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Structure and Function of Male Bottlenose Dolphin Alliances in Northeast Florida

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STRUCTURE AND FUNCTION OF MALE BOTTLENOSE DOLPHIN ALLIANCES IN
NORTHEAST FLORIDA

by

Kristin Amanda Karle

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in partial fulfillment of the requirements for the degree of

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TABLE OF CONTENTS

List of Tables	v
List of Figures	vi
Abstract	ix
Introduction	1
Chapter 1	
The effect of a mass mortality event on bottlenose dolphin social structure and male mating strategies in the Indian River Lagoon, Florida	4
Abstract.....	4
Introduction.....	5
Methods.....	9
Results.....	14
Discussion.....	16
Acknowledgements.....	22
Chapter 2	
The stability and function of male bottlenose dolphin alliances in the St. Johns River, Florida	27
Abstract.....	27
Introduction.....	28
Methods.....	33
Results.....	39
Discussion.....	43
Acknowledgements.....	49
Bibliography	65
Vita	76

LIST OF TABLES

Chapter 1

Table 1. Indian River Lagoon half-weight indices (HWIs). Pre-CeMV (January 2002 – December 2007) is shown in dark grey. Post-CeMV (January 2008 – December 2013) is shown in white.....24

Chapter 2

Table 1. Ethogram of behavioral states (adapted from Mann and Watson-Capps 2005). Activity categories are mutually exclusive.52

Table 2. Quasi-Akaike Information Criterion values weighted for each exponential decay model for lagged association rates of unstable (S1) and stable (S2) first-order alliances (FO) and of unstable and stable second-order alliances (SO) from April 2011 – March 2015 calculated via SOCPROG v. 2.6. Bolded numbers represent the probability that model is the actual expected best-fit. Association rates between individuals (g), as a function of time lag (d), were related to the proportion of constant companions (P_{cc}) and the proportion of casual acquaintances (P_{cas}) that lasted for time period τ_{cas} (but were not permanent), and to the proportion of casual associations (P_{perm}) that had more permanent associations (τ_{perm}) (see Whitehead 1995; Whitehead 2007).....55

Table 3. Quasi-Akaike Information Criterion or Akaike Information Criterion values weighted for each exponential decay model for lagged association rates of unstable (S1) and stable (S2) first-order alliances (FO) and of unstable and stable second-order alliances (SO) from April 2011 – March 2015 calculated via SOCPROG v. 2.6. Bolded numbers represent the probability that model is the actual expected best-fit. Social system models evaluate movement into and out of the study area where td indicates time delay in days, $a1$ is the emigration rate, $a2$ is the mean residence time, $a3$ is mean time out of study area, and $a4$ is the mortality rate.....59

LIST OF FIGURES

Chapter 1

Figure 1. The Indian River Lagoon lies within the white box, which is located 190-km south of the St. Johns River, denoted by the white star. A more detailed map of the Indian River Lagoon study area is shown on the right. Map adapted from Browning *et al.* 2014.....23

Figure 2. Distribution of top associations of FEM, MAL, and UNK categories pre- and post-CeMV (a and b, respectively). Top associations for all sex categories were highly variable and there was not a clear difference in top associations between the sexes.....25

Figure 3. Sociogram of all allied MAL/UNK dyads based on half-weight indices (HWI). Known males are indicated with a star. Only one dyad was observed during both data sets. Width of line indicates strength of association. 3a. Four dyads formed alliances pre-CeMV (January 2002 – December 2007). 3b. Seven dyads formed alliances post-CeMV (January 2008 – December 2013).26

Chapter 2

Figure 1. Survey route (reproduced from Ermak *et al.*, in review). Data were collected through weekly photo-identification surveys from the mouth of the St. Johns River (SJR; right dot) to downtown Jacksonville (left dot) along a 40-km transect, with the direction of travel alternating weekly.....51

Figure 2. Sociogram of all allied MAL/UNK dyads based on half-weight indices (HWI) calculated via SOCPROG v. 2.6. Width of line indicates strength of association. Known males are indicated with a star. Sociograms are divided for clarity. From Apr. 2011 – Mar. 2013, five dyads (a) formed only first-order alliances and ten dyads (b) formed more complex, second-order alliances ($HWI \geq 0.30$). From Apr. 2013 – Mar. 2015, thirteen dyads (c) formed only first-order alliances and two dyads (d) formed a more complex, second-order alliance ($HWI \geq 0.42$).....53

Figure 3. Lagged association rates (LAR) and null association rates (NAR) for first-order alliances with a stability index (SI) of 1 and a stability index of 2 from Apr. 2011 - Mar. 2015 calculated via SOCPROG v. 2.6. The NAR was calculated to represent the expected LAR if individuals were associating randomly. A moving average of 1500 associations was used for both stability indices to smooth the curve. Vertical bars indicate approximate standard errors, which were obtained by jack-knifing. Association rates between individuals, as a function of time lag (d), were related to the proportion of constant companions (P_{cc}) and the proportion of casual acquaintances (P_{cas}) that lasted for time period τ_{cas} (but were not permanent), and to the proportion of casual associations (P_{perm}) that had more permanent associations (τ_{perm}). The best fitting models for SI 1 ($P_{cc} + P_{cas} \times e^{-d/\tau_{cas}}$) and SI 2 (P_{cc}) are displayed.....54

Figure 4. Lagged association rates (LAR) and null association rates (NAR) for second-order alliances with a stability index (SI) of 1 and a stability index of 2 from Apr. 2011 - Mar. 2015 calculated via SOCPROG v. 2.6. The NAR was calculated to represent the expected LAR if individuals were association randomly. A moving average of 1500 associations was used for SI 1 and a moving average of 1000 associations was used for SI 2 to smooth the curve. Vertical bars indicate approximate standard errors, which were obtained by jack-knifing. Association rates between individuals, as a function of time lag (d), were related to the proportion of constant companions (P_{cc}) and the proportion of casual acquaintances (P_{cas}) that lasted for time period τ_{cas} (but were not permanent), and to the proportion of casual associations (P_{perm}) that had more permanent associations (τ_{perm}). The best fitting models for SI 1 ($P_{cas} \times e^{-d/\tau_{cas}}$) and SI 2 ($P_{cas} \times e^{-d/\tau_{cas}} + (1 - P_{cas}) \times e^{-d/\tau_{perm}}$) are displayed.....56

Figure 5. Lagged identification rates (LIR) for first-order alliances from Apr. 2011 – Mar. 2015 calculated via SOCPROG v. 2.6. Vertical lines indicate approximate standard errors, which were obtained by boot-straps of 100 replicates. Best-fitting models included emigration, reimmigration, and mortality where a_1 is the emigration rate, a_2 is the mean residence time, a_3 is mean time out of study area, and a_4 is the mortality rate. The best-fitting models for first-order alliances with a stability index (SI) of 1 (a) are given by $a_2 \times \exp(-a_1 \times td)$ and $\frac{1}{a_1} \times \exp(-\frac{td}{a_2})$. The best-fitting model for first-order alliances with an SI of 2 (b) is given by $\frac{1}{a_1} \times \frac{\frac{1}{a_3} + \frac{1}{a_2} \times \exp(-\frac{1}{a_3} + \frac{1}{a_2}) \times td}{\frac{1}{a_3} + \frac{1}{a_2}}$57

Figure 6. Lagged identification rates (LIR) for second-order alliances from Apr. 2011 – Mar. 2015 calculated via SOCPROG v. 2.6. Vertical lines indicate approximate standard errors, which were obtained by boot-straps of 100 replicates. Best-fitting models included emigration, reimmigration, and mortality where a_1 is the emigration rate, a_2 is the mean residence time, a_3 is mean time out of study area, and a_4 is the mortality rate. The best-fitting model for second-order alliances with an SI of 1 (a) are given by $\frac{\frac{1}{a_1} \times (\frac{1}{a_3} + \frac{1}{a_2} \times \exp(-(\frac{1}{a_3} + \frac{1}{a_2})) \times td)}{\frac{1}{a_3} + \frac{1}{a_2}}$ and $a_2 + a_3 \times \exp(-a_1 \times td)$. The best-fitting models for second-order alliances with a stability index (SI) of 2 (b) are given by $a_2 \times \exp(-a_1 \times td)$ and $\frac{1}{a_1} \times \exp(-\frac{td}{a_2})$60

Figure 7. Mean proportion of sightings focal first-order alliances were observed with their second-order alliance partners. Lines on each bar indicate standard error (April 2011 – March 2015). There was no significant difference between seasons (BR $\bar{x} = 0.59 \pm 0.05$, NB $\bar{x} = 0.51 \pm 0.11$, $t(9) = 0.534$, $p > 0.10$).....62

Figure 8. Activity budgets for first- and second-order alliances (FO and SO, respectively) for the breeding (BR) and non-breeding (NB) seasons. Predominant group activity was classified as one of four behavioral states: travel (TRV), forage (FOR), social (SOC), and rest (RST). Behaviors were unequally distributed (FO BR: $\chi^2(3, n = 197) = 257.1$, $p < 0.05$; FO NBR: $\chi^2(3, n = 111) = 119.4$, $p < 0.05$; SO BR: $\chi^2(3, n = 50) = 73.84$, $p < 0.05$; SO NBR: $\chi^2(3, n = 27) = 27.67$, $p < 0.05$).....63

Figure 9. Mean proportion of sightings alliances were observed with and without females (FEM) with respect to seasonality (breeding season: BR; non-breeding season: NB) from April 2011 – March 2015. First- and second-order alliances were significantly more likely to be observed with females during the breeding season (FO: Md = 0.50, n = 20; SO: $\bar{x} = 0.78 \pm 0.21$) than non-breeding season (FO: Md = 0.14, n = 20, Z = -3.73, p < 0.01; SO: $\bar{x} = 0.15 \pm 0.10$, t(6) = 5.78, p < 0.01). During the breeding season, second-order alliances significantly had a higher proportion of sightings with females than did first-order alliances (FO: $\bar{x} = 0.49 \pm 0.21$, SO: $\bar{x} = 0.78 \pm 0.21$, t(25) = -3.08, p < 0.01). There was no statistical significance between seasons or alliance structures when females were absent.....64

Abstract

Bottlenose dolphins exhibit fission-fusion social systems in which group size and composition change fluidly throughout the day. Societies are typically sexually segregated, and the quality and patterning of individual relationships in this social species shape the social structure of a population. Female dolphins usually have a large network of associates with whom they form recurring moderate bonds, while male associations are highly variable due to their mating strategies. Males employ one of two strategies; males may be solitary, and encounter and herd females individually, while others may form strong bonds with one to two other males and cooperatively herd individual females in the shape of a first-order alliance. Second-order alliances are more uncommon and have only been observed in Shark Bay, Australia, and more recently within the St. Johns River (SJR), Jacksonville, Florida. Given the inter-population variation in male mating strategies, greater documentation of social structure in neighboring populations along the Atlantic coast is needed. Therefore, chapter one documents the social structure of the Indian River Lagoon (IRL) estuarine system where dolphins have experienced recurrent cetacean morbillivirus (CeMV) epizootics. Although environmental disturbances can affect both social and mating systems, IRL dolphin sociality does not seem to be affected by the 2008 CeMV mass mortality event. Additionally, males only form first-order alliances within this population. Because multi-level alliances are unique to the SJR in this region, chapter two analyzes the stability and function of SJR alliances. Both first- and second-order alliances exhibited variation in stability, while alliance association appears dependent on female presence. Thus, SJR alliances likely function within a reproductive context. Together, this work provides insight into the social and mating systems of bottlenose dolphins, as well as the function of multi-level alliances at a relatively new study site.

Introduction

Everywhere they have been studied, bottlenose dolphins utilize fission-fusion social systems (Kummer 1971), in which group size and composition change fluidly throughout the day. In addition to balancing dynamically changing selection pressures, fission-fusion grouping patterns are thought to allow for association preferences within group membership (Connor *et al.* 2000). Due to differing socio-ecological pressures, the strongest bonds in bottlenose dolphins are often found within rather than between the sexes (Wells *et al.* 1987; Conradt and Roper 2000; Fury *et al.* 2013). The quality and patterning of both female and male relationships within these systems shape the social structure of a population (Hinde 1976; Trivers 1985; Lusseau and Newman 2004; Whitehead 2008). Female dolphins generally have a larger network of associates with whom they form recurring moderate bonds (Wells *et al.* 1987; Smolker *et al.* 1992). In contrast, males have a smaller network of associates (Quintana-Rizzo and Wells 2001; Smolker *et al.* 1992; Rogers *et al.* 2004), and their association patterns are highly variable due to their differing mating strategies.

Male bottlenose dolphins most commonly utilize one of two mating strategies. Some males encounter and herd females individually (Doubtful Sound, New Zealand: Lusseau *et al.* 2003; Bay of Islands, New Zealand: Mourão 2006; Moray Firth, Scotland: Einfeld and Robinson 2004), while others form strong, long-term relationships with two to three other males in the shape of a first-order alliance. Alliances can be defined as an enduring cooperative relationship in an aggressive or competitive context (de Waal and Harcourt 1992), and are thought to be critical to reproductive success in multiple populations (Sarasota, U.S.A, Wells *et al.* 1987; The Bahamas, Parsons *et al.* 2003; Port Stephens, Australia, Wiszniewski *et al.* 2009; Shark Bay, Australia, Connor *et al.* 1992a). However, not all males at these study sites form alliances, and

the strength of alliance bonds is highly variable both within and between populations. In addition, first-order alliances may form moderate bonds with one another within second-order alliances (Connor *et al.* 1992a,b) . Large second-order alliances in which males maintain fluctuating pair and trio formations between alliance members, yet exhibit partner preferences are termed super-alliances (Connor *et al.* 1999). Lastly, a third level of complexity is suspected, where agonistic interactions have been noted between multiple second-order alliances, indicative of third-order alliances (Connor *et al.* 2011). Both super-alliances and third-order alliances are thought to be unique to Shark Bay, Australia (Connor *et al.* 1999; Connor *et al.* 2011). Second-order alliances, however, have been documented in the genus *Stenella* in the Bahamas (Elliser and Herzing 2014a) and the genus *Tursiops* in Shark Bay (Connor *et al.* 1992a,b) and the St. Johns River, Florida (Ermak *et al.*, in review).

The recent research in the St. Johns River (SJR: Jacksonville, FL) was the first documentation of second-order alliances within bottlenose dolphins outside of Shark Bay, Australia (Ermak *et al.* in review). Given the inter-population variation in male mating strategies, a comparison between neighboring populations along the Atlantic coast is needed. Recent spatial analyses indicate there is some home range overlap between the St. Johns River (SJR) community and the Indian River Lagoon (IRL) dolphin population allowing for social structure comparison of nearly contiguous populations. Additionally, the IRL population has experienced recurrent cetacean morbillivirus (CeMV) epizootics since at least 1982 (Lipscomb *et al.* 1994; Diugnan *et al.* 1996; NOAA Fisheries 2008, 2015; Bossart *et al.* 2010). Chapter one investigates the demographic changes caused by the recent 2008 CeMV mass mortality event within the IRL, with the conclusion that sex-specific association patterns showed resilience to the mass mortality event and highlighted the overall social plasticity of the IRL bottlenose dolphins. With respect to

male mating strategies, only a subset of IRL males and unknowns formed first-order alliances, and of these, there was no indication of second-order alliance formation.

Chapter two builds upon the conclusion that multi-level alliances are unique to the SJR in the northeast Florida region, and further characterizes SJR alliances. Literature on the stability and function of first-order alliances is thus far limited to a few populations (Sarasota, Florida: Owen *et al.* 2002; Port Stephens, Australia: Wiszniewski *et al.* 2012; Shark Bay, Australia: Connor and Krützen 2015), while information on multi-level alliances is limited to Shark Bay (Connor *et al.* 1992a,b). Inclusion of a relatively new study site that contains second-order alliances gives greater insight into male alliances. Both first- and second-order alliances within the SJR exhibited variation in stability and formation, likely due to changes in association preferences over time. Both first- and second-order alliance associations appear dependent on female presence. Moreover, second-order alliances are rarely observed without females present. Thus, SJR alliances likely function within a reproductive context.

Together, this work allowed for a unique opportunity to examine both inter- and intra-population variation in association patterns and male mating strategies within nearly contiguous populations. The absence of second-order alliances in the Indian River Lagoon in contrast to the St. Johns River allows for analyses of varying ecological and demographic variables that may lead to second-order alliance formation. Additionally, the examination of stability and function of SJR male alliances adds to the current understanding of the adaptive significance of multi-level alliances in bottlenose dolphins. As such, this study highlights the importance of male-male cooperation in response to varying social environments.

Chapter 1

The Effect of a Mass Mortality Event on Bottlenose Dolphin Social Structure and Male Mating Strategies in the Indian River Lagoon, Florida

Abstract

Within fission-fusion societies, environmental disturbances can influence an individual's sociality, which consequently affects the social structure of the population. This study shows the effect of a cetacean morbillivirus (CeMV) epizootic on the Indian River Lagoon (IRL), Florida, bottlenose dolphins' (*Tursiops truncatus*) social structure, with an emphasis on male mating strategies. Boat-based photo-identification surveys were conducted from January 2002 to December 2013. Sighting histories were then split before and after a 2008 CeMV epizootic event. Data analyses were limited to sightings with complete photographic coverage of all animals ($n = 6779$), and individuals sighted ten or more times. Each individual was categorized as a known female (FEM), known male (MAL), or unknown sex (UNK). Pre-CeMV (January 2002 – December 2007) 320 individual dolphins met the sighting criteria (FEM = 159; MAL = 68; UNK = 93), while 258 individual dolphins met the sighting criteria post-CeMV (January 2008 – December 2013; FEM = 129; MAL = 51; UNK = 78). Half-weight indices (HWI), a test for preferred and avoided associations, and a Mantel test were calculated using SOCPROG 2.6 to examine within and between sex bonds. For both datasets, the overall population was found to interact non-randomly ($p = 0.0001$), with low mean levels of association between all individuals of the population pre- and post-CeMV at HWIs of 0.01 ± 0.03 . Within-sex bonds were

significantly stronger than between-sex bonds (Mantel test, $p = 1.00$), and FEMs had significantly lower mean top associations than MALs and UNKs. Mean top associations decreased for FEM-FEM bonds ($\bar{x} = 0.20 \pm 0.08$, 0.18 ± 0.11 ; $p < 0.05$) post-CeMV, whereas MAL-MAL and UNK-UNK top associations were more consistent between data sets (MAL-MAL: $\bar{x} = 0.30 \pm 0.26$, 0.30 ± 0.25 , $p = 0.07$; UNK-UNK: $\bar{x} = 0.27 \pm 0.21$, 0.27 ± 0.25 , $p = 0.38$). Eight MAL/UNK individuals pre-CeMV and fourteen MAL/UNK individuals post-CeMV met the criteria for first-order alliance status ($\text{HWI} \geq 0.8$) within four and seven dyads, respectively. Only one dyad met the criteria in both datasets. There were low levels of association between several alliances; however, none of the alliances met the second-order alliance criteria. These results suggest alliance formation is an alternative mating strategy within the IRL. Recent studies have indicated the prevalence of multi-level alliances at a nearby population within the St. Johns River, Jacksonville, Florida. Thus, there are potentially different ecological pressures on male mating strategies throughout northeast Florida. Recurrent CeMV epizootics have disrupted the IRL dolphin population since at least 1982. Although some changes to the IRL social structure occurred, these results illustrate the overall social plasticity of IRL bottlenose dolphins.

Introduction

Sociality evolves when the benefits of group living outweigh the costs. The most commonly cited advantages of group living are decreased predation risk (Hill and Lee 1998; Sorato *et al.* 2012) and increased transfer of information between individuals (Lusseau and Newman 2004; Clarin *et al.* 2014). The greatest disadvantages, however, are increased competition, both for food and mates (Asensio *et al.* 2009; Watts 1998), and the potential

transfer of infectious diseases (Rogers *et al.* 1998; Craft *et al.* 2011). The relative importance of these costs and benefits in turn determine optimal group size (Pulliam and Caraco 1984; Krause and Ruxton 2002). However, selection pressures like food availability and predation risk are not constant and may change dynamically across space and between habitats (Chapman *et al.* 1995). To balance these variable pressures, several taxa, including primates (Lehmann *et al.* 2007), elephants (Wittemyer *et al.* 2005), spotted hyenas (Smith *et al.* 2008), and dolphins (Wells *et al.* 1987), utilize fission-fusion grouping patterns in which group size and composition change fluidly in order to optimally adjust group size in response to the current environment (Kummer 1971).

Social systems comprise groups of conspecifics that regularly interact and organize in a cooperative manner more so with each other than with members of other such societies (Wilson 1975; Kappeler and van Schaik 2002). In turn, the quality and patterning of these relationships shape the social structure (Hinde 1976; Trivers 1985; Lusseau and Newman 2004; Whitehead 2008). Thus, disturbances, either anthropogenic or natural, that alter the social patterns of individuals will consequently affect a population's social structure. Anthropogenic disturbances, such as habitat fragmentation or restructuring (Banks *et al.* 2007; Richards *et al.* 2013), noise pollution (Nowacek *et al.* 2007), and eco-tourism (Bejder *et al.* 2006) are known to alter social interactions among individuals by affecting their ranging patterns, territoriality, group size, and antipredator behavior. Similarly, natural disturbances, such as hurricanes (Elliser and Herzing 2011, 2014a,b), harmful algal blooms (McHugh *et al.* 2011), and disease outbreaks (Genton *et al.* 2015) that result in death, emigration, immigration, and/or changes in resource availability may also lead to altered association patterns and ultimately a modified social structure. Any such changes to the social structure of a population could subsequently affect patterns of disease

transmission among individuals (Croft *et al.* 2008; Krause *et al.* 2009), thereby creating a cycle of disturbance and social structure modifications.

The degree of social structure reorganization in a population will vary depending on the frequency and intensity of disturbances encountered. In highly social animals, such as cetaceans, multiple concurrent or repeated disturbances could lead to significant changes in social structure. Over the past three decades, cetacean morbillivirus (CeMV), a highly contagious immunosuppressant, has caused several mass mortality events in cetaceans around the world (Van Bresse *et al.* 2014). Within the family Delphinidae, CeMV has shown increased viral infectivity and distribution (Shimizu *et al.* 2013); during mass mortality events, striped dolphins (*Stenella coeruleoalba*) and bottlenose dolphins (*Tursiops* spp.) had the highest documented strandings relative to other cetaceans (Van Bresse *et al.* 2009; Kemper *et al.* 2013; Stephens *et al.* 2014).

Along the southeast coast of the United States, a resident estuarine population of Atlantic bottlenose dolphins (*Tursiops truncatus*) in the Indian River Lagoon Estuarine System (IRL), Florida, has experienced recurrent CeMV epizootics since at least 1982 (Lipscomb *et al.* 1994; Diugnan *et al.* 1996; NOAA Fisheries 2008, 2015; Bossart *et al.* 2010). Since photo-identification studies began on the IRL dolphin population in 1996, two CeMV-related mass mortality events have occurred in 2008 and 2013-2015 (NOAA Fisheries 2008, 2015). Moreover, the IRL population is characterized by higher rates of infectious diseases, toxic responses, and human-related injuries compared to other southeast U.S. inshore populations (Bossart *et al.* 2003; Bossart *et al.* 2005; Reif *et al.* 2006; Murdoch *et al.* 2008; Bechdel *et al.* 2009; Bossart *et al.* 2011). Such recurrent epizootics within the same population provide opportunities to examine social structure reorganization in response to mass mortality events.

Knowledge of social affiliation patterns are relevant to epidemiological investigations due to the likelihood of contact transmission between individuals (Bossart *et al.* 2003; Kent *et al.* 2008). When association is used as a proxy for contact, the more time an individual spends with a carrier, the higher the risk of infection (Newman 2002). In most bottlenose dolphin populations, association patterns are sex-specific due to the sexually segregated nature of these societies (Wells *et al.* 1987; Connor *et al.* 2000; Fury *et al.* 2013). Female dolphins generally have a larger network of associates than males and may belong to a clique of other females with whom they form recurring moderate bonds (Wells *et al.* 1987; Smolker *et al.* 1992). Female bonds may be stable over years, but are more labile than male associations in that they are dependent on reproductive status (Reynolds *et al.* 2000; Möller and Harcourt 2008), home range overlap (Frère *et al.* 2010), and kinship (Connor *et al.* 2000; Möller *et al.* 2006; Frère *et al.* 2010). In contrast, males typically have a smaller network of associates (Quintana-Rizzo and Wells 2001; Smolker *et al.* 1992; Rogers *et al.* 2004) and the strength of male associations and subsequently mating strategies varies considerably among populations.

Adult males often form strong, long-term relationships in the shape of a first-order alliance, which can be defined as an enduring cooperative relationship in an aggressive or competitive context (de Waal and Harcourt 1992). Although alliance partners are observed together during all behavioral states, the apparent primary function of first-order alliances is to cooperate and sequester individual female dolphins (Connor *et al.* 1992a,b; Connor and Krützen 2015; see Chapter 2). Moreover, alliance formation is thought to be critical to reproductive success (Connor *et al.* 1992b; Krützen *et al.* 2004). Although first-order alliances are observed in multiple dolphin populations (Sarasota, U.S.A, Wells *et al.* 1987; The Bahamas, Parsons *et al.* 2003; Port Stephens, Australia, Wiszniewski *et al.* 2009; Shark Bay, Australia, Connor *et al.*

1992a.), not all males at these study sites form alliances and the strength of alliance bonds is variable. In bottlenose dolphins, second-order alliances, consisting of teams of first-order alliances have been observed in Shark Bay, Australia (Smolker *et al.* 1992; Connor and Krützen 2015), and more recently in the St. Johns River, Jacksonville, Florida (SJR; Ermak *et al.*, in review).

The primary aim of this study is to investigate potential effects of the 2008 CeMV mass mortality event on IRL bottlenose dolphin social structure. At least 44 dolphin mortalities, spanning all age classes, were documented during this event (NOAA Fisheries 2008). Therefore, it is hypothesized that this mortality event resulted in altered intra- and intersexual association patterns. In addition, recent spatial analyses of Northeast Florida (NEFL) dolphins indicate there is some home range overlap between the IRL and SJR populations (Nekolny and Gibson, in review). These resident estuarine populations are separated by approximately 190-km and connected by the Intracoastal Waterway and Atlantic Ocean. Given this overlap, the social structure within the IRL is predicted to be similar to that of the SJR. Thus, a comparison of these two populations will also determine if the multi-level male alliances documented in the SJR are present throughout the Northeast Florida geographic region.

Methods

Field Sampling

The Indian River Lagoon (IRL) estuarine system is a 250-km linear estuary located along the central east coast of Florida, covering 876-km² (Figure 1). It is comprised of four water bodies: the Mosquito Lagoon, the Banana River, the Indian River, and the St. Lucie River. The IRL system is bisected by the Intracoastal Waterway (ICW) that extends from Maine to Miami,

Florida. The average depth of the IRL is 1.5-m, with the exception of the dredged ICW channel, which averages a depth of 3.7-m; width ranges from a few meters to 8.9-km (Gilmore *et al.* 1977). Due to the unique linear nature of the study area, animals move within the IRL along a north-south axis (Mazzoil *et al.* 2004, 2008; Durden *et al.* 2011), whereas movement between the estuarine system and the Atlantic Ocean is possible via four inlets and the Canaveral Lock. Despite the potential to move out of the study area, Mazzoil *et al.* (2011) found a high level of residency within the IRL dolphin population. The entire IRL dolphin population is currently recognized by NOAA as one estuarine stock (Waring *et al.* 2011). However, a recent study found six distinct social communities that occupy relatively discrete core areas along the north-south axis of the IRL (Titcomb *et al.* 2015).

Boat-based photo-identification surveys were conducted monthly from January 2000 to December 2013 following standard protocols (Mazzoil *et al.* 2005). Due to the size of the study area, multiple days were needed to cover the entire survey area, and survey dates were consecutive whenever possible. Data collection took place on vessels ranging from 6- to 8-m in length, traveling at a consistent speed of 10-12-km/hr until dolphins were sighted. Proximity was maintained until the dorsal fins of all individuals in the group were photographed using a professional grade digital camera with 400-mm telephoto lens. In addition to photographs, group size and composition, GPS location, environmental conditions, and behavior were recorded. Groups were defined as an aggregation of dolphins within 100-m of each other engaged in similar behavior (Wells *et al.* 1987).

Data Analyses

Photographs were analyzed using standard photo-identification techniques (Würsig and Jefferson 1990; Mazzoil *et al.* 2004). The best photograph of each individual dolphin was

selected and compared to a master catalog. Dorsal fin shape, nick pattern, and scars were utilized to identify individual dolphins. When distinctive dorsal fins could not be matched, dolphins were added to the catalogue as new individuals. Only identified, adult individuals sighted ten or more times were included in analyses to eliminate transient individuals. Calves and juveniles were excluded based upon estimated birth dates when available; sexual maturity criteria followed Mazzaro *et al.* (2012) with females maturing at age seven and males maturing at age ten. Sex determination was based on all available sighting data collected since August 1996. Adults were categorized as female (FEM) based on consistent sightings with a dependent calf in infant position (Mann *et al.* 2000) and as male (MAL) based on direct observation of the genital region or genetically via biopsy sampling. All other individuals were categorized as unknown sex (UNK).

Any sightings without complete photographic coverage and sightings that were less than 30% different from a previous group the same day were excluded (Smolker *et al.* 1992), for a total of 6,779 group sightings analyzed with 1,487 individual dolphins encountered. In order to measure the impact of a significant cetacean morbillivirus epizootic (CeMV) that began in 2008, sightings were split into two 6-year data sets (January 2002- December 2007 and January 2008 – December 2013) before and after the CeMV (NOAA Fisheries 2008). The pre-CeMV data set begins after the 2001 unusual mortality event, which was suspected to be caused by the biotoxin saxitoxin, but is unconfirmed (NOAA Fisheries 2008), while the post-CeMV data set ends near the onset of the more recent 2013-2015 CeMV epizootic (NOAA Fisheries 2015). This CeMV stretched along the Atlantic coast and did not reach Florida until later in 2013 (NOAA Fisheries 2015) and is unlikely to affect the post-CeMV data set that ends in December 2013. For this study 320 individual dolphins were sighted 10+ times pre-CeMV (FEM = 159; MAL = 68; UNK

= 93), while 258 individual dolphins were sighted 10+ times post-CeMV FEM = 129; MAL = 51; UNK = 78). One hundred and eighty-four individual dolphins fit the sighting constraint both pre- and post-CeMV, while the other individuals were unique to each period (42.5% pre- and 38.26% post-CeMV).

Coefficients of association (COAs), specifically half-weight indices (HWIs), were used to approximate the strength of social bonds among individuals (Cairns and Schwager 1987). Half-weight association coefficients are defined as $\frac{2N_{ab}}{N_a + N_b}$, where N_{ab} is the number of times individuals a and b are sighted together and N_a and N_b are the total number of sightings of individuals a and b, respectively (Cairns and Schwager 1987; Smolker *et al.* 1992). Association indices range from 0 (individuals never sighted together) to 1 (individuals always sighted together). SOCPROG version 2.6 was used to calculate all HWIs between individuals (Whitehead 2009). The half-weight index is useful in that it is the most commonly used association index for dolphin studies, and it reduces the bias of photo-identification studies which may underestimate joint sightings, or miss individuals that were truly there (Cairns and Schwager 1987; Wells *et al.* 1987; Smolker *et al.* 1992; Quintana-Rizzo and Wells 2001).

The coefficient of variation of the HWI (S) and the correlation coefficient of the true and estimated association matrices (r) using maximum likelihood procedures were calculated with SOCPROG 2.6 (Whitehead 2008, 2009). The coefficient of variation (S) is a measure of social differentiation in a population with <0.3 indicating homogeneous societies, >0.5 well differentiated societies, and >2.0 extremely differentiated societies (Whitehead 2008). The correlation coefficient (r) is an indicator of the power of the analysis to detect the true social system with values close to 0 a poor representation, values close to 0.4 a moderate representation, and values close to 1.0 indicating a perfect representation of the true social

system (Whitehead 2008). Half-weight index measurements included the mean HWI, which is the average association of all individuals, the mean non-zero HWI, where individuals whom never associate are removed, and the mean top association, which is the average of each individual's maximum bond. In addition, a Mantel test was run to test for differences in associations within and between the sexes, and a two-tailed permutation test (20,000 permutations) for preferred and avoided associates was performed to test for dyads that associate non-randomly ($\alpha = 0.05$) (Whitehead 1995; Bejder *et al.* 1998). Specifically, the "permute groups within samples" test was conducted because it accounts for individuals not present in each sampling interval due to birth, death, and migration (Whitehead 1995). A significantly higher coefficient of variation (CV) of observed association indices in the real data set vs the random data set indicates that preferred companions are present in the populations, while a lower proportion of non-zero association indices in the real data than in the random indicates avoidances (Bejder *et al.* 1998). Half-weight indices for pre- and post-CeMV data sets were compared for FEM-FEM, MAL-MAL, and UNK-UNK top bonds within and between data sets using Mann-Whitney U tests using IBM SPSS Statistics v.22.

Results from the above analyses were further used to identify potential alliances within the MAL and UNK categories combined. First-order alliances were MAL/UNK 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 (Connor *et al.* 1992b, 1999; Möller *et al.* 2001; Parsons *et al.* 2003; Wiszniewski *et al.* 2012; Ermak *et al.*, in review). Second-order alliances are indicated by separate first-order alliances that maintain average coefficients of association either greater than 0.20 with one another (Smolker *et al.* 1992), or greater than or equal to twice the male non-zero average (Elliser and Herzing 2014b;

Ermak *et al.*, in review). Because the average non-zero HWI between MALs in the IRL community was 0.09, we conservatively raised our second-order alliance criterion to $\text{HWI} \geq 0.20$.

Results

Social differentiation, via the likelihood method, suggested a well-differentiated population both pre- and post-CeMV ($S = 0.733$ and $S = 0.736$, respectively). The estimate of correlation between true and estimated association was low with $r = 0.206$ and $r = 0.221$, which typically indicates a below moderate representation of the social system. Pre- and post- CeMV, a test for preferred associations found both the standard deviation and the coefficient of variation to be greater than random, indicating the presence of long-term preferred companions ($p < 0.001$). Additionally, a test for avoided companions found the proportion of real non-zero elements to be less than random, indicating the presence of avoided associations within the IRL population ($p < 0.001$).

Mean levels of association between all individuals of the population were low both pre- and post-CeMV at HWIs of 0.01 ± 0.03 . The overall maximum HWIs for the IRL were found to be 0.29 ± 0.19 and 0.28 ± 0.21 pre- and post-CeMV, respectively. (See Table 1 for a complete list of HWIs within and between the sexes for both data sets). When examining within and between sex associations, mean HWIs within the sexes were significantly stronger than between the sexes during both time periods (Mantel test, $p = 1.00$). Mean HWIs for FEM-FEM, MAL-MAL, and UNK-UNK categories were similar within data sets and there was no change in mean HWIs between data sets.

Pre-CeMV, FEMs had their top association with another FEM in 65.95% of cases with the majority (81.13%) of FEM maximum bonds lying between a HWI of 0.10 and 0.30 (range: 0.07 – 0.64). This pattern remained the same post-CeMV ($U = 9286.50$, $n_1 = 159$, $n_2 = 125$, $p > 0.10$) with females having another FEM as their top associate in 71.95% of cases (78.29% with maximum HWI between 0.10 – 0.30), and a similar range (0.08 – 0.65; Figure 2). Maximum FEM bonds were significantly lower than maximum MAL and UNK bonds within both data sets (Pre-CeMV FEM & MAL: $U = 3742.50$, $n_1 = 171$, $n_2 = 68$, $p < 0.01$; Pre-CeMV FEM & UNK: FEM $U = 5621.00$, $n_1 = 171$, $n_2 = 93$, $p < 0.01$; Post-CeMV FEM & MAL: $U = 1564.00$, $n_1 = 129$, $n_2 = 51$, $p < 0.01$; Post –CeMV FEM & UNK: $U = 3799.50$, $n_1 = 129$, $n_2 = 78$, $p < 0.01$). Top associations for MAL-MAL bonds were similar for both data sets ($U = 1690.50$, $n_1 = 68$, $n_2 = 51$, $p > 0.10$). Males had a same sex top associate in 46.98% and 46.15% of cases, respectively, and their maximum HWIs were higher and more variable than FEM maximum associations (range: 0.09 - 0.87; 0.10 - 0.93). Top associations of UNK-UNKs followed a similar pattern and were not significantly different pre- and post-CeMV ($U = 3181.50$, $n_1 = 93$, $n_2 = 78$, $p > 0.10$). Unknowns had a same sex top associate in 47.57% and 53.33% of cases, respectively, were highly variable, and had a similar range to MAL maximum bonds (range: 0.08 - 0.87; 0.08 - 0.92). There was no significant difference in maximum bonds between MAL and UNK categories pre-CeMV ($U = 2607.00$, $n_1 = 93$, $n_2 = 68$, $p > 0.05$) while post-CeMV MALs had a higher mean top association than UNKs ($U = 1524.50$, $n_1 = 51$, $n_2 = 78$, $p < 0.05$). When MAL and UNK sex categories were combined, 72.58% and 75.35% of MAL/UNK individuals had an individual of the same sex as their top associate pre- and post-CeMV, respectively.

When addressing our alliance criteria, eight MAL/UNK individuals (4.94% of MAL/UNKs) met the criteria for allied males with the formation of four dyads pre-CeMV

(Figure 3a). No first-order alliances had HWIs ≥ 0.20 with another first-order alliance, indicating a lack of second-order level alliance formation. Only two allied dyads associated (mean HWI of 0.04), while all others had zero association between alliances. Only one of these four dyads also met the alliance criteria post-CeMV. This is due to the death/disappearance of one dyad while the other two failed to meet the alliance (HWI > 0.80) criteria. However, post-CeMV, fourteen individuals (10.85% MAL/UNKs) formed seven allied dyads (Figure 3b). All seven of the new dyads had associated with their alliance partner pre-CeMV but with lower HWIs (range: 0.40 – 0.76). There were low levels of association between several alliances; however, none of the alliances met the second-order alliance criteria.

Discussion

Despite the loss of at least 44 individuals, association analyses revealed that the 2008 cetacean morbillivirus (CeMV) mass mortality event did not alter the overall patterns of the Indian River Lagoon (IRL) social structure. Social differentiation analyses suggested a well-differentiated population of non-random associates during both time periods. Although the correlation between true and estimated association was low ($r = 0.206$ and 0.221 , respectively), Titcomb *et al.* (2015) found the population to have a linear distribution, with the lowest HWI values between northern and southern communities. The high social S value and the low coefficient correlation value (r) could be due in part to the low spatial overlap, and therefore a lower chance of inhabitants of the northern and southern communities interacting (Titcomb *et al.* 2015). Thus, these results are likely indicative of the true association patterns of the entire IRL population.

Mean and mean maximum levels of association between all individuals were consistently low both pre- and post-CeMV ($\bar{x} = 0.01 \pm 0.03$ each), with a wide range of association strengths. Moreover, IRL mean HWIs were the lowest relative to other studies on bottlenose dolphins: St. Johns River, Florida ($\bar{x} = 0.05 \pm 0.02$, Ermak *et al.*, in review), Panama City, Florida ($\bar{x} = 0.11 \pm 0.04$, Bouveroux and Mallefet 2010), Moray Firth, Scotland ($\bar{x} = 0.11 \pm 0.04$, Eisfeld and Robinson 2004), and Doubtful Sound, New Zealand ($\bar{x} = 0.47 \pm 0.04$, Lusseau *et al.* 2003). It should be noted that group definition, and subsequently association calculations, vary by study site with most studies using a 100-m diameter rule. Groups were defined using a more conservative definition of group membership (10-m chain rule) in select locations: Shark Bay, Australia (Smolker *et al.* 1992), Bay of Islands, New Zealand (Lusseau *et al.* 2003), and St. Johns River, Florida (Ermak *et al.*, in review). With this in mind, the IRL utilizes the 100-m radius group definition yet still documents the lowest mean levels of association. These results suggest that the majority of IRL dolphins do not associate.

The overall low association rates in the IRL observed in this study are possibly an artifact of the six distinct social communities found pre-CeMV along the north-south axis of the estuary, which exhibit minimally overlapping core areas (Titcomb *et al.* 2015). Communication between these communities can influence the rate and patterning of disease transmission in the IRL (Whitehead 2008), and mortality of community brokers can disrupt this communication (Lusseau and Newman 2004). For example, in Doubtful Sound, New Zealand (Lusseau and Newman 2004) and Little Bahama Bank, Bahamas (Elliser and Herzing 2011), community brokers had a disproportionate effect on communication between communities. These key individuals played a crucial role in the social cohesion of the population as a whole, and network connectivity was broken after their removal despite redundant paths of communication (Lusseau and Newman

2004; Elliser and Herzing 2011). After the loss of community brokers in the Bahamas, both the population's mean COAs and social cohesion within each community increased due to the removal of low COAs (Elliser and Herzing 2011). In contrast to the Bahamas study, there were no apparent changes to the mean HWIs of IRL dolphins following the 2008 CeMV. Two possible explanations exist for this lack of change: either no key individuals were lost during the mass mortality event or because the majority of associations within the IRL were already low, then despite communication disruption between social communities the IRL upheld its association patterns (Lusseau 2003; Lusseau and Newman 2004).

Within the IRL, group size is low ($\bar{x} = 4.1 \pm 3.43$, Kent *et al.* 2008) and strong associations are uncommon. Dolphins that are more solitary are at a lower risk of infection than their more social counterparts, and will likely have a higher survival rate after an epizootic. This pattern has been demonstrated in the Congo gorilla population affected by recurring Ebola outbreaks (Caillaud *et al.* 2006; Genton *et al.* 2015). Similar to the IRL dolphin population, six years after a catastrophic Ebola outbreak gorilla social dynamics had returned to pre-Ebola levels (Genton *et al.* 2015). Further, disease transmission relies not only on the association patterns within populations, but also between them. Mazzoil *et al.* (2011) found minimal interaction between the southern portion of the IRL and the coastal Atlantic population. This high site fidelity suggested low potential for disease transmission for these two populations. However, Durden *et al.* (2011) found that the IRL population experienced a winter influx with the greatest increase in the northern regions of the estuarine system. This northern influx is suggestive of higher rates of transmission within these areas that could then transmit along the north-south axis of the IRL. The origin of the 2008 CeMV is unknown, yet the majority of stranded individuals occurred in the northern IRL region (NOAA Fisheries, 2008). Additionally, the more recent

2013-2015 CeMV migrated south along the Atlantic coastline from New York to Florida and reached the IRL during the winter when the population density is highest (Durden *et al.* 2011; NOAA Fisheries, 2015). Future work, examining intra-community changes may show that the northern communities are the most affected by CeMV epizootics due to their greater rates of interactions with other populations.

With respect to sex-specific associations, the majority of female relationships were low to moderate in strength. This pattern of limited female interactions within the IRL could be a result of foraging specializations within each community (Mann and Sargeant 2003), reduced grouping pressure due to a lack of predation (Weiss 2006), or asynchronous reproductive cycles (Möller and Harcourt 2008). The variability in female maximum association is largely a result of a few outliers: two mixed-sex dyads whose relation to each other is unknown (pre-CeMV) and an immigrating female dyad (post-CeMV). It is hypothesized these females retained a strong association with each other as a result of moving into a novel environment. Studies have shown that female residents are less accepting of female immigrants due to increased feeding and mating competition (Kahlenberg *et al.* 2008; Elliser and Herzing 2011), and residents may even aggressively chase away immigrants (Karczmarski *et al.* 2005). Resistance to immigration of new individuals following the CeMV could have caused reduced social cohesion of the population (i.e., between communities), while at the same time retaining the population's sex-specific association patterns (Lin *et al.* 2004).

In contrast to female relationships, male and unknown top associations were highly variable, and only a small percentage of individuals within the MAL/UNK category formed alliances both pre- and post-CeMV (4.94% and 10.85%, respectively). The doubling in the number of alliances within the IRL contrasts with patterns documented in spotted dolphins

(*Stenella frontalis*) in Little Bahama Bank, Bahamas, following two major hurricanes. Prior to the hurricanes there were multiple first- and second-order alliances, however, after the loss of 36% of the population, multiple first-order alliances were lost and only one second-order alliance remained (Elliser and Herzing 2014b). While some allied males were lost due to the hurricane, the reduced population density within the population potentially may have also contributed to the decrease in alliance complexity. Community structure remained intact and immigration was low after the hurricanes (Elliser and Herzing 2014b); thus, decreased encounter rates with rival males reduced the need for remaining and new first-order alliances to form multi-level alliances (Connor and Whitehead 2005). In addition to increasing reproductive success (Green *et al.* 2011), second-order alliances in spotted dolphins function in agonistic interspecific interactions with sympatric bottlenose dolphins (Herzing and Johnson 1997; Elliser and Herzing 2014a). The bottlenose dolphin community significantly restructured after the hurricanes and aggressive interspecific encounters were rare afterwards (Elliser 2010). The absence of these aggressive encounters likely also reduced the need for second-order alliances (Elliser and Herzing 2014b).

Following the IRL mortality event, the increase in the number of first-order alliances may be explained by compounding variables. Although the ages of alliance members are unknown, alliances crystallize in their early teens (Owen *et al.* 2002) and some individuals may have been too young to form alliances prior to the disturbance. Additionally, in contrast to the spotted dolphin population (Elliser and Herzing 2014b) immigration into the IRL did not significantly decrease. If mortality and immigration rates were sex-biased, encounter rates with rival males could have been altered throughout the population (Lin *et al.* 2004). In areas in which males encounter many rivals, sharing copulations (within a cooperative alliance) presumably has a greater pay off than constantly competing (Whitehead and Connor 2005; Connor *et al.* 2000). As

reviewed in Ermak *et al.* (in review), increased male-male competition appears to be the most useful indicator of dolphin alliance formation, with the highest density locations containing multi-level alliances (2.40 dolphins/km², Shark Bay, Australia: Watson-Capps 2005; 6.76 dolphins/km², SJR: Ermak *et al.*, in review). Thus, demography and density changes by community may have resulted in the increased number of MAL/UNKs that utilized alliances post-CeMV.

The results of this study suggest that IRL alliance formation may be an alternative mating strategy, similar to the neighboring dolphin population within the St. Johns River (SJR), Florida, where a subset of MAL/UNK individuals (29.13%) form multi-level alliances (Ermak *et al.*, in review). Given this similarity and the home range overlap between these two populations (Nekolny and Gibson, in review), it would be expected for the IRL dolphins to exhibit multi-level alliances. However, IRL MAL/UNKs showed no indication of forming multi-level alliances, and display little to no association between first-order alliances. This disparity in alliance complexity may be due to contrasting patterns in seasonal population density influx between the IRL and SJR. The IRL dolphin population is extremely variable, and density estimates show an elevated density of 1.406 dolphins/km² during the winter, whereas the summer is low at 0.387 dolphins/km² (Durden *et al.* 2011). This is in sharp contrast to the SJR where the influx of seasonal residents and transients occurs during the breeding season, when mate competition is highest (Gibson, unpublished data). Because the IRL influx does not occur during the highest competition for mates, it is likely fewer MAL/UNK individuals need to utilize alliance formation to increase their reproductive success.

Conclusions

Recurrent CeMV epizootics have disrupted the IRL dolphin social system since at least 1982 (Lipscomb *et al.* 1994), with subclinical infections occurring in between mass mortality events (Bossart *et al.* 2010). The population showed resilience to demographic changes after the 2008 CeMV despite impairment in adaptive immunity related to chronic exposure of infectious diseases (Reif *et al.* 2006; Murdoch *et al.* 2008), multiple organic pollutants (Fair *et al.* 2007a, 2007b, 2010), and human-related injuries (Bechdel *et al.* 2009). These anthropogenic and natural stressors within the IRL may synergistically interact to favor repeated CeMV epizootics, and over time these factors may have an accumulative impact on the population (Reif *et al.* 2006; Van Bresse *et al.* 2009). Future studies on the effects of the larger, and more recent 2013-2015 CeMV on IRL association and mating patterns will determine if this population continues to be resilient to multiple disturbances.

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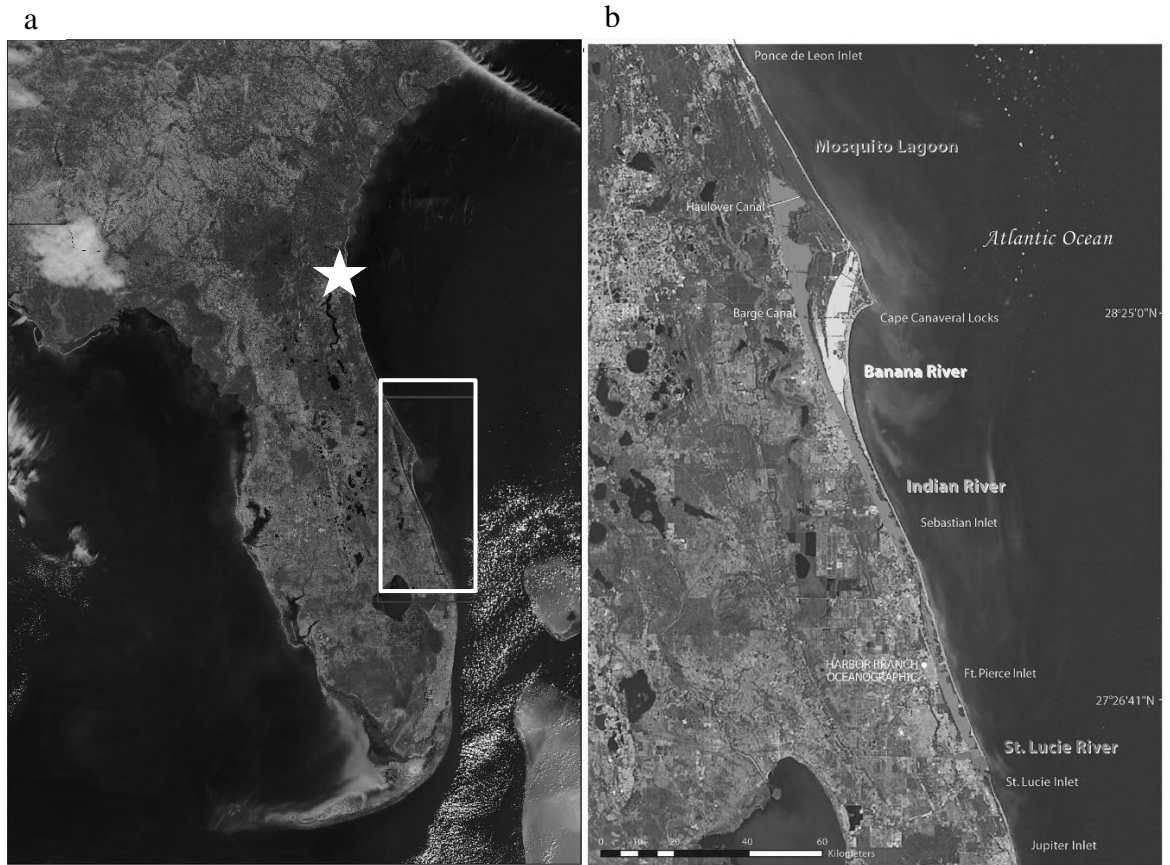
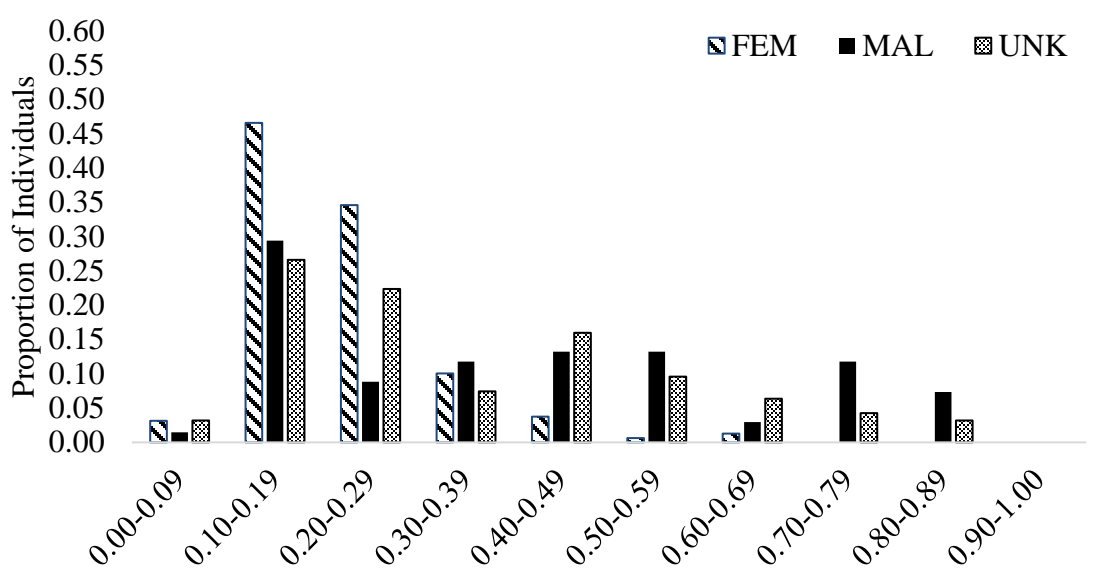


Figure 1. The Indian River Lagoon lies within the white box, which is located 190-km south of the St. Johns River, denoted by the white star. A more detailed map of the Indian River Lagoon study area is shown on the right. Map adapted from Browning *et al.* 2014.

Table 1. Indian River Lagoon half-weight indices (HWIs). Pre-CeMV (January 2002 – December 2007) is shown in dark grey. Post-CeMV (January 2008 – December 2013) is shown in white.

	Mean HWI	Mean Non-zero HWI	Mean Top Association
Overall	0.01 ± 0.03	0.07 ± 0.06	0.29 ± 0.19
	0.01 ± 0.03	0.07 ± 0.06	0.28 ± 0.21
FEM : All	0.01 ± 0.03	0.07 ± 0.05	0.21 ± 0.10
	0.01 ± 0.03	0.07 ± 0.05	0.21 ± 0.11
MAL : All	0.01 ± 0.04	0.07 ± 0.08	0.40 ± 0.24
	0.01 ± 0.04	0.07 ± 0.08	0.41 ± 0.24
UNK : All	0.01 ± 0.04	0.08 ± 0.07	0.35 ± 0.21
	0.01 ± 0.04	0.08 ± 0.07	0.33 ± 0.25
FEM : FEM	0.01 ± 0.03	0.07 ± 0.05	0.19 ± 0.08
	0.01 ± 0.03	0.07 ± 0.05	0.19 ± 0.10
MAL : MAL	0.01 ± 0.06	0.09 ± 0.12	0.31 ± 0.26
	0.02 ± 0.06	0.08 ± 0.11	0.29 ± 0.25
UNK : UNK	0.01 ± 0.04	0.10 ± 0.10	0.27 ± 0.20
	0.01 ± 0.05	0.09 ± 0.10	0.25 ± 0.24
FEM : MAL	0.01 ± 0.03	0.06 ± 0.04	0.13 ± 0.07
	0.01 ± 0.03	0.07 ± 0.05	0.13 ± 0.08
FEM : UNK	0.01 ± 0.03	0.08 ± 0.05	0.16 ± 0.10
	0.01 ± 0.03	0.07 ± 0.04	0.14 ± 0.07
FEM : MAL/UNK	0.01 ± 0.03	0.07 ± 0.05	0.16 ± 0.09
	0.01 ± 0.03	0.07 ± 0.04	0.16 ± 0.08
MAL : UNK	0.01 ± 0.03	0.08 ± 0.08	0.18 ± 0.17
	0.01 ± 0.04	0.08 ± 0.09	0.19 ± 0.19
MAL : MAL/UNK	0.01 ± 0.04	0.09 ± 0.10	0.39 ± 0.25
	0.01 ± 0.05	0.08 ± 0.10	0.39 ± 0.25
MAL/UNK : MAL/UNK	0.01 ± 0.04	0.09 ± 0.10	0.35 ± 0.23
	0.01 ± 0.05	0.08 ± 0.10	0.35 ± 0.26

a)



b)

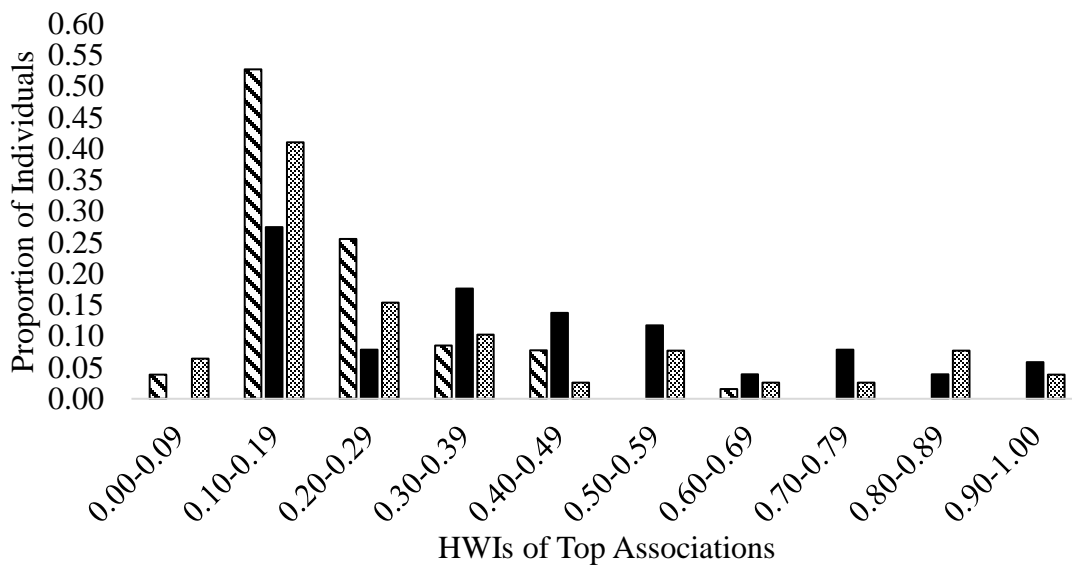


Figure 2. Distribution of top associations of FEM, MAL, and UNK categories pre- and post-CeMV (a and b, respectively). Top associations for all sex categories were highly variable and there was not a clear difference in top associations between the sexes.

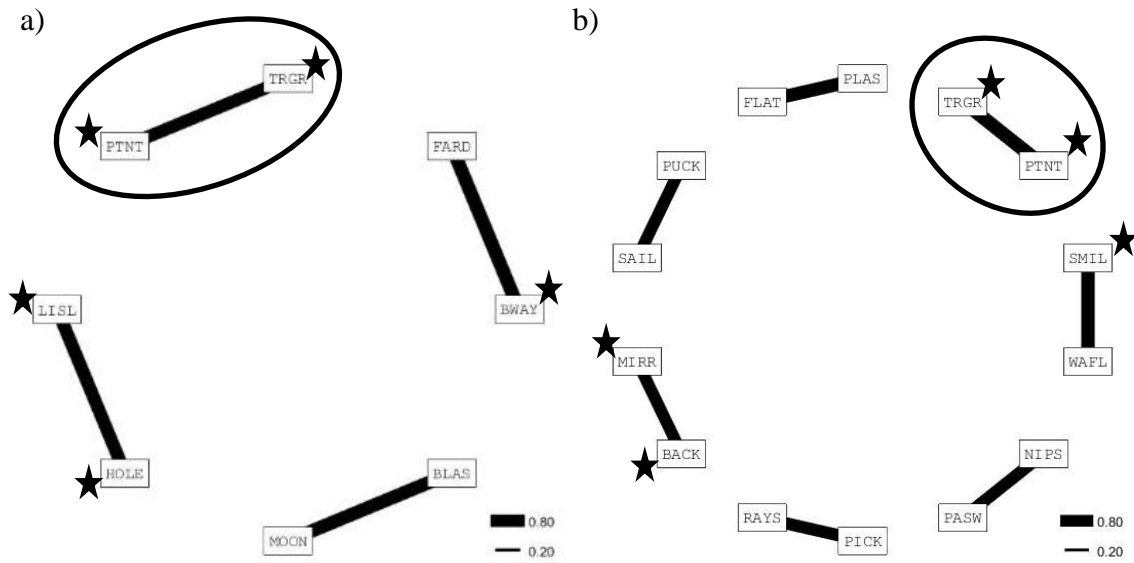


Figure 3. Sociogram of all allied MAL/UNK dyads based on half-weight indices (HWI). Known males are indicated with a star. Only one dyad was observed during both data sets indicated by the circled dyads. Width of line indicates strength of association. 3a. Four dyads formed alliances pre-CeMV (January 2002 – December 2007). 3b. Seven dyads formed alliances post-CeMV (January 2008 – December 2013).

Chapter 2

The Stability and Function of Male Bottlenose Dolphin Alliances in the St. Johns River, Florida

Abstract

Multi-level alliances in bottlenose dolphins have only been observed in a few geographically distinct areas around the world. Recently, both first- and second-order alliances (teams of first-order males cooperating to sequester females) have been documented within the St. Johns River (SJR), Jacksonville, Florida. This study aims to elucidate the stability and function of both first- and second-order alliances within the SJR. Data were collected along a 40-km transect via photo-identification surveys from April 2011 – March 2015. To determine stability, survey data were stratified into two equal time periods (April 2011 – March 2013 and April 2013 – March 2015), and male and unknown sex individuals sighted 5+ times ($n = 126$ and 112 , respectively) were included in data analyses. Using the program SOCPROG v. 2.6, first-order alliances (FO) were identified with criteria adapted from previous publications with the addition of a half-weight index (HWI) cut-off ≥ 0.80 . Second-order alliances (SO) were defined as twice the mean male HWI between first-order alliances for each time period ($\text{HWI} \geq 0.30$ and 0.42 , respectively). Alliances were assigned stability indices based on their maintenance of alliance partners. Patterns of temporal stability were analyzed using lagged association rates (LARs) and lagged identification rates (LIRs). Sighting histories from the entire study were then combined, and alliance association patterns were analyzed with respect to seasonality (breeding vs. non-breeding), female presence, and behavioral state. Results showed considerable variation

in stability for both first- and second-order alliances. No simultaneous falls in LARs and LIRs indicated changes were due to association preferences rather than demographic parameters. With respect to function, results indicated both alliance structures associated year-round. For both alliance structures, a higher proportion of sightings contained females during the breeding season (FO: Md = 0.50, n = 20; SO: M = 0.78, SD = 0.21) compared to the non-breeding season (FO: Md = 0.14, n = 20, Z = -3.73, p < 0.01; SO: M = 0.15, SD = 0.10, t(6) = 5.78, p < 0.01). Additionally, herding events were documented year-round, but were more common in the breeding season (herding events: χ^2 (1, n = 74) = 12.16, p < 0.05). Intra-population variability in alliance stability and formation suggests similar to other areas, alliance formation is a conditionally dependent strategy with males responding to their current social environment. Additionally, SJR alliances likely function within a reproductive context, with second-order alliances more dependent on female presence than first-order alliances.

Introduction

According to socio-ecological theory, ecological parameters (e.g., food resources) are the driving force behind female distribution (Wrangham 1980; van Schaik 1989; Sterck *et al.* 1997), while male distribution is dependent on the distribution of fertile females (Bateman 1948; Trivers 1972; Clutton-Brock 1989). When food resources are patchily distributed both spatially and temporally, and females are defensible resources, males may attempt to guard females (Emlen and Oring 1977). Mate guarding can be an effective strategy to increase reproductive success, though it can also generate increased competition between males (Andersson 1994; Watts 1998). In an effort to decrease intrasexual competition and receive increased relative reproductive output (Watts 1998; Feh 1999; Clutton-Brock and Isvaran 2006), some males

cooperatively mate guard estrous females, even though fertilizations are non-divisible (Noë 1992; van Hooff and van Schaik 1994). This alternative mating strategy has been observed in the shape of coalitions where two or more males opportunistically cooperate during agonistic interactions against other males competing for access to a female (de Waal and Harcourt 1992; van Hoof and van Schaik 1994; Diaz-Munoz *et al.* 2014).

Coalitions are more likely to develop in species where social factors (e.g., estrous duration, group size, and/or dominance hierarchy) reduce the feasibility of individual monopolization of a female (reviewed in Olson and Blumstein 2009). Moreover, complex coalitionary behavior is distinct in that individuals exhibit mutual tolerance, cooperation, and partner preferences (Olson and Blumstein 2009). This is shown in an unusually large group of chimpanzees in Ngogo, Uganda, where high-ranking males were observed switching mating tactics from single to coalitionary mate guarding when group size increased to a point where males were no longer successful at mate guarding alone (Watts 1998). Recurrent coalition formation in this population is influenced by the quality of social bonds, with the most egalitarian coalitions lasting at least seven years (Watts 2002; Mitani 2009). When individuals maintain their cooperative relationships over years, coalitions are then referred to as alliances (de Waal and Harcourt 1992). Increased success in mate guarding through alliance formation has been observed in several species (lions, *Panthera leo*, Packer *et al.* 1991; chimpanzees, *Pan troglodytes*, Watts 1998; bottlenose dolphins, *Tursiops* spp., Krützen *et al.* 2004, Wiszniewski *et al.* 2012). Most notably, the multi-level alliances of dolphins are one of the most complex male mating strategies observed in the animal kingdom (Connor 2007).

The atomistic fission-fusion (Kummer 1971; Rodseth *et al.* 1991) social system of bottlenose dolphins is thought to reduce resource competition for patchily distributed food

resources, while allowing for association preferences within group membership (Connor *et al.* 2000). Due to differing socio-ecological priorities of males and females, bottlenose dolphins most commonly live in sexually segregated societies, with the strongest bonds found within the sexes (Wells *et al.* 1987; Conradt and Roper 2000; Fury *et al.* 2013). Female dolphins generally maintain a larger network of associates than males and may belong to a clique of other females with whom they form recurring moderate bonds (Wells *et al.* 1987; Smolker *et al.* 1992). Some female bonds may be stable over years, but most associations are labile in that they depend upon reproductive status (Reynolds *et al.* 2000; Möller and Harcourt 2008), home range overlap (Frère *et al.* 2010), and kinship (Connor *et al.* 2000; Möller *et al.* 2006; Frère *et al.* 2010). Despite enduring associations, female dolphins gain little from coalitionary behavior since food resources are patchily distributed and hard to defend (Sterck *et al.* 1997). In contrast to females, male dolphins typically have a smaller network of associates (Wells *et al.* 1987), and the strength of male associations and subsequently, coalitionary behavior (i.e., cooperative mate guarding), varies considerably across populations.

Male bottlenose dolphins most commonly utilize one of two mating strategies. Some males are solitary, and encounter and herd females individually (Doubtful Sound, New Zealand: Lusseau *et al.* 2003; Bay of Islands, New Zealand: Mourão 2006; Moray Firth, Scotland: Einfeld and Robinson 2004). Other males may operate within a first-order alliance by forming strong bonds with one or two other males and cooperatively mate guarding individual females (Sarasota, Florida: Wells *et al.* 1987; Shark Bay, Australia: Connor *et al.* 1992a,b; Little Bahama Bank, Bahamas: Parsons *et al.* 2003; Wiszniewski *et al.* 2009). Although several populations exhibit first-order alliances, not all males at these study sites form alliances, and the strength and duration of alliance bonds are variable due to ecological and social variation (Kappeler 2000;

Whitehead and Connor 2005; Gehrt 2008; Ermak *et al.*, in review). Similar to the Ngogo chimpanzees (Watts 1998), alliance formation is thought to increase relative reproductive success for alliance members in areas of high population density (Connor *et al.* 2000; Ermak *et al.*, in review). Preferred first-order alliance partners typically crystallize as juveniles (Owen 2003; Tsai and Mann 2013), but flexibility in partnership has been demonstrated by older males joining younger alliances (Connor and Krützen 2015). Stability of first-order alliances can vary considerably (Wiszniewski *et al.* 2012), and some have been documented to last at least 20 years (Owen *et al.* 2002; Connor 2007). Maintenance of these strong associations over time is dependent on demographic parameters (e.g., death; Connor 2007) and changes in association preferences (Wiszniewski *et al.* 2012).

Alliances of increased social complexity in bottlenose dolphins are uncommon, but some males exhibit second-order alliances in the shape of moderate associations between members of first-order alliances (Connor *et al.* 1992a,b). Information on the behavior of second-order alliances is largely limited to Shark Bay, Australia (Connor *et al.* 1992a,b), where they are thought to cooperate to defend against or participate in a theft of a female from another alliance. Similar to first-order alliances, second-order alliances may last at least 20 years, but membership in second-order alliances is more flexible due to gradual attrition (Connor and Krützen 2015). In Shark Bay, researchers have documented a continuum of second-order alliance sizes (4-14) with no simple relationship between alliance size and long-term stability (Connor *et al.* 2001). These second-order alliances are termed super-alliances, and maintain fluctuating pair and trio formations among members while exhibiting partner preferences within the larger group (Connor *et al.* 1999; Connor and Krützen 2015). Third-order alliances, noted as cooperation between two or more second-order alliances, are also suspected in this area and are thought to increase the

chances of having allies nearby (Connor *et al.* 2011; Connor and Krützen 2015). Both super-alliances and third-order alliances are thought to be unique to Shark Bay, Australia, while second-order alliances have recently been documented in the St. Johns River, Florida (Ermak *et al.*, in review). This was the first report of second-order male alliances in bottlenose dolphins (*Tursiops truncatus*) outside of Shark Bay, Australia.

The recent research in the St. Johns River (SJR; Jacksonville, FL) indicates that the social structure of this dolphin community is surprisingly similar to that observed in Shark Bay. St. Johns River dolphins appear to form both first- and second-order alliances (Ermak *et al.*, in review), in which a reduced portion of SJR males and unknown sex individuals (presumed males) form first-order (29%) or second-order (19%) alliances. These results suggest male alliances may be an alternative mating strategy in this population, however, these numbers may be an underestimate confounded by the inclusion of juvenile individuals (Ermak *et al.*, in review). Thus far, analyses on bottlenose dolphin male alliances are limited to a few populations in which the majority of adult males form alliances (Sarasota, Florida: Owen *et al.* 2002; Port Stephens, Australia: Wiszniewski *et al.* 2012; Shark Bay, Australia: Connor and Krützen 2015). This study will expand the current literature on male alliances by analyzing a population in which alliance formation is uncommon, yet allied males exhibit increased social complexity. More specifically, this study will determine if both first- and second-order alliances maintain strong associations over time, and if alliance association strength can predict alliance stability for this area. Additionally, in an effort to determine if SJR male alliances function within a reproductive context, association patterns will be examined with respect to seasonality, female presence, and behavioral state.

Methods

Field Sampling

The St. Johns River (SJR) is a 500-km well-mixed mesohaline riverine system that drains into the Atlantic Ocean at Mayport Inlet in Jacksonville, Florida (DeMort 1991). The brackish water flows from south to north and can reach depths up to 18-m within dredging zones (DeMort 1991). In the Jacksonville area, the SJR is an urbanized waterway that contains a major international shipping port, U.S. Naval and Coast Guard stations, and commercial fishing fleets. Additionally, it is bisected by the Intracoastal Waterway (an inland waterway that runs north to south paralleling the coast) 8-km from the mouth of the river (DeMort 1991; Benke and Cushing 2005; University of North Florida and Jacksonville University 2013). Previous work on the Jacksonville estuarine stock of bottlenose dolphins from 1994-1997 indicated several behaviorally and genetically distinct communities including the SJR community studied here (Caldwell 2001; NOAA Fisheries 2014). Recent work on the SJR dolphin community indicates over 300 dolphins utilize the river annually, with at least half of these being year-round residents (Nekolny and Gibson, in review).

Boat-based photo-identification surveys were conducted from April 2011 to March 2015 along a fixed 40-km transect in the St. Johns River (SJR). Surveys extended from Mayport Inlet (N30.39904, W-81.39396) at the mouth of the SJR to the Hart Bridge in downtown Jacksonville (N30.31479, W-81.62987), alternating direction of travel each week (Figure 1). Surveys were conducted from either a 6.4-m Carolina skiff or 7.9-m Twin Vee catamaran while traveling at a consistent survey speed of 10-12 km/hr until dolphins were sighted.

During each dolphin sighting, the dorsal fins of all individuals within a group (conservatively defined using a 10-m chain rule as in Smolker *et al.* 1992) were photographed

for later identification (Würsig and Jefferson 1990) using a professional grade digital camera with 400mm telephoto lens. Photographs were analyzed using standard photo-identification techniques (Würsig and Jefferson 1990; Mazzoil *et al.* 2004), with the best photograph of each individual dolphin from each sighting selected and compared to a master catalog. Dorsal fin shape, nick pattern, and scars were utilized to identify individual dolphins. All distinctive, unmatched dolphins were added as new individuals to the catalog. Any sightings without complete photographic coverage and sightings that were less than 30% different from a previous group the same day were excluded (Smolker *et al.* 1992). Along with photo-identification data, detailed behavioral and environmental variables (e.g., salinity and water temperature), as well as GPS coordinates were collected.

For sex identification purposes, all available sighting data were used (March 2011 – February 2016). Individuals were categorized as females (FEM) by the current or past presence of a calf in infant position (Mann *et al.* 2000) in at least two sightings. Males (MAL; n=23) were identified based on the direct observation of the genital region or genetically via biopsy sampling (NOAA Fisheries, unpublished data). All other individuals were categorized as unknown sex (UNK), which includes both presumed males (based on behavior) and non-reproductive females. Thus, some groups within the analyses may have been miscategorized when examining the effect of female presence. However, as demonstrated in Ermak *et al.*'s (in review) social structure analyses, the vast majority of UNK individuals are likely true males.

Alliance Stability

Data were stratified into two equal time periods (April 2011 – March 2013 and April 2013 – March 2015), and only identified male and unknown sex individuals sighted five or more times during each time period were included in analyses (n = 126 and 112, respectively). Male

alliance members were identified by coefficients of association (COA), specifically half-weight indices (HWIs), generated within SOCPROG version 2.6 (Cairns and Schwager 1987; Whitehead 2009). Half-weight association coefficients are defined as $2N_{ab}/(N_a + N_b)$, where N_{ab} is the number of times individuals a and b are sighted together, and N_a and N_b are the total number of sightings of individuals a and b, respectively (Cairns and Schwager 1987; Smolker *et al.* 1992). Association indices range from 0 (individuals never sighted together) to 1 (individuals always sighted together). The half-weight index is useful in that it is the most commonly used association index for dolphin studies, and it reduces the bias of photo-identification studies which may underestimate joint sightings or miss individuals that were truly present (Cairns and Schwager 1987; Wells *et al.* 1987; Smolker *et al.* 1992; Quintana-Rizzo and Wells 2001).

First-order alliances were defined as MAL/UNK individuals that: 1) had $HWI \geq 0.80$, 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 (Connor *et al.* 1992b, 1999; Möller *et al.* 2001; Parsons *et al.* 2003; Wiszniewski *et al.* 2012; Ermak *et al.*, in review). Second-order alliances consisted of separate first-order alliances that maintained moderate coefficients of association greater than twice the average association of males (Elliser and Herzing 2014a; Ermak *et al.*, in review). The half-weight indices of each first- and second- order alliance were compared between two equal time periods (April 2011 – March 2013 and April 2013 – March 2015) to assess stability. Each alliance was assigned a stability index of one if they only met the alliance criteria during one time period or switched partners between time periods, and a stability index of two if they were identified as an alliance during both time periods (procedure adapted from Silk *et al.* 2006; Mitani 2009; Wiszniewski *et al.* 2012). Half-weight indices for each alliance were averaged across the two time periods, and then logistic regression analyses were

performed to describe the relationship between the mean HWI of each alliance and alliance stability. Alliances with a stability index of one will be referred to as unstable, and alliances with a stability index of two will be referred to as stable. One first-order and one second-order alliance were excluded from regression analyses due to these individuals not meeting the minimum of five sightings criterion during both time periods. To assess temporal changes in alliance stability across the entire study period (Apr. 2011 – Mar. 2015), lagged association rates (LARs; Whitehead 1995) were generated within each stability index category. The LAR is the probability of two individuals associating τ time units after a previous association (Whitehead 1995; Whitehead 2008). Standard errors and precision estimates of LARs were obtained with a temporal jackknife procedure using a grouping factor of one day (Whitehead 2008). Calculated LARs were then compared to the null association rate (NAR), which demonstrates the temporal stability of individuals if they associated randomly (Whitehead 2007, 2008). Temporal association patterns were then compared to six simulated models of social structure for each stability index using maximum likelihood and binomial loss methods to determine the best-fit social system model (Whitehead 1995, 2008). These models consider associations of constant companions (individuals associating for long periods of time), casual acquaintances (individual associate for some time and then disassociate, possibly re-associating again), and rapid disassociations (associates disassociate in a short time; Whitehead 2007, 2008).

To account for demographic effects on the temporal association patterns, such as emigration or mortality, the LAR was compared to the nonsocial lagged identification rate (LIR), which is the probability of an individual remaining within the study area (Whitehead 2001, 2008). LIRs are constant in a closed population, but decline when individuals are leaving the population through emigration or mortality, whereas leveling off after a fall indicates re-

immigration, or a mixed population of residents and transients (Whitehead 2001, 2008). A simultaneous fall in LAR and LIRs indicate demographic factors and not association preferences are affecting alliance stability (Whitehead 2008). Standard errors were obtained using the bootstrap technique (Whitehead 2007). Similar to the LAR analyses, best-fit models were fitted to the observed LIR data using maximum likelihood and binomial loss methods (Whitehead 1995, 2008). Parameters of the LIR models were estimated by maximizing the summed log likelihoods (Whitehead 2001). Demographic parameters examined in LIR analyses included population size, mean residence time, mean time outside the study area, emigration, immigration, and mortality rates. To select the best-fit model for both LAR and LIR analyses, either the minimum Akaike's Information Criterion (AIC) or Quasi-Akaike's Information Criterion (QAIC) value was used depending on evidence of overdispersion (Burnham and Anderson 2002; Whitehead 2007). The $\Delta\text{AIC}/\Delta\text{QAIC}$ value for each model was then weighted to determine the relative likelihood of the model, given the data (Burnham and Anderson 2002).

Alliance Function

Regardless of changes in alliance membership (i.e., stability), the function of both first- and second-order alliances was not expected to differ between time periods. Thus, association data from the two time periods were combined (April 2011 – March 2015) to assess alliance function. However, data on individual alliances were only analyzed during the time periods these individuals met all of the alliance criteria. For example, first-order alliance BONO and EDGE only met the alliance criteria (e.g., $\text{HWI} > 0.80$) during April 2011 – March 2013, therefore, no data were analyzed for these individuals from April 2013 – March 2015.

To examine the seasonality of second-order alliances, sighting histories were first stratified by season: breeding (BR; April – September) and non-breeding (NBR; October –

March). These seasons are based on reproductive analyses within the SJR specifically (Gibson, unpublished data). Next, the percentage of sightings in which focal first-order alliance pairs were observed with their second-order alliance partners were compared between these seasons.

Seasonal activity budgets were then assessed for focal first- and second-order alliances. Predominant group activity was classified as one of four behavioral states: travel, forage, social, and rest (defined in Table 1). Chi-square goodness-of-fit tests were used to determine if behavioral states were equally distributed across seasons. Of the behavioral states, social behavior is thought to be most closely linked to the function of alliances. Thus, the frequency of social behavior was then compared between focal first- and second-order alliances and between the breeding and non-breeding seasons. It is important to note that for all analyses comparing alliance structures, focal first-order alliance data did not include sightings that contained their second-order alliance partners in order to reduce bias

To examine the effect of female presence on alliance association, the percentage of sightings in which focal first- and second-order alliances were with females was analyzed, and then further compared between seasons (breeding vs. non-breeding). The frequency of social behavior for both alliance structures was then examined to determine if alliances socialized more when females were present compared to when females were absent. Data were analyzed using either parametric (Independent and paired t-tests) or non-parametric (Mann-Whitney U and Wilcoxon Signed-Rank Tests) statistics as required.

Lastly, the seasonality of herding events was examined. Herding events can be short-lived (Connor *et al.* 1992), thus, these events could be documented *ad libitum* within surveys (Altmann 1974). Herding events were identified by males consistently surfacing synchronously and swimming in formation (flanking) behind a known female (Connor *et al.* 1996).

Additionally, herding events were documented if a capture attempt of a female, escape attempt by the female, or physical aggression towards the female were observed (adapted from Connor *et al.* 1992b, Connor *et al.* 1996, Möller *et al.* 2001, Watson-Capps 2005). Chi-square goodness-of-fit tests were used to determine if herding events were equally distributed between seasons, and were restricted to cooperative herding between alliance partners only during the time period dyads met the alliance criteria.

Results

Alliance Stability

Based on our alliance criteria, there were 15 first-order and 7 second-order alliances during the first time period (Figure 2a,b), comprising 11.90% of male and unknown sex individuals. During the second time period (Figure 2c,d), there were 15 first-order and 1 second-order alliances, comprising 13.39% of male and unknown sex individuals. Although the number of first-order alliances remained the same, alliance identity changed between time periods resulting in 20 unique first-order alliances and 7 unique second-order alliances. When assessing first-order alliance stability, 10 alliances were observed in only one of the two time periods (50%) and 10 alliances remained with the same alliance partner during both time periods (50%). Six second-order alliances met the alliance criteria during only the first time period (85.71%), while only one second-order alliance met the criteria during both time periods (14.29%). Of the alliances that did not last the whole study period only two first-order alliances (which formed a second-order alliance together) ended due to the disappearance of alliance partners.

The mean strength of association within alliances varied considerably for both first-order (FO; \bar{x} HWI ranging from 0.56 to 1.00) and second-order alliances (SO; \bar{x} HWI ranging from

0.26 to 0.70). However, logistic regression models were able to distinguish between stability indices for both first- and second-order alliances (FO: $\chi^2(1, n = 18) = 14.91, p < 0.05$; SO: $\chi^2(1, n = 6) = 5.407, p < 0.05$). The logistic regression model explained between 56.3% (Cox and Snell R^2) and 75.4% (Nagelkerke R^2) of the variance in first-order alliance stability and correctly classified 77.8% of cases. For second-order alliances, the logistic regression model explained between 59.4% (Cox and Snell R^2) and 100.0% (Nagelkerke R^2) of the variance in alliance stability and correctly classified 83.3% of cases. The close relationship between association strength within alliances and the duration of alliances was further supported by lagged association rate (LAR) analyses. LARs of all comparisons remained above the null association rates, indicating alliances associated non-randomly. Within each category, data include association both within and between alliances in that category, which is why these association values are lower than the alliance criteria of $HWI \geq 0.80$. Association rates of unstable first-order alliances were initially high (0.65), but gradually decreased and dropped below the association levels of stable first-order alliances after approximately one year (Figure 3). Association rates decreased again to 0.30 after two years. Stable first-order alliances' association rates remained around 0.50 for a duration of at least three years. The most parsimonious LAR social system model (minimum QAIC value) for unstable first-order alliances described rapid disassociation, constant companions, and casual acquaintances (see Table 2 for complete list of LAR best-fit social system models). Stable first-order alliances, however, had a social system model that only described two levels of association: constant companions and rapid disassociation.

Association rates between the six unstable second-order alliances were initially moderate (0.55), but decreased after one year, and again after two years similar to the unstable first-order alliances (Figure 4). The one stable second-order alliance association levels were consistently

higher (0.80) than the unstable second-order alliances, and even began to increase after two years. The best-fit model for unstable second-order alliances described rapid dissociation and casual acquaintances. More stable second-order alliances fit a model that suggests two levels of casual acquaintances.

The lagged identification rates (LIRs) for all alliance structure and stability indices were highly variable for the first 10 days and began to stabilize close to 100 days. Unstable first-order alliances were suggested to be affected by emigration and mortality (Figure 5; see Table 3 for a complete list of LIR best-fit social system models), while stable first-order alliances were suggested to be affected by emigration and re-immigration. Unstable second-order alliances had two best-fit models (Figure 6a), that indicated the occurrence of emigration and re-immigration. Stable second-order alliances (Figure 6b) also had two best-fit models indicating the occurrence of both emigration and mortality. However, the LIRs for all stability and alliance categories did not coincide with the LAR plots, indicating association rates were not affected by these demographic parameters.

Alliance Function

Second-order alliances were found to associate year-round. There was no significant difference in the proportion of sightings focal first-order alliances associated with their second-order alliance partners during the breeding ($M = 0.59$, $SD = 0.05$) and non-breeding seasons ($M = 0.51$, $SD = 0.11$, $t(9) = 0.534$, $p > 0.10$; Figure 7). Activity budgets for both focal first- and second-order alliances were unequally distributed among behavioral states for both the breeding and non-breeding seasons (FO BR: $\chi^2(3, n = 197) = 257.1$, $p < 0.05$; FO NBR: $\chi^2(3, n = 111) = 119.4$, $p < 0.05$; SO BR: $\chi^2(3, n = 50) = 73.84$, $p < 0.05$; SO NBR: $\chi^2(3, n = 27) = 27.67$, $p <$

0.05; Figure 8). Both alliance structures were most likely to be observed traveling year-round ($\bar{x} = 68.19\%$).

When evaluating social behavior, focal first-order alliances were more likely to be observed socializing during the non-breeding (Md = 0.10) than breeding season (Md = 0.00, $Z = -2.55$, $p = 0.01$), whereas there was no significant difference in the proportion of social sightings between the breeding (Md = 0.17) and non-breeding (Md = 0.17) seasons for focal second-order alliances ($Z = -0.52$, $p > 0.50$). Additionally, during the breeding season focal second-order alliances were more likely to be observed socializing than focal first-order alliances (FO: Md = 0.07, $n = 20$; SO: Md = 0.12, $n = 7$, $U = 21$, $p < 0.01$). During the non-breeding season, focal first- and second-order alliances socialized at similar proportions (FO: Md = 0.10, $n = 20$; SO: Md 0.17, $n = 7$, $U = 65.5$, $p > 0.50$).

When examining the effect of female presence on alliance association, both focal first- and second-order alliances were more likely to be observed with known females (FO: $\bar{x} = 0.62 \pm 0.24$; SO: $\bar{x} = 0.92 \pm 0.15$) compared to without females (FO: $\bar{x} = 0.38 \pm 0.24$, $t(19) = 2.315$, $p < 0.05$; SO: $\bar{x} = 0.08 \pm 0.15$, $Z = -2.41$, $p < 0.05$). Focal second-order alliances had a higher proportion of sightings with females than focal first-order alliances (FO: Md = 0.65, $n = 20$; SO: Md = 1.00, $n = 7$, $U = 18.5$, $p < 0.01$). Analyses were further stratified by season to determine if there were seasonal effects on female presence and alliance association (Figure 9). For both alliance structures, a higher proportion of sightings contained females during the breeding season (FO: Md = 0.50, $n = 20$; SO: $\bar{x} = 0.78 \pm 0.21$) compared to the non-breeding season (FO: Md = 0.14, $n = 20$, $Z = -3.73$, $p < 0.01$; SO: $\bar{x} = 0.15 \pm 0.10$, $t(6) = 5.78$, $p < 0.01$). During the breeding season, focal second-order alliances had a higher proportion of sightings with females than did focal first-order alliances (FO: $\bar{x} = 0.49 \pm 0.21$, SO: $\bar{x} = 0.78 \pm 0.21$, $t(25) = -3.08$, $p < 0.01$).

Moreover, there was only one sighting containing a second-order alliance without females present during the breeding season. When known females were absent, there was no difference in the seasonal proportion of sightings for both first- and second-order alliances (FO BR: Md = 0.13, n = 20; FO NBR: Md = 0.17, n = 20, Z = -0.10, p > 0.50; SO BR: Md = 0.00, n = 7; NBR: Md = 0.00, n = 7, Z = -1.34, p > 0.10).

When analyzing social behavior with respect to female presence, focal first-order alliances were more likely to socialize when females were present (Md = 0.07, n = 20) compared to absent (Md = 0.00, n = 20, Z = -2.41, p < 0.05). In contrast, focal second-order alliances socialized at similar levels with (Md = 0.13, n = 7) and without females (Md = 0.00, n = 7, Z = -0.41, p > 0.50). When comparing alliance structures, focal first- and second-order alliances socialized with and without females at similar proportions to each other (with females: FO Md = 0.07, n = 20; SO Md = 0.13, n = 7, U = 50.0, p > 0.50; without females: FO Md = 0.00, n = 20; SO Md = 0.00, n = 7, U = 51.0, p > 0.10). Analyses of cooperative herding events revealed focal first-order alliances herded females year-round, with 34.74% of sightings with females containing herding events. However, herding events were more likely to be observed during the breeding season (70.3%) than the non-breeding season (29.7%; χ^2 (1, n = 74) = 12.16, p < 0.05)).

Discussion

Alliance Stability

Consistent with previous St. Johns River (SJR) social structure analyses (Ermak *et al.*, in review) a low proportion of male and unknown sex individuals formed alliances (23.81% and 26.79%, respectively). These proportions are reduced compared to other study sites where the proportion of allied males range from 57% in Sarasota, FL (Owen *et al.*, 2002) to 85% in Shark

Bay, Australia (Smolker *et al.*, 1992), with other study sites falling in between (Little Bahamas Bank, Bahamas, Parsons *et al.* 2003; Port Stephens, Australia, Wiszniewski *et al.* 2012).

Although calves were excluded from analyses, it is likely the SJR proportions are somewhat diluted with sexually immature females, and immature males who have not yet formed an alliance or are between partners (Owen *et al.* 2002). Despite the small number of SJR alliances, several alliances formed second-order alliances, which were previously thought to be unique to Shark Bay, Australia (Connor *et al.* 1992a,b). However, the frequency of SJR multi-level alliance formation changed over time, with more alliances participating in second-order alliances during the first time period (Figure 2).

Alliances exhibited intra-population variation in their stability and structure, in which males formed strong and highly stable first-order alliances, strong but unstable first-order alliances, highly stable second-order alliances, or unstable second-order alliances. Of the first-order alliances, some formed either stable or unstable second-order alliances, while others never associated within a second-order alliance. Additionally, logistic regression analyses were able to distinguish between stability indices for both alliance structures. These findings reflect those in other areas, in which alliances of shorter duration have been described by lower mean association rates (Connor *et al.* 2000; Owen 2003), while alliances with higher mean association rates were more likely to maintain a relationship over time (Wiszniewski *et al.* 2012). The relationship between association strength and duration of alliances was further supported by the lagged association rate analyses.

First- and second-order alliances within both stability indices were determined to be non-random associates, and there was no simultaneous fall in LARs and LIRs. These results suggest that changes in temporal stability were a product of association preferences within the alliances

and not a result of demographic variables (i.e., emigration, immigration, mortality). Unstable first-order alliances exhibited a variety of temporal associations, with an exponential model of best fit that described constant companions, casual acquaintances, and rapid disassociations. This potentially indicates that the long-term relationships within first-order alliances began to degrade over time, while new first-order alliances were forming, and short-term relationships were formed and terminated with others. In contrast, the temporal associations of stable first-order alliances were characterized as constant companions and rapid disassociations. This illustrates that the long-term relationships within stable first-order alliances were maintained throughout the study, while short-term associations occurred with other individuals. Unstable second-order alliance associations were described as casual acquaintances and rapid disassociations, demonstrating short-term relationships between individuals that lasted at least a year and rapid disassociations from all others. The one stable second-order alliance was defined as two levels of casual acquaintances, which is potentially a consequence of the differing association rates within and between the two first-order alliances that comprised the stable second-order alliance.

Interestingly, unstable first- and second-order alliances LARs had concurrent falls near the end of the first time period (Figures 3 and 4). These falls coincided with a partner switch that occurred within one of the second-order alliances. These individuals were members of multiple second-order alliances, and their partner switch may have had a disproportionate effect on the social interactions with other second-order alliances (Lusseau and Newman 2004). Consequently, this potentially resulted in the degradation of several second-order alliances; thereby, reducing the number of males that associated in second-order alliances during the second time period. Thus far, this is the only known first-order alliance partner switch in the SJR where all individuals remained in the area. However, future investigations are required within a

larger data set to determine if partner switching is an uncommon occurrence within the SJR. Additionally, examination of group size and social network could shed light into the variation of SJR alliance stability. Unstable alliances in Port Stephens, Australia, were found to associate within a much larger male social network than stable alliances (Wiszniewski *et al.* 2012). Associating within a larger network may reduce the cost of switching allies and potentially increase reproductive success for those individuals (Whitehead and Connor 2005; Wiszniewski *et al.* 2012).

Alliance Function

First-order alliances associated year-round, and were more likely to socialize when females were present and during the non-breeding season. Forging and maintaining an alliance within a fission-fusion society is a cognitively demanding process that requires maintenance often exhibited in the form of synchrony (Connor *et al.* 2006), affiliative contact (Connor *et al.* 2000), or consorting females (Connor *et al.* 1996; Connor and Mann 2006). Thus, year-round formation of first-order alliances is likely an essential component of alliance formation and stability. Furthermore, association during the non-breeding season, when mating competition is reduced, may be an important time for males to interact with each other (Owen *et al.* 2002). Increased social behavior during the non-breeding season could indicate instability in social bonds, as seen in Shark Bay (Connor and Smolker 1995). Males may be attempting to strengthen established bonds by consorting non-receptive females (Connor *et al.* 1996; Connor and Mann 2006), improve their social position within their alliance, or compete for future alliance partners (Connor and Smolker 1995). Due to the turbidity of the water in the SJR, it is difficult to observe agonistic actions; however, rates of aggression can be documented by the presence of tooth rake marks. Previous tooth rake analyses within the SJR showed males and unknown sex individuals

to have a greater prevalence of new rake marks than females (Ermak 2014). There was also a trend towards males/unknowns receiving more new rake marks during the non-breeding season (Ermak 2014), which is consistent with the increased social behavior observed during this study.

Similar to first-order alliances, second-order alliances were more likely to be observed year-round and when females were present. Given that second-order alliances are thought to function within a reproductive context, their association should largely occur within the breeding season. Potentially, these perplexing findings are explained by the documentation of first-order alliances herding year-round. Results from this study mirror those in Shark Bay, where consortships of females occur year-round but lasted longer during the breeding season (Connor *et al.* 1996). Additionally, even in Shark Bay thefts are relatively uncommon, highlighting the importance of female defense (Smolker *et al.* 1992; Connor *et al.* 1992a, 1999; Connor and Mann 2006; Connor 2007). If SJR first-order alliances are herding females year-round, then the presence of their second-order alliance partners may function to opportunistically assist in capturing females, while deterring rival males from attempting thefts. These multi-functions are supported by behavioral observations of a second-order alliance cooperatively capturing a female in February 2016 (non-breeding season; Gibson, unpublished data). After the female was captured and guarded by one of the first-order alliances, the second-order partners increased their distance to 100-m yet remained in the area.

Year-round herding may be a result of females cycling outside of the breeding season. This cycling is unlikely conceptive, given the seasonal reproduction within the SJR (Gibson, unpublished data) and the year long gestation of bottlenose dolphins (Schroeder and Keller 1989; Schroeder 1990). Females may undergo anovulatory cycling during the non-breeding season to reduce the risk of infanticide or to assess male quality prior to the breeding season (Connor *et al.*

1996; Moors 1997; Owen *et al.* 2002). In addition to anovulatory cycling by females or strengthening male-male bonds, males may be intimidating females and herding them prior to their maximum attractiveness when increased competition makes monopolizing a female more difficult; similar to what has been observed in chimpanzees (Goodall 1986; Connor *et al.* 1996). Aggressive behavior was not analyzed within this study; however, herding events were identified by alliance members flanking their female consort. Flanking a female enables male alliances to maintain closer proximity to their consort for longer periods of time, and in combination with synchrony may give male alliances more control over their female consort (Connor *et al.* 1992b; Owen 2003). Additionally, previous tooth rake analyses found that while SJR females received new rake marks year-round, with the highest occurrence of new rake marks during the winter (non-breeding season) and spring (Ermak 2014). Thus, there is likely a coercive nature to herding within the SJR similar to other areas (Shark Bay: Connor *et al.* 1996, Connor and Vollmer 2009; Clarence River estuary: Fury *et al.* 2013).

Conclusions

Despite the increased alliance complexity within the SJR, a reduced proportion of male and unknown individuals form alliances. Although this number is somewhat diluted by immature individuals, alliance formation within the SJR is likely a conditionally dependent strategy utilized by a subset of males/unknowns (DuVal 2007). Similar to other areas that support male alliances, intra-community variation in stability and structure suggests that SJR male alliances form in response to their social environment. A review of ecological and demographic variables found that increased male-male competition best predicted alliance formation, with areas of elevated population density supporting second-order alliances (Ermak *et al.*, in review). Further

investigations comparing SJR alliance stability to demography changes would allow for an examination of this predictive value within the same population.

While alliance stability was highly variable, both first- and second-order alliance association was dependent on female presence suggesting SJR alliances likely function within a reproductive context. Moreover, second-order alliances were rarely observed without a female, indicating second-order alliances are more dependent on female presence than first-order alliances. Ultimately, SJR first-order alliances likely function to cooperatively herd females, while second-order alliances assist in capture and defense of their first-order alliance partners' female consorts. Because second-order alliances associate frequently, they may also function to increase the chances of having allies nearby, similar to the suspected third-order alliances in Shark Bay (Connor *et al.* 2011). Moreover, year-round association within first- and second-order alliances suggests maintaining relationships during the non-breeding season may play an important role in mating success the following breeding season (Connor *et al.* 1996; Owen *et al.* 2002). Prior to Ermak *et al.*'s (in review) social structure analyses, documentation of multi-level alliances in bottlenose dolphins were limited to Shark Bay, Australia, where the majority of males form alliances (85%, Smolker *et al.* 1992). The reduced proportion of allied individuals in the SJR provides a sharp contrast to Shark Bay, and enriches the current understanding of the adaptive significance of multi-level alliances in bottlenose dolphins.

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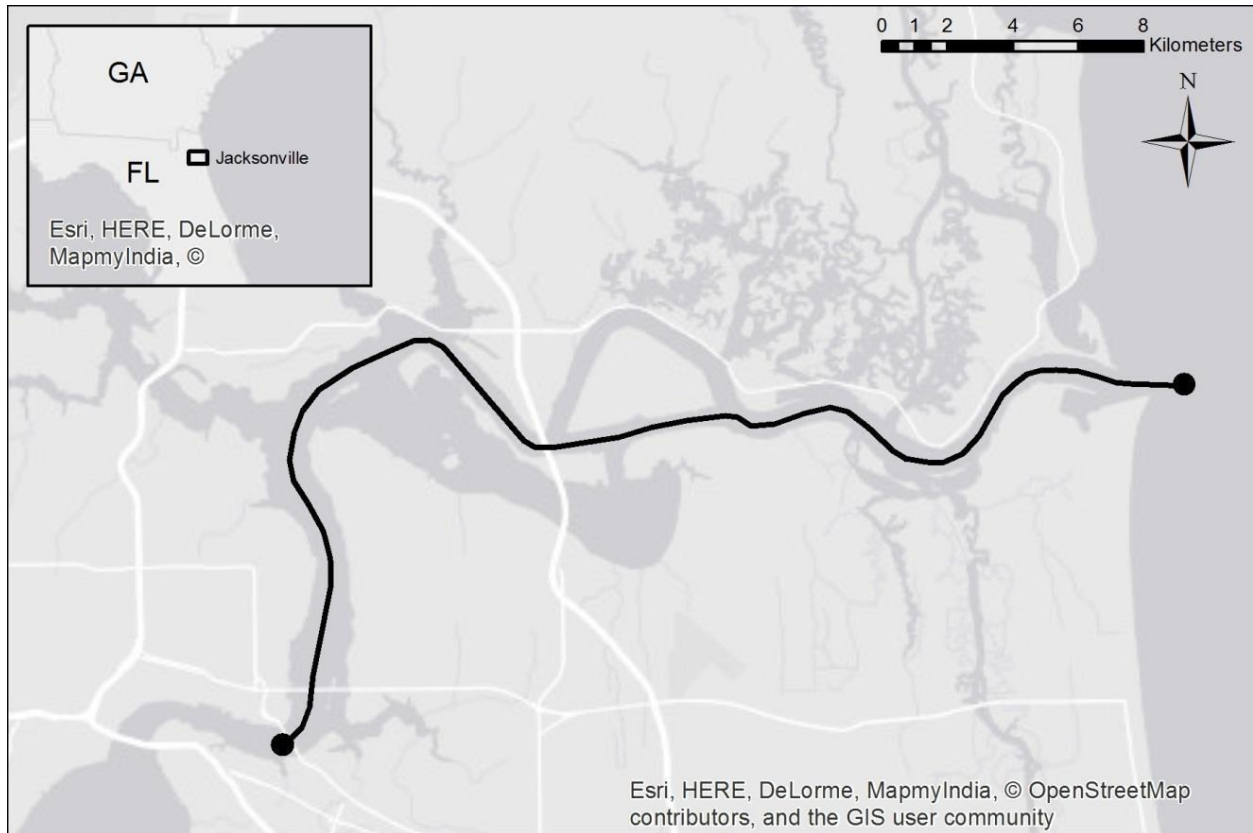


Figure 1. Survey route (reproduced from Ermak *et al.*, in review). Data were collected through weekly photo-identification surveys from the mouth of the St. Johns River (SJR; right dot) to downtown Jacksonville (left dot) along a 40-km transect, with the direction of travel alternating weekly.

Table 1. Ethogram of behavioral states (adapted from Mann and Watson-Capps 2005). Activity categories are mutually exclusive.

Activity	Definition
Travel	Steady, moderate, or fast (>3 km/h) directional movement.
Forage	Fast swimming, rapid direction changes, fish catches, and fish fleeing.
Social	Rubbing, petting (flipper or flukes actively moving on a body part of another), displays, chasing, mounting, poking, contact swimming, and other forms of active contact
Rest	Slow (< 3 km/h) nondirectional movement, frequent hanging at the surface.

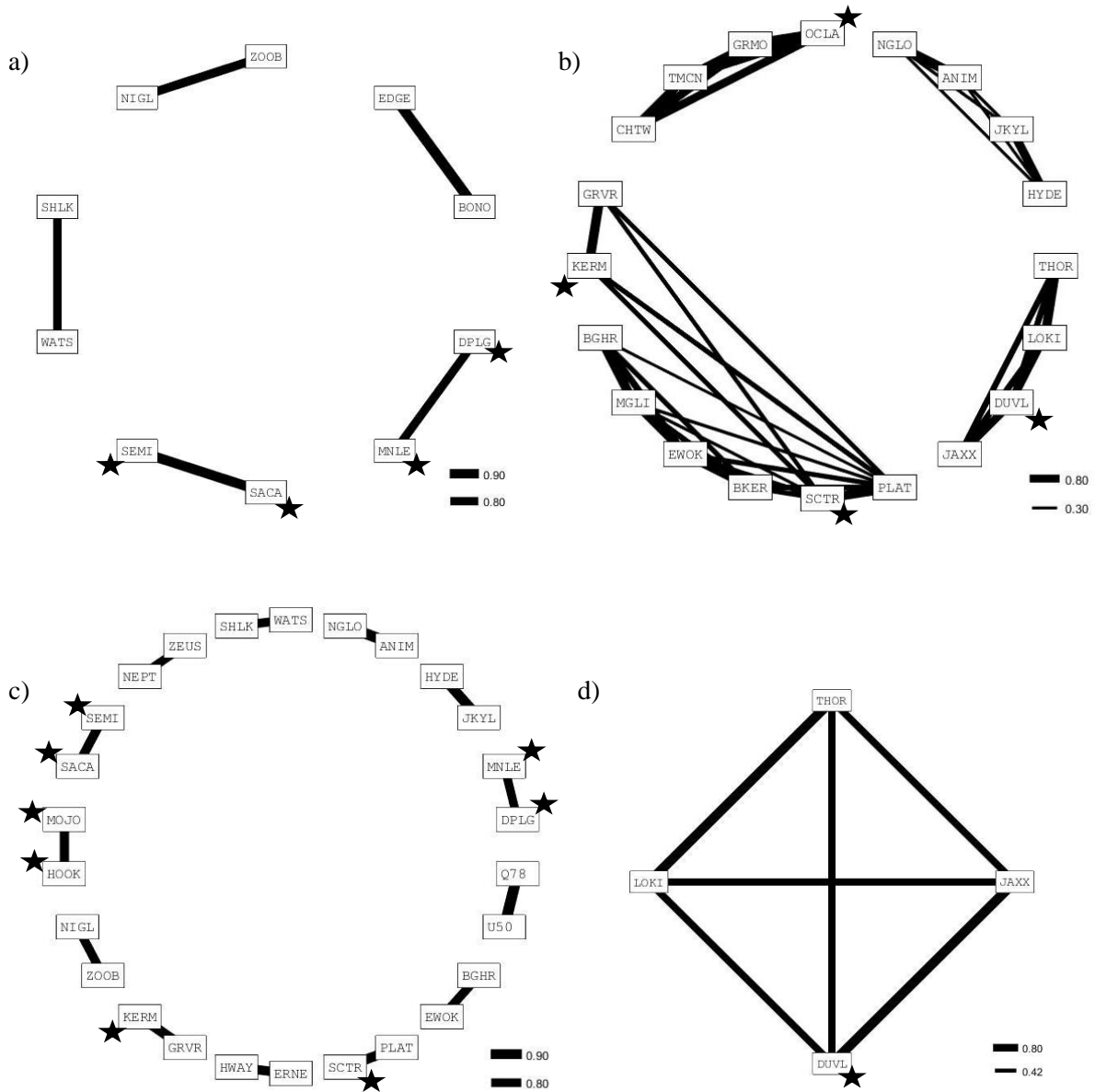


Figure 2. Sociogram of all allied MAL/UNK dyads based on half-weight indices (HWI) calculated via SOCPROG v. 2.6. Width of line indicates strength of association. Known males are indicated with a star. Sociograms are divided for clarity. From Apr. 2011 – Mar. 2013, five dyads (a) formed only first-order alliances and ten dyads (b) formed more complex, second-order alliances ($\text{HWI} \geq 0.30$). From Apr. 2013 – Mar. 2015, thirteen dyads (c) formed only first-order alliances and two dyads (d) formed a more complex, second-order alliance ($\text{HWI} \geq 0.42$).

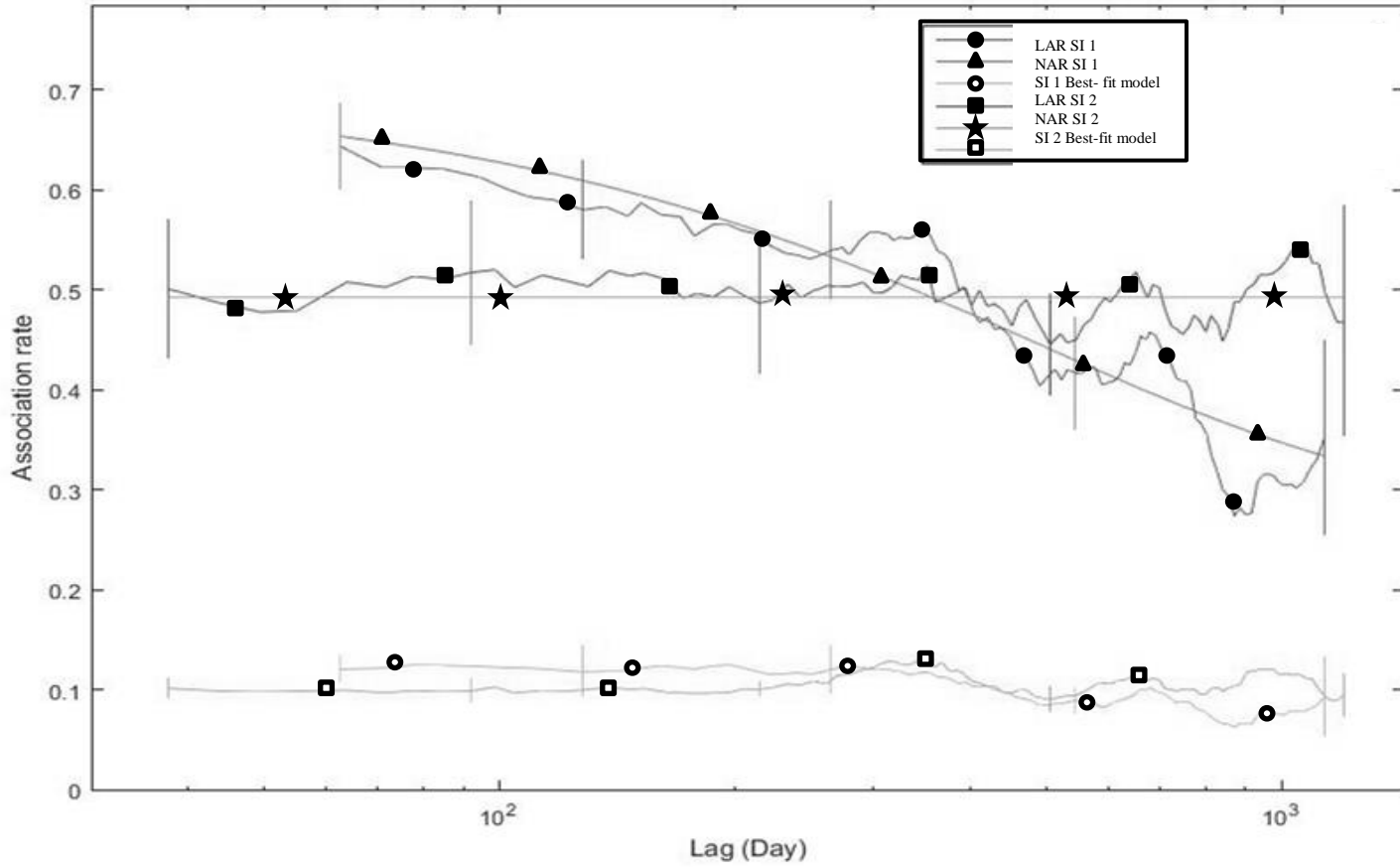


Figure 3. Lagged association rates (LAR) and null association rates (NAR) for first-order alliances with a stability index (SI) of 1 and a stability index of 2 from Apr. 2011 - Mar. 2015 calculated via SOCPROG v. 2.6. The NAR was calculated to represent the expected LAR if individuals were associating randomly. A moving average of 1500 associations was used for both stability indices to smooth the curve. Vertical bars indicate approximate standard errors, which were obtained by jack-knifing. Association rates between individuals, as a function of time lag (d), were related to the proportion of constant companions (P_{cc}) and the proportion of casual acquaintances (P_{cas}) that lasted for time period τ_{cas} (but were not permanent), and to the proportion of casual associations (P_{perm}) that had more permanent associations (τ_{perm}). The best fitting models for SI 1 ($P_{cc} + P_{cas} \times e^{-d/\tau_{cas}}$) and SI 2 (P_{cc}) are displayed.

Table 2. Quasi-Akaike Information Criterion values weighted for each exponential decay model for lagged association rates of unstable (S1) and stable (S2) first-order alliances (FO) and of unstable and stable second-order alliances (SO) from April 2011 – March 2015 calculated via SOCPROG v. 2.6. Bolded numbers represent the probability that model is the actual expected best-fit. Association rates between individuals (g), as a function of time lag (d), were related to the proportion of constant companions (P_{cc}) and the proportion of casual acquaintances (P_{cas}) that lasted for time period τ_{cas} (but were not permanent), and to the proportion of casual associations (P_{perm}) that had more permanent associations (τ_{perm}) (see Whitehead 1995; Whitehead 2007).

LAR model $g(d)$	Biological interpretation	FO S1	FO S2	SO S1	SO S2
$P_{cc} + P_{cas} \times e^{-d/\tau_{cas}}$	Rapid disassociation + constant companions + casual acquaintances	0.999974747	0.054982237	1.4483×10^{-66}	1.1131×10^{-18}
$P_{cas} \times e^{-d/\tau_{cas}}$	Rapid dissociation + casual acquaintances	2.49154×10^{-5}	0.20174614	0.999775183	0
$\frac{P_{cas} \times e^{-d/\tau_{cas}} + (1 - P_{cas}) \times e^{-d/\tau_{perm}}}{P_{cas} \times e^{-d/\tau_{perm}}}$	Two levels of casual acquaintances	3.38066×10^{-7}	0.024705112	0.000224817	0.869891526
$\frac{P_{cas} \times e^{-d/\tau_{cas}} + P_{perm} \times e^{-d/\tau_{perm}}}{P_{perm} \times e^{-d/\tau_{perm}}}$	Rapid disassociation + two levels of casual acquaintance	7.26231×10^{-32}	0.004987876	5.15192×10^{-54}	0.130108474
$\frac{P_{cc} + (1 - P_{cas}) \times e^{-d/\tau_{cas}}}{e^{-d/\tau_{cas}}}$	Constant companions + casual acquaintances	8.51777×10^{-55}	0.165175769	3.93689×10^{-66}	3.7826×10^{-27}
P_{cc}	Rapid disassociation + constant companions	5.65553×10^{-90}	0.548402866	2.90899×10^{-65}	2.79498×10^{-26}
$e^{-d/\tau_{cas}}$	Casual acquaintances	5.0592×10^{-279}	0	0	0

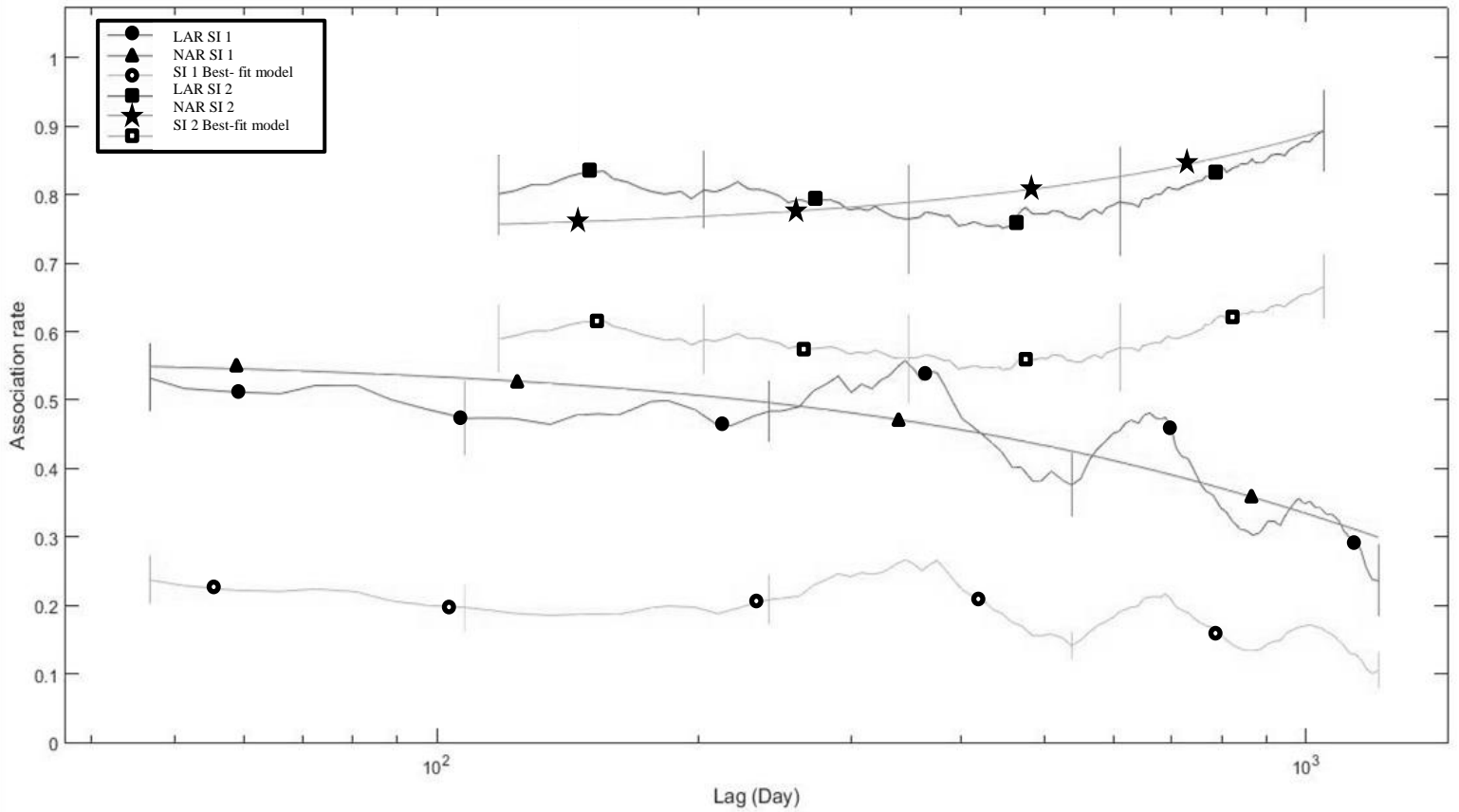
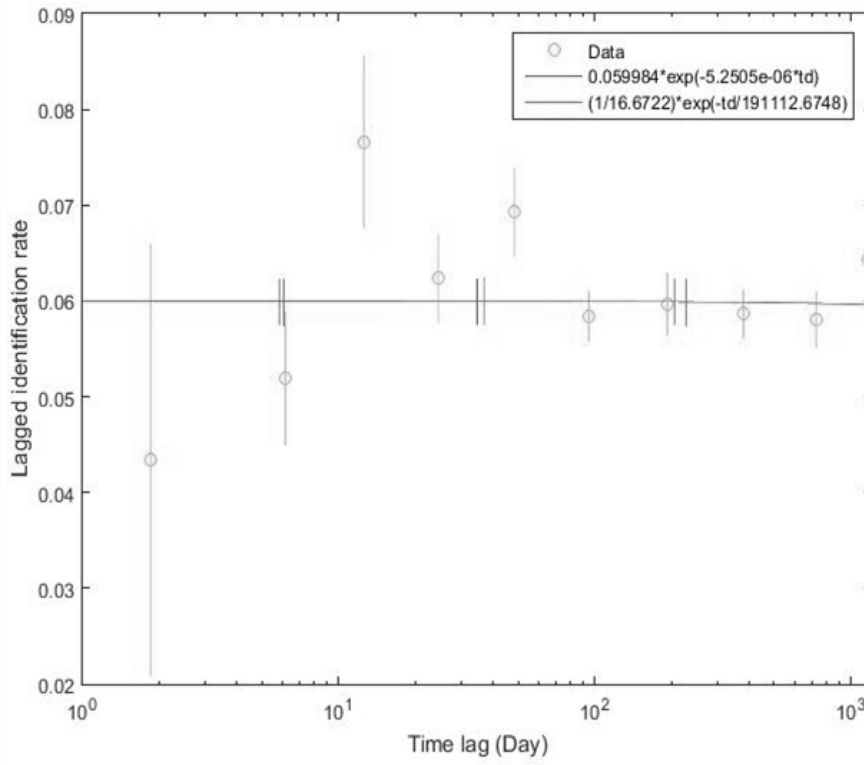


Figure 4. Lagged association rates (LAR) and null association rates (NAR) for second-order alliances with a stability index (SI) of 1 and a stability index of 2 from Apr. 2011 - Mar. 2015 calculated via SOCPROG v. 2.6. The NAR was calculated to represent the expected LAR if individuals were association randomly. A moving average of 1500 associations was used for SI 1 and a moving average of 1000 associations was used for SI 2 to smooth the curve. Vertical bars indicate approximate standard errors, which were obtained by jack-knifing. Association rates between individuals, as a function of time lag (d), were related to the proportion of constant companions (P_{cc}) and the proportion of casual acquaintances (P_{cas}) that lasted for time period τ_{cas} (but were not permanent), and to the proportion of casual associations (P_{perm}) that had more permanent associations (τ_{perm}). The best fitting models for SI 1 ($P_{cas} \times e^{-d/\tau_{cas}}$) and SI 2 ($P_{cas} \times e^{-d/\tau_{cas}} + (1 - P_{cas}) \times e^{-d/\tau_{perm}}$) are displayed.

a)



b)

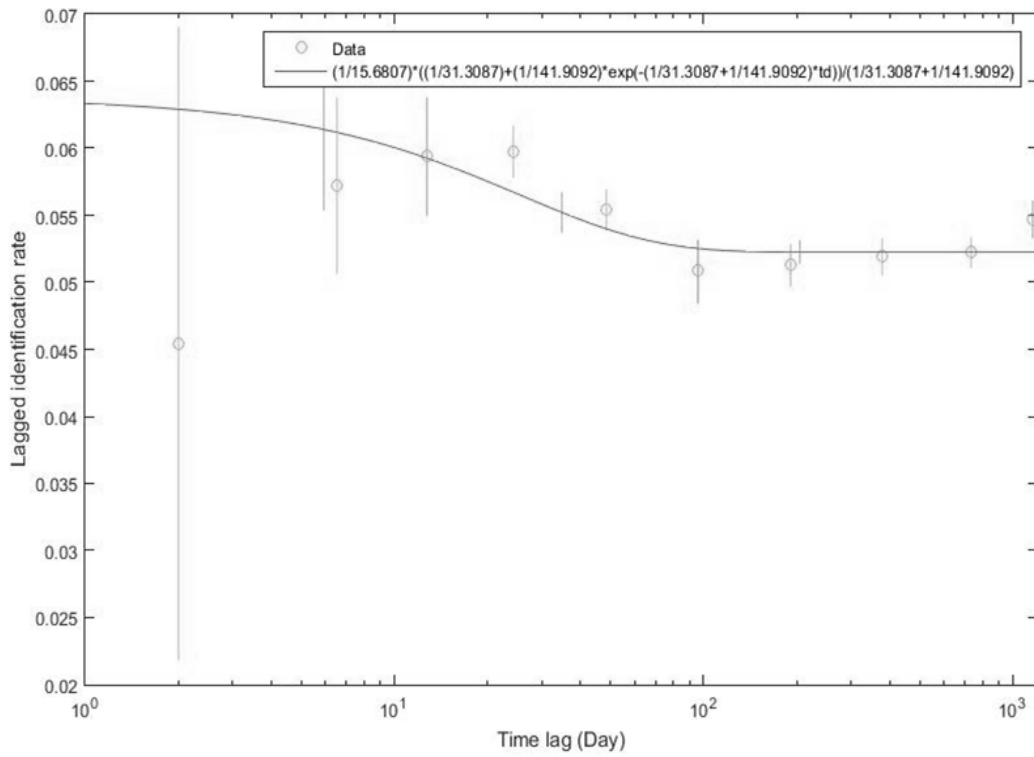


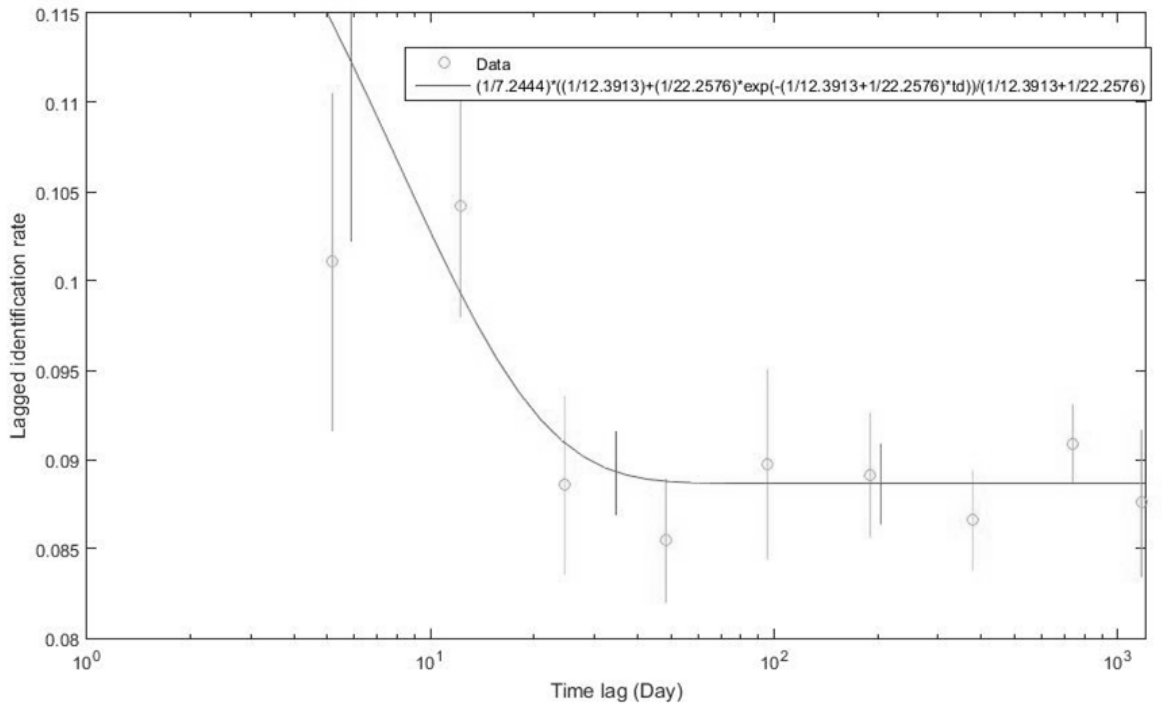
Figure 5. Lagged identification rates (LIR) for first-order alliances from Apr. 2011 – Mar. 2015 calculated via SOCPROG v. 2.6. Vertical lines indicate approximate standard errors, which were obtained by boot-straps of 100 replicates. Best-fitting models included emigration, reimmigration, and mortality where a_1 is the emigration rate, a_2 is the mean residence time, a_3 is mean time out of study area, and a_4 is the mortality rate. The best-fitting models for first-order alliances with a stability index (SI) of 1 (a) are given by $a_2 \times \exp(-a_1 \times td)$ and $(\frac{1}{a_1} \times \exp(-\frac{td}{a_2}))$. The best-fitting model for first-order alliances with an SI of 2 (b) is given by $\frac{1}{a_1} \times$

$$\frac{\frac{1}{a_3} + \frac{1}{a_2} \times \exp(-\frac{1}{a_3} + \frac{1}{a_2}) \times td}{\frac{1}{a_3} + \frac{1}{a_2}}.$$

Table 3. Quasi-Akaike Information Criterion or Akaike Information Criterion values weighted for each exponential decay model for lagged association rates of unstable (S1) and stable (S2) first-order alliances (FO) and of unstable and stable second-order alliances (SO) from April 2011 – March 2015 calculated via SOCPROG v. 2.6. Bolded numbers represent the probability that model is the actual expected best-fit. Social system models evaluate movement into and out of the study area where td indicates time delay in days, $a1$ is the emigration rate, $a2$ is the mean residence time, $a3$ is mean time out of study area, and $a4$ is the mortality rate.

LIR model $g(d)$	Biological interpretation	FO S1	FO S2	SO S1	SO S2
$a2 \times \exp(-a1 \times td)$	Emigration/mortality ($a1$ = emigration RATE; $\frac{1}{a2}$ = N)	0.432646281	0.190547521	0.12076	0.437367
$\frac{1}{a1} \times \exp(-\frac{td}{a2})$	Emigration/mortality ($a1$ = emigration RATE; $a2$ = mean residence time)	0.432646281	0.115572913	0.12076	0.437367
$a2 + a3 \times \exp(-a1 \times td)$	Closed : Emigration + reimmigration ($a1$ = emigration rate; $\frac{a2}{a2+a3}$ = proportion of population in study area at any time)	0.058552307	0.094623098	0.362784	0.059191
$\frac{\frac{1}{a1} \times (\frac{1}{a3} + \frac{1}{a2} \times \exp(-(\frac{1}{a3} + \frac{1}{a2})) \times td)}{\frac{1}{a3} + \frac{1}{a2}}$	Emigration + reimmigration ($a1$ = N; $a2$ = mean time in study area; $a3$ = mean time out of study area)	0.058552307	0.468671275	0.362784	0.065416
$a3 \times \exp(-a1 \times td) + a4 \times \exp(-a2 \times td)$	Emigration + reimmigration + mortality	0.009678631	0.00285737	5.6E-285	0.000658
$\frac{\exp(-a4 \times td)}{a1} \times (\frac{1}{a3} + \frac{1}{a2} \times \exp(-(\frac{1}{a3} + \frac{1}{a2}) \times td))$	Emigration + reimmigration + mortality ($a1$ = N; $a2$ = mean time in study area; $a3$ = mean time out of study area; $a4$ = mortality rate)	0.007924193	0.127727823	0.032911	0

a)



b)

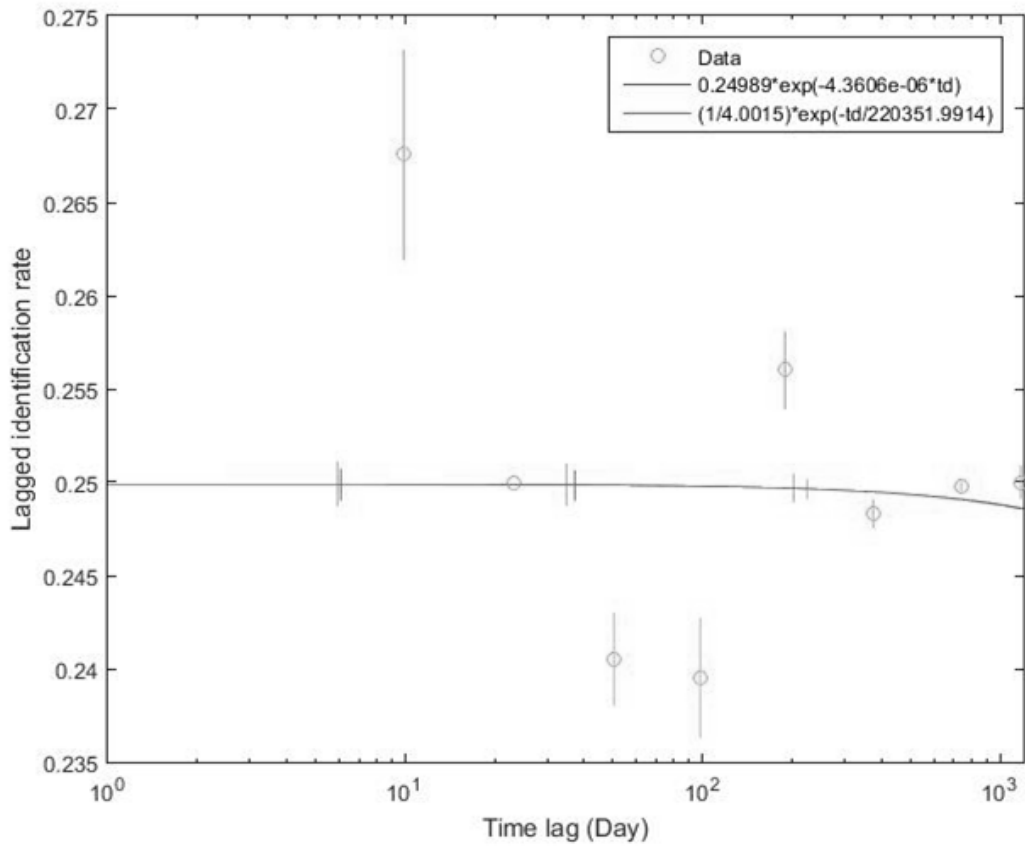


Figure 6. Lagged identification rates (LIR) for second-order alliances from Apr. 2011 – Mar. 2015 calculated via SOCPROG v. 2.6. Vertical lines indicate approximate standard errors, which were obtained by boot-straps of 100 replicates. Best-fitting models included emigration, reimmigration, and mortality where a_1 is the emigration rate, a_2 is the mean residence time, a_3 is mean time out of study area, and a_4 is the mortality rate. The best-fitting model for second-order alliances with an SI of 1 (a) are given by $\frac{\frac{1}{a_1} \times (\frac{1}{a_3} + \frac{1}{a_2} \times \exp(-(\frac{1}{a_3} + \frac{1}{a_2})) \times td)}{\frac{1}{a_3} + \frac{1}{a_2}}$ and $a_2 + a_3 \times \exp(-a_1 \times td)$. The best-fitting models for second-order alliances with a stability index (SI) of 2 (b) are given by $a_2 \times \exp(-a_1 \times td)$ and $\frac{1}{a_1} \times \exp(-\frac{td}{a_2})$.

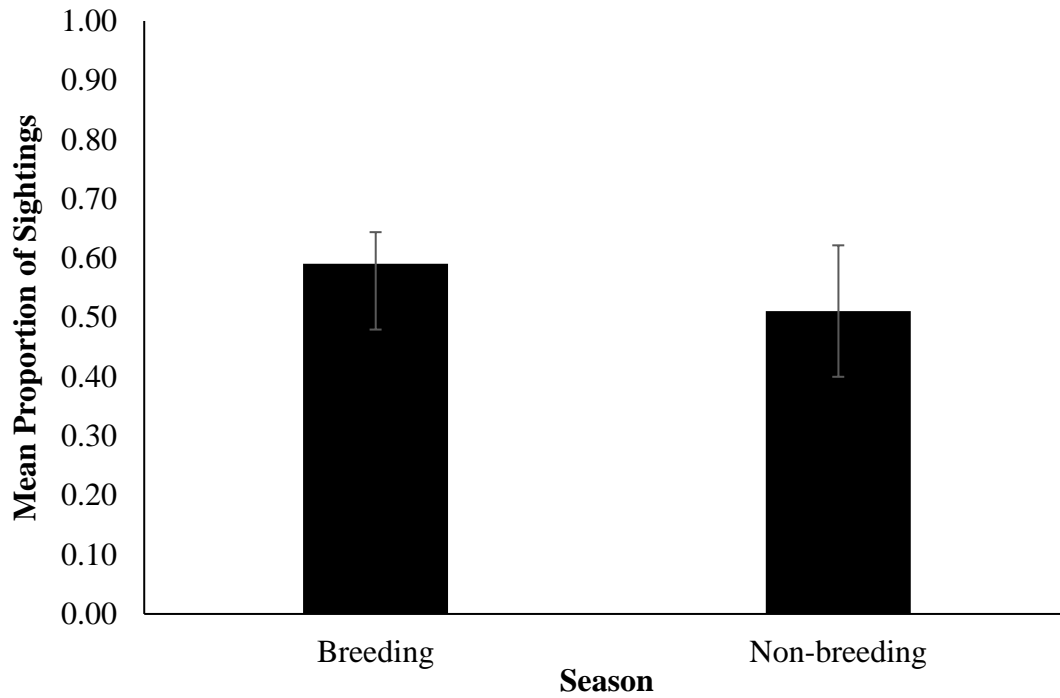


Figure 7. Mean proportion of sightings focal first-order alliances were observed with their second-order alliance partners. Lines on each bar indicate standard error (April 2011 – March 2015). There was no significant difference between seasons (BR $\bar{x} = 0.59 \pm 0.05$, NB $\bar{x} = 0.51 \pm 0.11$, $t(9) = 0.534$, $p > 0.10$).

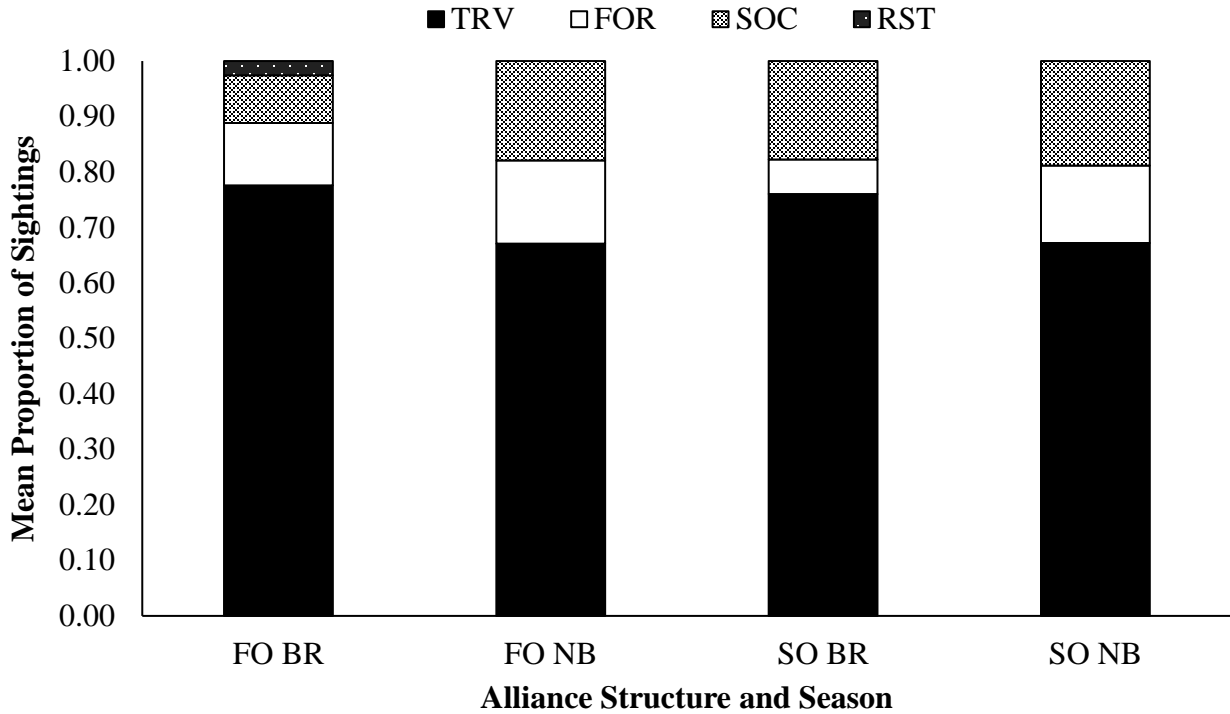


Figure 8. Activity budgets for first- and second-order alliances (FO and SO, respectively) for the breeding (BR) and non-breeding (NB) seasons. Predominant group activity was classified as one of four behavioral states: travel (TRV), forage (FOR), social (SOC), and rest (RST). Behaviors were unequally distributed (FO BR: $\chi^2(3, n = 197) = 257.1, p < 0.05$; FO NBR: $\chi^2(3, n = 111) = 119.4, p < 0.05$; SO BR: $\chi^2(3, n = 50) = 73.84, p < 0.05$; SO NBR: $\chi^2(3, n = 27) = 27.67, p < 0.05$).

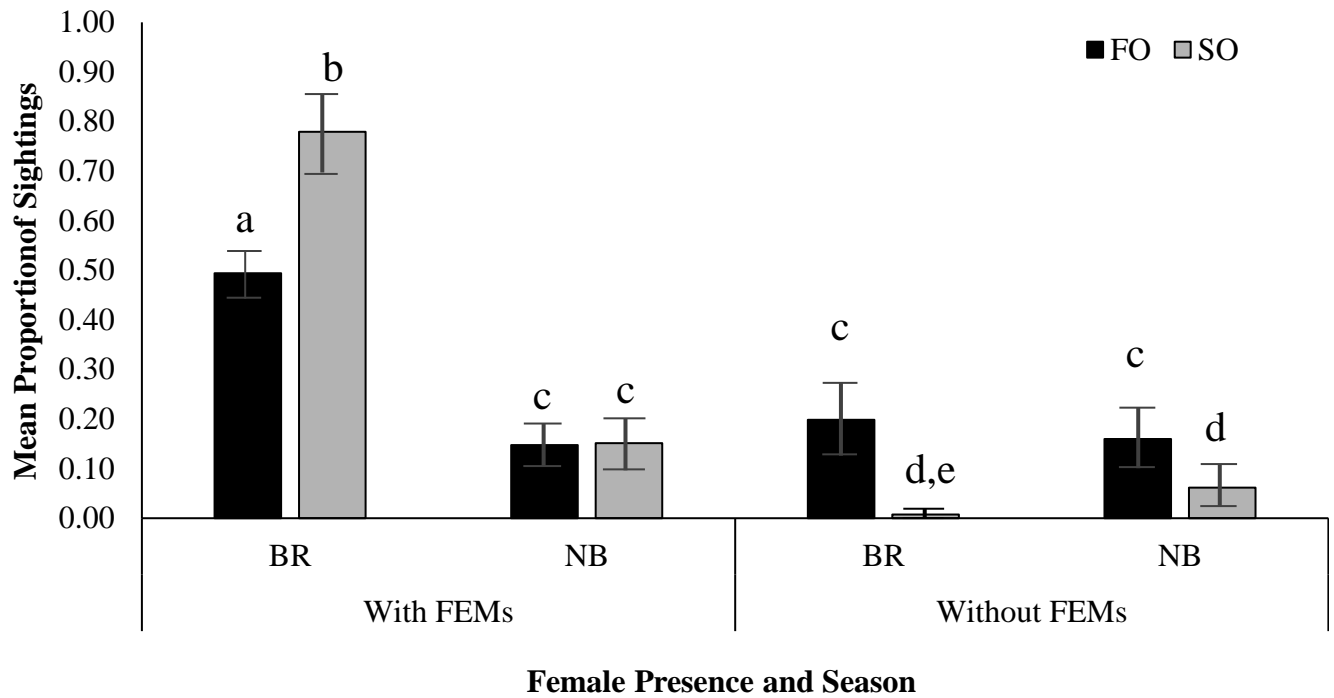


Figure 9. Mean proportion of sightings alliances were observed with and without females (FEM) with respect to seasonality (breeding season: BR; non-breeding season: NB) from April 2011 – March 2015. First- and second-order alliances were significantly more likely to be observed with females during the breeding season (FO: Md = 0.50, n = 20; SO: $\bar{x} = 0.78 \pm 0.21$) than non-breeding season (FO: Md = 0.14, n = 20, Z = -3.73, p < 0.01; SO: $\bar{x} = 0.15 \pm 0.10$, t(6) = 5.78, p < 0.01). During the breeding season, second-order alliances significantly had a higher proportion of sightings with females than did first-order alliances (FO: $\bar{x} = 0.49 \pm 0.21$, SO: $\bar{x} = 0.78 \pm 0.21$, t(25) = -3.08, p < 0.01). There was no statistical significance between seasons or alliance structures when females were absent.

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VITA

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