Nature* 351: 562-565.
- PALAGI, E., T. PAOLI, AND S. BORGOGNINI TARLI. 2006. Short-term benefits of play behavior and conflict prevention in *Pan paniscus*. *International Journal of Primatology* 27: 1257-1270.
- PARSONS, K.M., J.W. DURBAN, D.E. CLARIDGE, K.C. BALCOMB, L.R. NOBLE, AND P.M. THOMPSON. 2003. Kinship as a basis for alliance formation between male bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. *Animal Behaviour* 66: 185-194.
- PAZOL, K. 2003. Mating in the Kakamega Forest blue monkeys (*Cercopithecus mitis*): does female sexual behavior function to manipulate paternity assessment? *Behaviour* 140: 473-499.
- PEARSON, H.C. 2011. Sociability of female bottlenose dolphins (*Tursiops* spp.) and chimpanzees (*Pan troglodytes*): understanding evolutionary pathways towards social convergence. *Evolutionary Anthropology* 20: 85-95.
- PEREIRA, A. F. MARTINHO, C. BRITO, AND I. CARVALHO. 2013. Bottlenose dolphin *Tursiops truncatus* at São Tomé Island (Sao Tome and Príncipe)- relative abundance, site fidelity and social structure. *African Journal of Marine Science* 35: 501-510.
- PLAVCAN, J.M. AND C.P. VAN SCHAIK. 1997. Intrasexual competition and body weight dimorphism in Anthropoid primates. *American Journal of Physical Anthropology* 103: 37-68.
- POLO, P., V. HARNANDEZ-LLOREDA, AND F. COLMENARES. 2014. Male takeovers are reproductively costly to females in hamadryas baboons: a test of the sexual coercion hypothesis. *PLoS One* 9: e90996.
- PUSEY, A., J. WILLIAMS, AND J. GOODALL. 1997. The influence of dominance rank on the reproductive success of female chimpanzees. *Science* 277: 828-831.
- QUINTANA-RIZZO, E. AND R.S. WELLS. 2001. Resighting and association patterns of bottlenose dolphins (*Tursiops truncatus*) in the Cedar Keys, Florida: insights into social organization. *Canadian Journal of Zoology* 79: 447-456.
- RANDIĆ, S., R.C. CONNOR, W.B. SHERWIN, AND M. KRÜTZEN. 2012. A novel mammalian social structure in Indo-Pacific bottlenose dolphins (*Tursiops* sp.): complex male alliances in an open social network. *Proceedings of the Royal Society London, Series B: Biological Sciences* 279: 3083-3090.
- READ, A.J., R.S. WELLS, A.A. HOHN, AND M.D. SCOTT. 1993. Patterns of growth in wild bottlenose dolphins, *Tursiops truncatus*. *Journal of Zoology* 231: 107-123.
- RODSETH, L. ET AL. 2001. The human community as a primate society [and comments]. *Current Anthropology* 32: 221-254.

- ROGERS, C.A., B.J. BRUNNICK, D.L. HERZING, AND J.D. BALDWIN. 2004. The social structure of bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. *Marine Mammal Science* 20: 688-708.
- ROLLAND, M. ET AL. 2012. Evidence that ship noise increases stress in right whales. *Proceedings of the Royal Society, Series B: Biological Sciences* 279: 2363-2368.
- ROMANO, T.A. ET AL. 2004. Anthropogenic sound and marine mammal health: measures of the nervous and immune systems before and after intense sound exposure. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 1124-1134.
- ROSSBACH, K.A. AND D.L. HERZING. 1999. Inshore and offshore bottlenose dolphin (*Tursiops truncatus*) communities distinguished by association patterns near Grand Bahama Island, Bahamas. *Canadian Journal of Zoology* 77: 581-592.
- ROSVALL, K.A. 2011. Intrasexual competition in females: evidence for sexual selection? *Behavioral Ecology*: arr106.
- SAMUELS, A. AND T. GIFFORD. 1997. A quantitative assessment of dominance relations among bottlenose dolphins. *Marine Mammal Science* 13: 70-99.
- SCHREIER, A.L. AND L. SWEDELL. 2012. Ecology and sociality in a multi-level society: ecological determinants of spatial cohesion in hamadrayas baboons. *American Journal of Physical Anthropology* 148: 580-588.
- SCHROEDER, J.P. AND K.V. KELLER. 1989. Seasonality of serum testosterone levels and sperm density in *Tursiops truncatus*. *Journal of Experimental Zoology* 249: 316-321.
- SCOTT, E.M., J. MANN, J.J. WATSON-CAPPS, B.L. SARGEANT, AND R.C. CONNOR. 2005. Aggression in bottlenose dolphins: evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behavior. *Behaviour* 142: 21-44.
- SEELEY, C. AND R. DUKAS. 2011. Teneral matings in fruit flies: male coercion and female response. *Animal Behaviour* 81: 595-601.
- SMITH, J.E., J.M. KOLOWSKI, K.E. GRAHAM, S.E. DAWES, AND K.E. HOLEKAMP. 2008. Social and ecological determinants of fission-fusion dynamics in the spotted hyaena. *Animal Behaviour* 76: 619-636.
- SMOLKER, R., A. RICHARDS, R. CONNOR, AND J. PEPPER. 1992. Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behavior* 123: 38-69.
- SMUTS, B.B. AND R.W. SMUTS. 1993. Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Advances in the study of behavior* 22: 1-63.
- STEINER, A. AND M. BOSSLEY. 2008. Some reproductive parameters of an estuarine population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *Aquatic Mammals* 34: 84-92.
- STERCK, E., D. WATTS, AND C. SCHAIK. 1997. The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology* 41: 291-309.
- STOCKLEY, P. AND J. BRO-JØRGENSEN. 2011. Female competition and its evolutionary consequences in mammals. *Biological Reviews* 86: 341-366.
- STUMPF, R.M. AND C. BOESCH. 2010. Male aggression and sexual coercion in wild West African chimpanzees, *Pan troglodytes verus*. *Animal Behaviour* 79: 333-342.
- SUEUR, C. ET AL. 2011. Collective decision-making and fission-fusion dynamics: a conceptual framework. *Oikos* 120: 1608-1617.

- SYMINGTON, M.M. 1990. Fission-fusion social organization in *Ateles* and *Pan*. *International Journal of Primatology* 11: 47-61.
- TEZANOS-PINTO, G. 2009. Population structure, abundance and reproductive parameters of bottlenose dolphins (*Tursiops truncatus*) in the Bay of Islands (Northland, New Zealand). PhD thesis, University of Auckland, Auckland, New Zealand.
- THAYER, V.G. 2008. Life history parameters and social associations of female bottlenose dolphins (*Tursiops truncatus*) off North Carolina, U.S.A. PhD thesis, Duke University, Durham, North Carolina.
- TOLLEY, K.A., A.J. READ, R.S. WELLS, K.W. URIAN, M.D. SCOTT, A.B. IRVINE, AND A.A. HOHN. 1995. Sexual dimorphism in wild bottlenose dolphins (*Tursiops truncatus*) from Sarasota, Florida. *Journal of Mammalogy* 76: 1190-1198.
- TOMKINS, J.L. AND G.S. BROWN. 2004. Population density drives the local evolution of a threshold dimorphism. *Nature* 431: 1099-1103.
- TRIVERS, R. 1972. Parental investment and sexual selection. Pages 136-179 in *Sexual selection and the descent of man 1871-1971* (B. Campbell, ed.). Aldine Publishing Company, Chicago, Illinois.
- TRIVERS, R.L. 1974. Parent-offspring conflict. *American Zoologist* 14: 249-264.
- TSAI, Y.J. AND J. MANN. 2013. Dispersal, philopatry, and the role of fission-fusion dynamics in bottlenose dolphins. *Marine Mammal Science* 29: 261-279.
- URIAN, K.W., D.A. DUFFIELD, A.J. READ, R.S. WELLS, AND E.D. SHELL. 1996. Seasonality of reproduction in bottlenose dolphins, *Tursiops truncatus*. *Journal of Mammalogy* 77: 394-403.
- VAN SCHAIK, C.P. 1983 Why are diurnal primates living in groups? *Behaviour* 87: 120-144.
- VERMEULEN, E. AND A. CAMMARERI. 2009. Residency patterns, abundance, and social composition of bottlenose dolphins (*Tursiops truncatus*) in Bahia San Antonio, Patagonia, Argentina. *Aquatic Mammals* 35: 378-385.
- WATSON-CAPPS, J.J. 2005. Female mating behavior in the context of sexual coercion and female ranging behavior of bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia. PhD thesis, Georgetown University, Washington D.C.
- WATTS, D.P. 1998. Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology* 44: 43-55.
- WEISS, J. 2006. Foraging habits and associated preferential foraging specializations of bottlenose dolphins (*Tursiops truncatus*) mother-calf pairs. *Aquatic Mammals* 32: 10-19.
- WELLS, R.S. 1991a. Reproductive success and survivorship of free-ranging bottlenose dolphins relative to group size and stability. Abstract, Ninth Biennial Conference on the Biology of Marine Mammals, Chicago.
- WELLS, R.S. 1991b. The role of long-term study in understanding the social structure of a bottlenose dolphin community. Pages 199-225 in *Dolphin Societies: discoveries and puzzles* (K. Pryor and K.S. Norris, eds.). University of California Press, Los Angeles, California.
- WELLS, R.S. 1993. Parental investment patterns of wild bottlenose dolphins. Pages 58-64 in *Proceedings of the 18th International Marine Animal Trainers Association Conference* (N.F. Hecker, ed.). Chicago, Illinois.
- WELLS, R.S. 2000. Reproduction in wild bottlenose dolphins: Overview of patterns observed during a long-term study. *Bottlenose Dolphins Reproduction Workshop*. Silver Springs, AZA marine mammal taxon advisory group.

- WELLS, R.S. 2003. Dolphin social complexity: lessons from long-term study and life history. Pages 32-56 in *Animal Social Complexity: Intelligence, Culture, and Individualized Societies* (F.B.M. de Waal and P.L. Tyack, eds.). Harvard University Press: Cambridge, Massachusetts.
- WELLS, R.S. 2013. Social structure and life history of bottlenose dolphins near Sarasota Bay, Florida: insights from four decades and five generations. Pages 149-172 in *Primates and Cetaceans: Field Research and Conservation of Complex Mammalian Societies* (J. Yamagiwa and L. Karczmarski, eds.). Springer, Japan.
- WELLS, R.S., M.D. SCOTT AND A.B. IRVINE. 1987. The social structure of free-ranging bottlenose dolphins. Pages 247-305 in *Current Mammalogy*, Vol. 1 (H. Genoways, ed.). Plenum Press, New York, New York.
- WHITEHEAD, H. 2009. SOCPROG programs: analyzing animal social structures. *Behavioral Ecology and Sociobiology* 63:765-778.
- WHITEHEAD, H. AND R. CONNOR. 2005. Alliances I. How large should alliances be? *Animal Behaviour* 69: 117-126.
- WILLIAMS, T.M. 1999. The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 354: 193-201.
- WILSON, B., P. THOMPSON, AND P. HAMMOND. 1993. An examination of the social structure of a resident group of bottle-nosed dolphins (*Tursiops truncatus*) in the Moray Firth, N.E. Scotland. Pages 54-56 in *European Research on Cetacean Proceedings of the Seventh Annual Conference of the European Cetacean Society*. European Cetacean Society (G.G.H Evans, ed.). Cambridge, UK.
- WILSON, B., P.M. THOMPSON, AND P.S. HAMMOND. 1997. Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *Journal of Applied Ecology* 34: 1365-1374.
- WILSON, B., P.S. HAMMOND, AND P.M. THOMPSON. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecological Applications* 9: 288-300.
- WISZNIEWSKI, J., C. BROWN, AND L.M. MÖLLER. 2012. Complex patterns in male alliance formation in a dolphin social network. *Journal of Mammalogy* 93: 239-250.
- WISZNIEWSKI, J., S.J. ALLEN, AND L.M. MÖLLER. 2009. Social cohesion in a hierarchically structured embayment population of Indo-Pacific bottlenose dolphins. *Animal Behaviour* 77: 1449-1457.
- WITTEMYER, G., I. DOUGLAS-HAMILTON, AND W.M. GETZ. 2005. The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal Behaviour* 69: 1357-1371.
- WOOD, F.G., D.K. CALDWELL, AND M.C. CALDWELL. 1970. Behavioral interactions between porpoises and sharks. *Investigations on Cetacea* 2: 264-277.
- WRANGHAM, R. 1980. An ecological model of female-bonded primate groups. *Behavior* 75: 262-300.
- WRANGHAM, R.W. AND B.B. SMUTS. 1980. Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. *Journal of Reproduction and Fertility*. Supplement: 13-31.
- ZINNER, D. AND T. DESCHNER. 2000. Sexual swellings in female hamadryas baboon after male take-overs: "deceptive" swellings as possible female counter-strategy against infanticide. *American Journal of Primatology* 52: 157-168.

VITA

Jessica graduated with her B.S. from the University of Delaware with a major in Wildlife Conservation and a minor in Biology. During her time in Jacksonville at the University of North Florida she has dedicated her time to the research of marine mammal behavior, with a specific interest in bottlenose dolphin social structure and mating strategies, as evidenced within her Master's thesis. A portion of this research was presented at the international 2013 Conference on the Biology of Marine Mammals. In addition, Jessica has remained active in the local marine mammal world by volunteering with the Fish and Wildlife Commission, where she assisted with strandings, necropsies, and public outreach. Jessica plans to publish her research collected at the University of North Florida and continue her career as a wildlife biologist.