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The Function of Second-Order Male Alliances in St. Johns River Dolphins (Tursiops truncatus)

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THE FUNCTION OF SECOND-ORDER MALE ALLIANCES IN ST. JOHNS RIVER
DOLPHINS (*TURSIOPS TRUNCATUS*)

by

Arien D. Widrick

A thesis submitted to the Honors Program

in partial fulfillment of the requirements for

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April, 2016

CERTIFICATE OF APPROVAL

The thesis of Arien D. Widrick is approved: (April 2016)

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Abstract

Bottlenose dolphins (*Tursiops truncatus*) have a sexually segregated fission-fusion society, in which males and females form different types of social groups for different purposes. Social interactions among dolphins are frequent, and group composition changes just as often. Male-male association patterns reveal the formation of alliances, which range in complexity. Recently, second-order alliance formation was confirmed in the St. Johns River, but the function of these alliances is unknown. To investigate their function, this research analyzes the seasonality of first and second-order alliance formation, and whether female presence plays a role. It was hypothesized that higher level male alliances form in order to improve mating opportunities in a society dominated by male-male competition. It follows then that more male alliances will form during the breeding season, including second-order alliances, and alliances of both levels will form more often in the presence of females. By analyzing boat-based photo-identification survey data, it was found that the average number of alliances was 1.5 per group in all seasons, if there was at least one alliance present. More alliances were sighted in groups with females, and this trend followed for the second-order alliances. The percent of sightings with first-order alliances was higher in the breeding season as expected. However, most of the second-order alliances were sighted in the non-breeding season, which correlates with increased aggression in the non-breeding season. This suggests that second-order alliances may be integral in establishing male dominance prior to the start of the breeding season.

Introduction

Bottlenose dolphins (*Tursiops truncatus*) lead complex social lives. The underlying community structure is a sexually segregated fission-fusion society, with sex biased differences in association patterns (Morteo et al. 2014, Connor et al. 2000). Dolphin society is considered fission-fusion because group size and membership changes frequently (Wells et al. 1987, Smolker et al. 1992). Females compete for nutritional resources, and thus cooperation isn't highly selected for, since fish are not easily defendable resources. Thus, females are observed forming large groups of moderately bonded individuals, usually including matrilineal family members (Wells et al. 1987, Smolker et al. 1992). Female bottlenose dolphins in Sarasota, Florida interacted with approximately 95% of the local female population, and associations were usually highly variable, though reproductive status was shown to play a role (Wells et al. 1987).

The high mobility of dolphins (Randić et al. 2012), and high rates of encounter (Connor and Whitehead 2004) increase competition for mates among male dolphins, thus encouraging the formation of male alliances. It is reproductively beneficial to form alliances with other males, if the male is unable to monopolize the female by himself, and therefore protect reproductively available females from other groups of males (Connor and Whitehead 2004). Male-male associations are, in general, tightly bonded and stable over the long term (Connor et al. 2011, Wiszniewski et al. 2012*a*). Coefficients of association (COAs) are used to measure the strength of bonds between individuals. One type of COA is the half weight index (HWI), which is used here to detect the presence of alliances. A HWI of 0.8 or higher between two dolphins indicates that they are first-order alliance pairs. Further, the HWI can be used to examine interactions between first-order alliances to determine if second-order alliances are also present (Ermak 2014, Elliser and Herzing 2014). The level of complexity exhibited in male alliances varies by location

(Wiszniewski et al. 2012*a*). The most common alliance type across populations is the first-order alliance. Connor et al. (1992) describes a first-order alliance as a pair or trio of males that cooperates to aggressively herd an individual female for reproductive purposes; pregnant or recently pregnant females are rarely herded (Connor et al. 1992). These first-order allied males are typically together 80-100% of the time (HWI = 0.8 or greater), the same amount of time a mom and dependent calf spend together (Connor et al. 1999). Additionally, males within a first-order alliance can form a second-order alliance. This is when two first-order alliances associate together, this association can be used to steal a female from another alliance (Connor et al. 1992). After a "theft", only one of the paired first-order alliances would retain and herd the female (Connor et al. 1992). These second-order alliances could be composed of $4 - 6$ dolphins, and remain stable for several years independent of size of the alliance (Connor et al. 2011). The coefficient of association criterion used to identify second-order alliances was set conservatively higher than normal at 0.32 for the present study, twice the average non-zero HWI between males/unknown sex individuals in this community (Ermak 2014). There is also a special type of second-order alliance called the superalliance. This alliance is composed of approximately 14 males, none of whom have a stable first-order alliance partner, but rather the males split into pairs and trios to herd females, but these pairs and trios vary frequently (Connor et al. 1999). In Port Stephens, Australia, the size of alliance was the best predictor of reproductive success in Indo-Pacific bottlenose dolphins, which could lend some insight on the formations of large male-male alliances (Wiszniewski et al. 2012*b*). More recently, third-order alliances have been suspected to form in Shark Bay, Australia. These consist of a loosely associated alliance between second-order alliances, and can be used in large fights to keep or steal females (Connor et al. 2011). Third-order alliances are defined as having a coefficient of association around $0.1 - 0.17$

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(Connor et al. 2011). Finally, a male can be solitary and have no stable alliance partner. This occasionally occurs when one of the alliance members passes away, leaving a solitary male, or it is simply his personality to be a loner (Wells 1991).

Dolphins are very intelligent animals, allowing for a complex social structure (Connor et al. 2007), which has been shown to vary among populations (Connor et al. 1992, Wells et al. 1987, Elliser and Herzing 2014). The majority of research on bottlenose dolphin social dynamics comes from studies in Shark Bay, Australia, the site currently recognized for the highest levels of complexity in alliance formation. It is important to conduct comparative studies between different geographic locations in order to assess differences and commonalities between their behaviors, which could elucidate the reasons certain levels of alliance formation develop in some areas but not in others. Ermak (2014) confirmed that second-order alliances are present in the St. Johns River, Jacksonville, Florida (Figure 8 shows the alliance structure in the St. Johns River). However, the function of second-order alliance formation in the St. Johns River is not fully understood. The present study examines the function of multi-level male alliances in the St. Johns River, and provides a comparison to second-order alliances in Shark Bay, Australia.

To investigate the function of alliance formation with St. Johns River dolphins, several factors were examined: seasonality of first-order alliance formation, seasonality of second-order alliance formation, and whether female presence was correlated with second-order alliance formation. It was hypothesized that more male alliances, both first- and second-order, would form during the breeding season. Additionally, if alliance formation functions to improve reproductive opportunities, alliances would form more often in the presence of females. This study will expand the knowledge on the St. Johns River dolphins, allowing for more notable comparisons to other study sites around the world.

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Methods

Data Collection

   The St. Johns River in Jacksonville, Florida, is utilized by over 300 dolphins annually. It is home to at least 70 year-round resident dolphins, in addition to a number of seasonal resident dolphins and transient dolphins (Gibson, unpublished data). This river runs from the Atlantic Ocean and past downtown Jacksonville. The dolphins in this habitat deal with boat traffic, anthropogenic noise, pollution, and other disturbances, which have been shown to impact dolphin behavior (Constantine et al. 2004, Rolland et al. 2012, Romano et al. 2004). Data were collected weekly via boat-based photo-identification surveys along a fixed 40 km length of the river, from Mayport Inlet to the Jacksonville Landing (Figure 9, Appendix). Direction of travel along the river alternated each week, and speed of travel was maintained between 10 – 12 km/hr. Environmental data (salinity, water temperature, wave strength, water depth), location variables (proximity of other vessels, particularly large shipping boats) and behavioral information (group activity, group size, dive type, etc) were recorded. Photographs of dorsal fins were taken and these images were used to identify dolphins. The 10-meter chain rule defined by Smolker et al. (1992) was used to determine group composition.

Data Analysis

   Meaningful group composition studies require that the sex of the dolphins be known. Males are identified using opportunistic views of genitals, stranding data, or genetic biopsies (NOAA Fisheries, unpublished data). Additionally, a dolphin is determined to be female if she is spotted consistently with a dependent calf, or by using stranding data and genetic biopsy data. All other dolphins are considered unknown sex. Dolphin sexes are updated continuously as new data are collected, though analyses for this study were limited to March 2011 to February 2013.

Half weight indices (HWIs), which ranges from 0 to 1, were used to determine the presence of alliances, (Cairns and Schwager 1987). HWI is calculated by: $HWI = 2N_T/(N_a + N_b)$, where N_T is the number of times two individuals are sighted together. N_a and N_b are the numbers of times each individual was sighted (Cairns and Schwager 1987, Ermak 2014). HWIs were calculated for all dolphins, and the sociogram (Figure 8, Appendix) illustrates the bonds that met the HWI criterion for alliance membership (0.80 for first-order, and 0.32 for second-order alliances) (Ermak 2014).

Data used for this study were restricted to a two-year period, March 2011 – February 2013. This included a total of 798 group sightings, 229 of which contained first-order alliances. Of these, 44 sightings contained second-order alliances. Second-order alliances were only counted if all members of each paired first-order alliance were present. Sighting data were separated by season. The calendar year was divided by three month periods into seasons: spring (March to May), summer (June to August), autumn (September to November), and winter (December to February). These four seasons were then consolidated into two categories: breeding season (spring and summer) and non-breeding season (autumn and winter). Statistical analyses were used to determine if there were significant differences between the two study years, across seasons, or in different group compositions. For all Chi-Squared Goodness of Fit tests, the expected values were assumed to be an even split across group types and seasons.

Results

The average number of alliances per group (in sightings with at least one alliance) did not differ among seasons. There was an average of 1.5 alliances per group in the breeding season for both years, and 1.55 and 1.47 alliances per group in the non-breeding season for 2011 and 2012

respectively (Figure 1). Though the average number of alliances per sighting was approximately the same for both years and seasons, when comparing the raw, non-averaged number of alliances per sighting for statistical analyses, significant differences were found. There was a seasonal difference (breeding vs. non-breeding) for 2011 (χ^2 (1) = 15.0, p < 0.05) and 2012 (χ^2 (1) = 7.191, p < 0.05). There was a difference between years for the breeding season (χ^2 (1)= 6.0, p < 0.05), but there was no difference between years during the non-breeding seasons (χ^2 (1) = 1.532, p > 0.05).
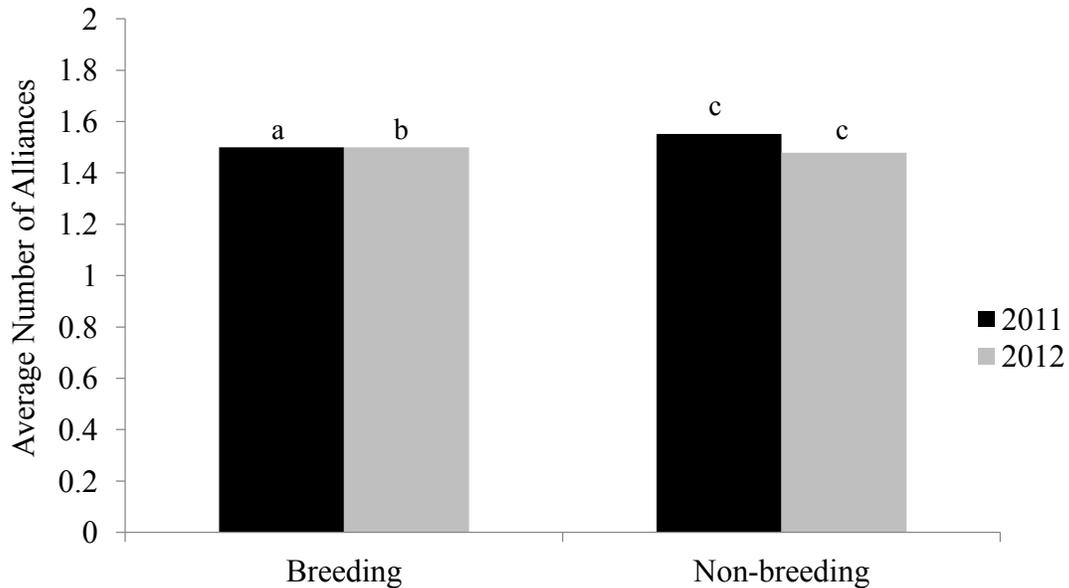
Figure 1 The average number of alliances per group. Data were restricted to group sightings that contained at least one alliance. Different letters indicate statistically significant differences. Within years, there was a significant difference between breeding and non-breeding seasons in both 2011 and 2012. Between years, the average number of alliances per group did not differ during the non-breeding seasons. However, there was a significant difference between the 2011 and 2012 breeding seasons.

The percentage of group sightings containing at least one alliance was greatest in spring (both years). In 2011, the percentage of sightings containing alliances was lowest in the winter (14%) (Figure 2). However, in 2012, the lowest percentage of sightings with alliances was in autumn (8.2%), and increased into the winter season (21%). The only significant difference between years was during the summer (χ^2 (1) = 8.967, p < 0.05). Within years, there was a seasonal difference in 2011 (χ^2 (3) = 21.88, p < 0.05), though not in 2012 (χ^2 (3)= 6.65, p > 0.05).

Figure 2 Percent of total sightings of groups containing at least one alliance. The total number of sightings for 2011 and 2012 are 404 and 394 respectively. Different letters indicate statistically significant differences within year. Within years, there was a seasonal difference for 2011 but no seasonal difference for 2012. Between years, only summer was significantly different.

For both years of the study, the percentage of sightings with at least one alliance present was significantly higher in the breeding season than non-breeding season. In 2011, 28% of sightings contained alliances during the breeding season, compared to 15% in the non-breeding season (χ^2 (1) = 10.798, p < 0.05). In 2012, the percentage of sightings with alliances in the breeding season was 17.8%, which was significantly higher than the 13.6% of sightings with alliances in the non-breeding season (χ^2 (1) = 4.587, p < 0.05). There was no difference between the breeding seasons of 2011 and 2012, but there was a significant difference between years in the non-breeding season (χ^2 (1) = 4.0, p < 0.05) (Figure 3).

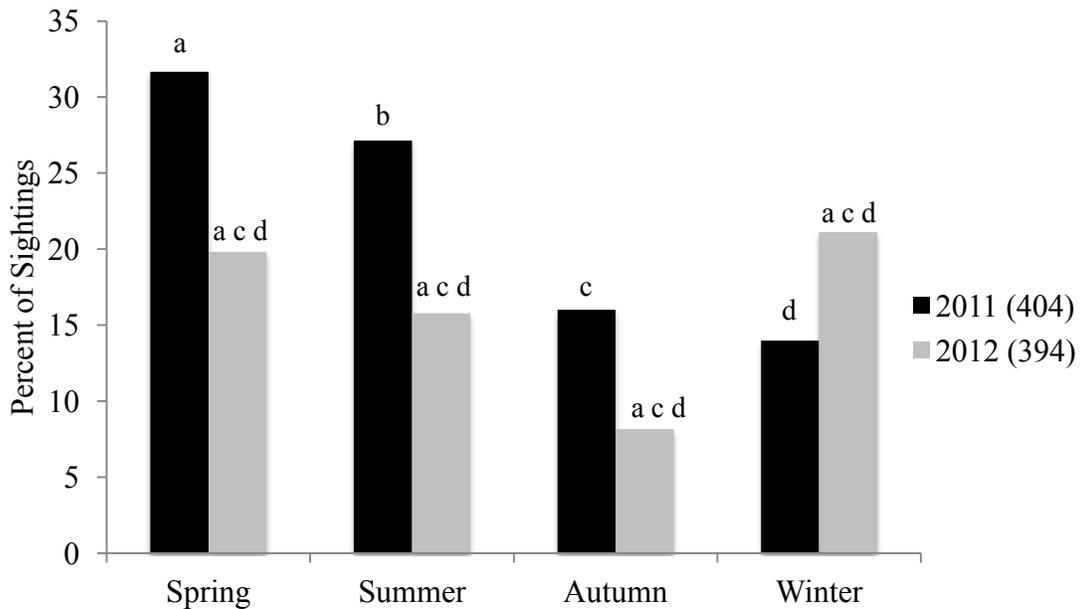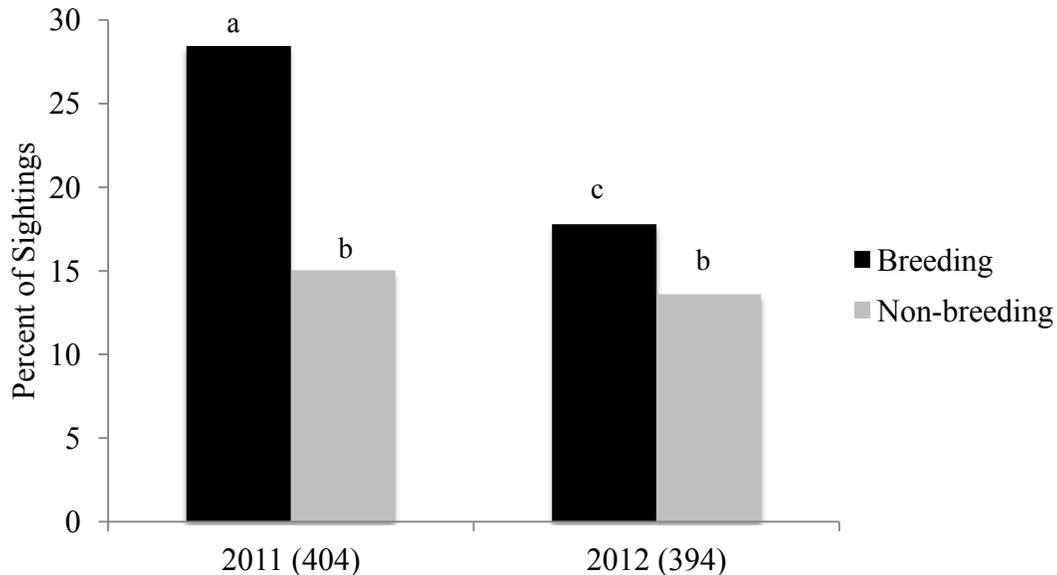Figure 3 Year and seasonal effects on the percent of sightings with at least one alliance. The total number of sightings for 2011 and 2012 are 404 and 394 respectively. Within years, there was a significant seasonal difference in both 2011 and 2012. Overall χ^2 test indicated no significant difference between years in the non-breeding season, though there was a difference between years in the breeding season.

The percent of sightings containing second-order alliances did not differ significantly across seasons (breeding and non-breeding) in either year (2011: χ^2 (1) = 1.286, p > 0.05; 2012: χ^2 (1) = 0.222, p > 0.05) (Figure 4). In 2011, 38% of sightings contained second-order alliances in the non-breeding season, and 28% of sightings contained second-order alliances in the breeding season. In 2012, 34.8% of sightings contained second-order alliances in the non-breeding season, whereas 25% of sightings in the breeding season had second-order alliances. Overall, there was also no significant difference between years for either season (breeding: χ^2 (1) = 1.815, p > 0.05; non-breeding: χ^2 (1) = 0.474, p > 0.05). (Figure 4).

Figure 4   The percent of sightings that contained a second-order alliance. Data restricted to group sightings containing at least one first-order alliance. Numbers in parentheses (89 and 63) indicate number of sightings included for each year. No significant differences were documented between years or seasons.

Female presence did not have a significant effect on the percent of sightings containing first-order alliances between years (with females: χ^2 (1) = 0.002, p > 0.05; and without females: χ^2 (1) = 0.251, p > 0.05). In 2011, 59% of sightings with first-order alliances occurred in groups with females, which was significantly higher than the 41% of sightings that occurred in groups without females (χ^2 (1) = 12.831, p < 0.05). In 2012, 60% of sightings with first-order alliances were sighted in groups with females, which was significantly higher than the 40% of sightings in groups without females (χ^2 (1) = 16.244, p < 0.05) (Figure 5).
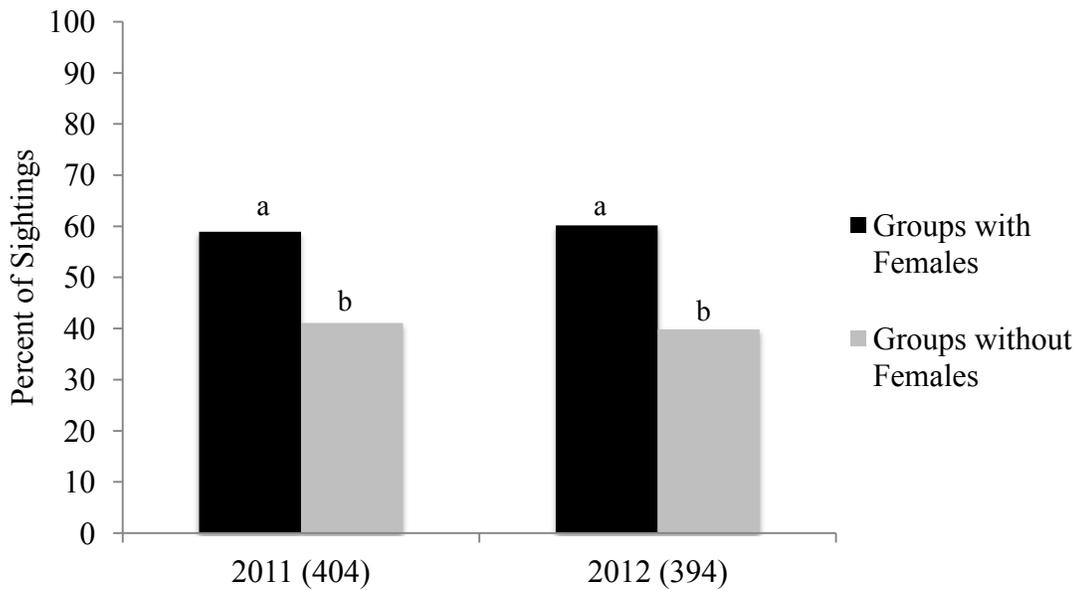
Figure 5   The effect of female presence on the percent of sightings containing first-order alliances. Numbers in parentheses (404 and 394) indicate number of sightings included for each year. Overall, there was a difference within 2011 and 2012 based on female presence; however there was no significant difference between years.

In both years, the majority of sightings containing second-order alliances also contained at least one female in the group. In 2011, 92.6% of sightings with second-order alliances, and in 2012, 88% of sightings with second-order alliances were sighted in groups with females. There was no difference between years (with females: χ^2 (1) = 2.5, p > 0.05; and without females: χ^2 (1) = 0, p > 0.05), but there was a significantly higher percentage of sightings with second-order alliances present in groups containing females than groups without females in 2011 (χ^2 (1) = 19.593, p < 0.05) and 2012 (χ^2 (1) = 9.941, p < 0.05) (Figure 6).
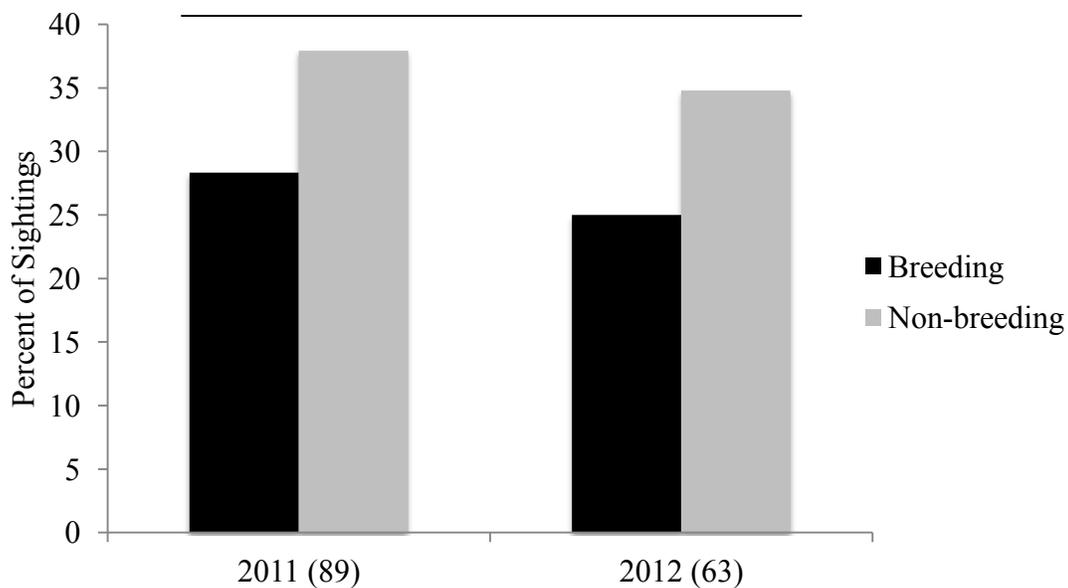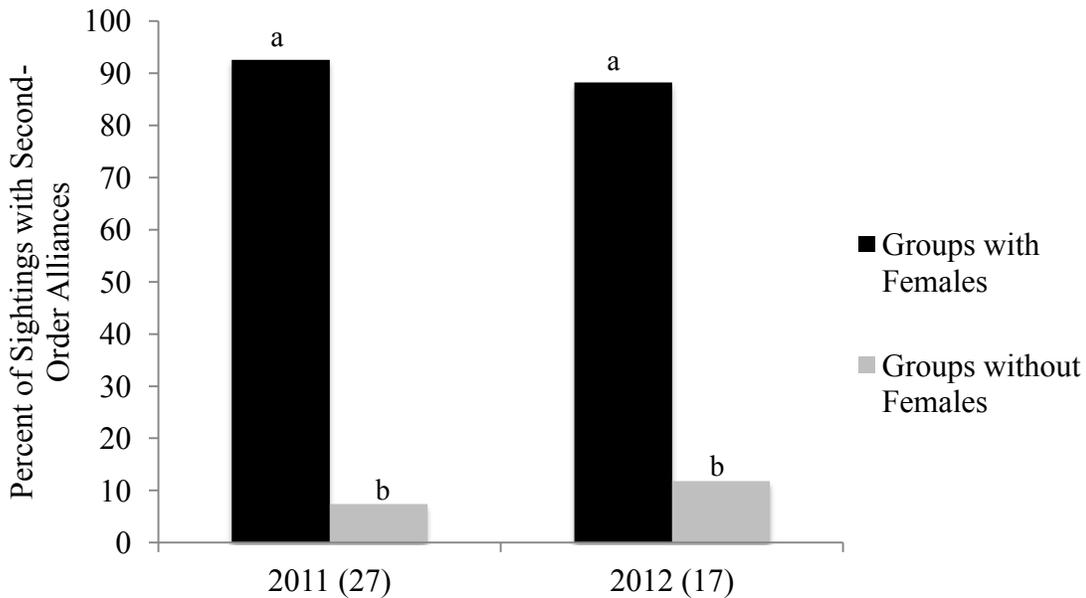

Figure 6 The effect of female presence on the percent of sightings containing at least one second-order alliance. Data restricted to sightings containing at least one first-order alliance. Female presence had a significant effect on the percent of sightings with second-order alliances in 2011 and 2012, though there was no significant difference between years.

The average number of alliances per group varied seasonally for groups with females (χ^2 (1) = 10.02, p < 0.05), but there was no seasonal difference for groups without females (χ^2 (1) = 0.08, p > 0.05) (Figure 7). For groups with females, the average number of alliances per group was 0.53 and 0.27 for breeding and non-breeding seasons respectively. For groups without females, the average number of alliances per group was 0.15 in both the breeding and non-breeding seasons.
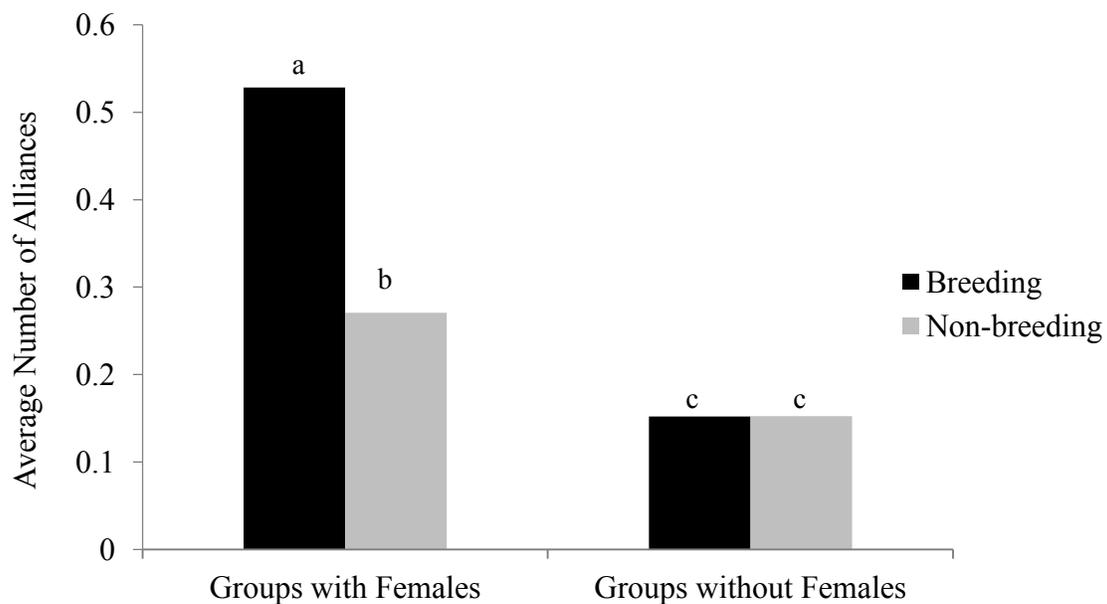

Figure 7 The effect of female presence on the average number of alliances per group, for 2011 and 2012 combined. Data restricted to sightings containing at least one first-order alliance. Female presence was significant. There was a significant difference between seasons in groups with females, however there was no significant difference between seasons in groups without females.

Discussion

The average number of first-order alliances sighted was approximately 1.5 alliances per group, year-round (Figure 1). Despite the average number of alliances per sighting being similar across years and seasons, when calculating the statistics and using the raw counts of alliances per sighting, the breeding season was significantly different from the non-breeding season. This is because raw alliance counts are required for the statistical analyses, and the raw numbers varied between years and seasons. When the percentage of sightings containing first-order alliances was divided into the four seasons, 2012 showed a large percentage of alliances sighted in the winter season, but 2011 did not follow this trend (Figure 2). The χ^2 test showed a significant seasonal difference for 2011, and no significant seasonal difference for 2012. Summer was the only season when 2011 and 2012 were significantly different. 2011 had 41 sightings with alliances in the summer, whereas there were only 18 in 2012. The sightings with alliances in 2012 were evenly spread throughout the year, but this was not the case in 2011.

The percentage of sightings containing second-order alliances was higher in the non-breeding season than the breeding season, though not significantly different (Figure 4). It was hypothesized that second-order alliances were forming to help with mate acquisition and defense, so it seems counterintuitive that second-order alliances were more prevalent in the non-breeding season, regardless of the difference not being significant. A significantly higher percentage of sightings with first-order alliances were sighted in the breeding season for both years (Figure 3), indicating that seasonality does play a role in alliance sightings. It is specifically the multilevel alliance formation that did not follow the expected pattern of being more prevalent during breeding season and no statistically significant difference was noted across seasons (Figure 4).

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Given that the seasonality patterns differ between first-order and second-order alliances, female presence was focused on for a clearer picture. The average number of alliances per group showed seasonal differences when females were present, and the average number of alliances per group was higher in groups with females (Figure 7). In addition, the percentage of sightings with alliances was significantly higher with females in the group for both years (Figure 5). On average 90.3% of sightings with second-order alliances occurred in groups with females (Figure 6). This pattern suggests a strong correlation between female presence and higher level alliance formation.

Research in Shark Bay, Australia has shown first and second-order alliance function is to increase access to females and expand mating opportunities (Connor et al. 2010, Randić et al. 2012). Since a higher percentage of second-order alliances were sighted in groups with females present than groups without females, the hypothesis that female presence is a driving factor in alliance function in the SJR was supported. Given that the proposed purpose of second-order alliances is to increase success in female acquisition and defense (Connor et al. 2010, Elliser and Herzing 2014, Randić et al. 2012), it was expected that more second-order alliances would be sighted in the breeding season in the St. Johns River. There was no difference in the percentage of sightings containing second-order alliances in the non-breeding season compared to the breeding season (Figure 4). Seasonality data did not show convincing patterns for sightings with increased alliance complexity. It can be concluded that female presence, not season, seems to be the common denominator for predicting alliance patterns.

With any highly intelligent animal, motives for behaviors are complex. Future studies should increase the number of years of data analyzed, in order to determine a clear pattern. With only two years of data, it is hard to tell if certain unexpected seasonal patterns were anomalies or

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stayed consistent from year to year. In addition, focal follow studies should be used to look at specific individuals' behavior and analyze results to draw conclusions on reasons specific dolphins participate in specific behaviors. Dolphins are highly intelligent animals (Connor 2007), and like humans, may not fit an overarching pattern for their behaviors. More individualized data would improve the dependability of conclusions made on the St. Johns River dolphin population. Finally, alliance complexity varies globally (Wells et al. 1987, Connor et al. 2011, Elliser and Herzing 2014), so it would be interesting to further investigate the types of alliances that are forming in the St. Johns River. Some areas have documented third-order alliances (Elliser and Herzing 2014, Connor et al. 1999, 2011) and superalliances (Connor et al. 1999, 2001). Ermak (2014) confirmed the formation of second-order alliances in the St. Johns River, but so far, third-order alliance or superalliance formation has not been studied in this location.

Appendix A

Supplemental Information
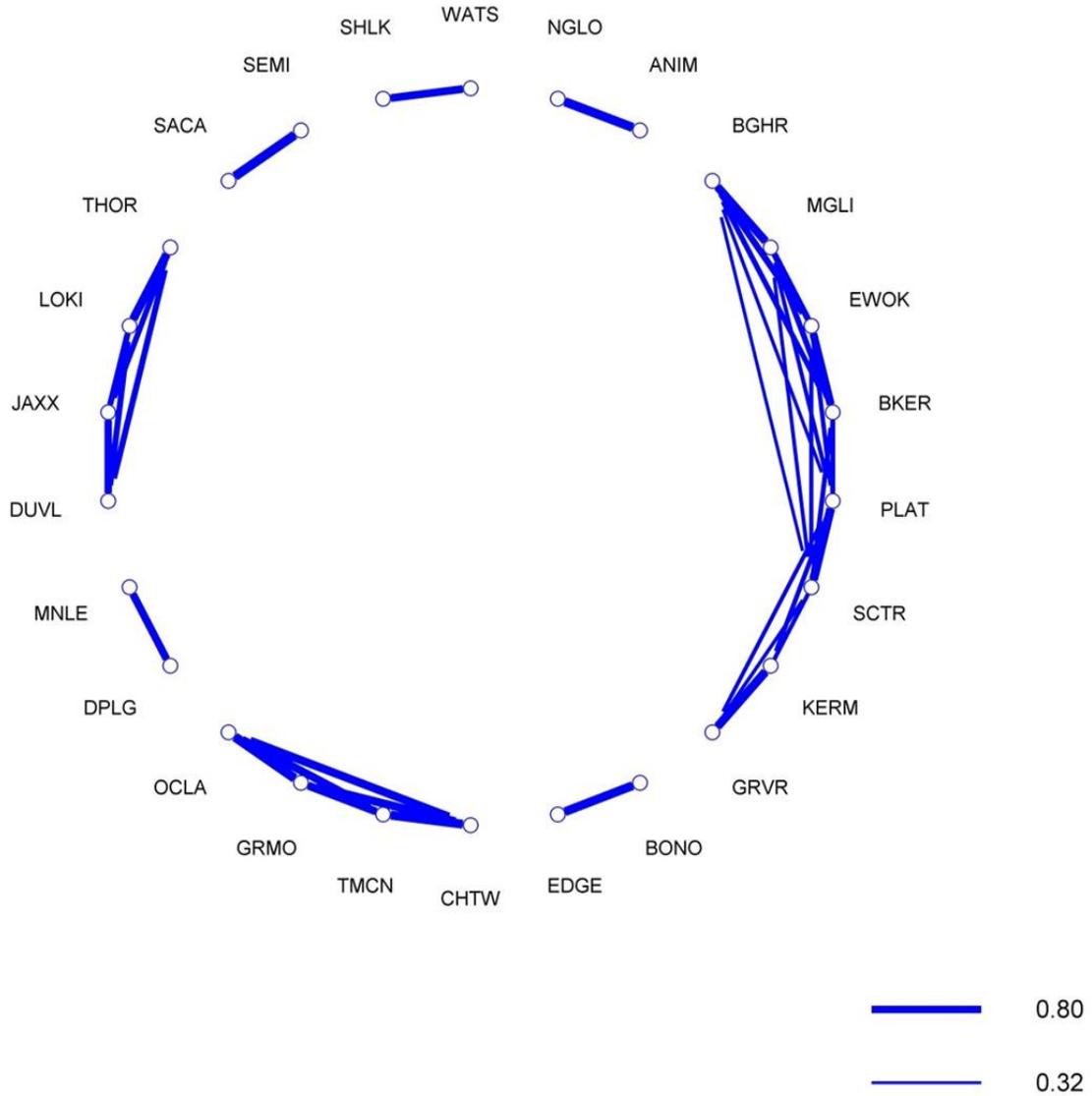
Figure 8 Sociogram of male alliances. Thicker lines corresponding to 0.8 HWI indicate first-order alliances, while thinner lines corresponding to 0.32 HWI indicate second-order alliances. Sociogram generated by Ermak (2014).

Figure 9 Map of 40 km survey transect of the St. Johns River, Jacksonville, Florida. Boat-based photo-identification surveys were conducted weekly between the two locations marked with triangles; direction of travel alternated each week..

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VITA

Arien Widrick received her B.S. in Biology from University of North Florida in Jacksonville, FL, in April 2016. Throughout her undergraduate career she completed two research projects and assisted with many more. She plans to continue her education and research while pursuing a M.S. degree at California State University, Northridge, in Dr. Peter Edmunds' coral physiological ecology lab. Upon completion of her M.S. degree she plans to pursue a doctorate degree and continue a career in marine science research and conservation.