School of Biological Sciences

BIOL20020

DOLPHIN BEHAVIOUR COMPUTATIONAL REPORT

STATISTICAL AND COMPUTATIONAL INVESTIGATION OF DOLPHIN SOCIAL NETWORKS

1876793

**Introduction**

*Tursiops aduncus* is a bottlenose dolphin studied in depth by Shark Bay Research in Australia (Connor*et al*., 2001).The aim of the research is to understand whether tool usage combined with sex influences foraging, socialising, traveling, and resting activity as well as social network structure among *T. aduncus* through a sample population of 120 dolphins. Their dorsal fins develop unique nicks/notches allowing the dolphins to be identified and their behaviour observed over time. The dolphins associate according to a fission fusion society and using social network metrics, such as strength and Eigenvector, their true social preferences and homophily can be measured. Short boat surveys took place, using photo-identification of the dolphin groupings that change by minute, hour, and day. The photos recorded which individuals associated together, the proportion of time they spend together, and which of the four activities they were performing. Using the program R, an undirected and weighted network can be built to identify homophylic clusters and individual influence among the population according to attributes such as sex (male or female) or “tool use” (spongers or non-spongers). To some dolphins, a sponge serves as a tool in accessing novel foraging niches such as, prey lacking a swim bladder that can’t be discovered by a dolphin’s echolocation (Kopps*et al*., 2013). The dolphins startle and capture these prey by covering their rostrum with a sponge and, protected from sharp objects, they may probe and scour the sea floor for them. Fatty acid signature analysis has indicated that spongers thus feed on select prey that their non-sponging counterparts do not consume. There is primarily a female bias among spongers as the technique is vertically transmitted between mother and female offspring, and thus highly significant data among female spongers is expected for foraging activity (Mann*et al*., 2008). This pronounced change in feeding habit among an increasingly individualized group within the population could be a preliminary indicator toward an allopatric speciation event (Yamaguchi and Iwasa, 2013). In contrast, strongly significant data is expected for socializing activity among male spongers and non-spongers as they actively need to be part of an alliance to access females and secure paternities, because competition for females is so high (Bizzozzero*et al*., 2019). Travelling and resting are likely similar among males and females, but of higher significance among spongers as their proportion of time spent on foraging should increase with tool-use.

**Methods**

Raw Data Collection

A sample population of 120 *T. aduncus* was observed in Shark Bay, Western Australia by Shark Bay Dolphin Research !!. Behaviour data on foraging, socializing, travelling, and resting was collected during short boat surveys of 5-minute snapshots of group composition and activity from 2007 to 2017. Photo identification of dorsal fins showed how many and which dolphins were present, their activity status, and with which dolphins they associated. The dolphins were assigned a three-letter identification code (ID), and data was recorded for: sex (male and females), tool-users (spongers and non-spongers). Observed unknown behaviours were omitted from the raw dataset.

Statistical Testing with R: Activity Budgets

The raw data of the four activity budgets was visualized through histograms and assigned means (Figure 1), to roughly overview whether the data is normally distributed or skewed. Variables sex and tool (categorical/qualitative variables) were set as factors. A categorical predictor variable was then created by combining sex and tool, resulting in variables: sponger females (SF), non-sponger females (NSF), sponger males (SM), and non-sponger males (NSM). For this dataset, assumption of independence of data points is met, as the individuals in the population freely mix with each other in a fission-fusion society and do not form stable social groups albeit forming alliances (Mann*et al*., 2012). Assumptions for normal distribution, normal residuals and homogeneity of variance, were tested for violation in each of the four activities with a General Linear Model (GLM) procedure detailed in a flow diagram in Figure 2. When assumptions were violated a non-parametric test was conducted because it removes underlying assumptions of normality by using ranks and measures differences via medians over means. When assumptions were met a parametric test was conducted because it assumes sample population distribution is normal. Foraging data violated normal residuals and homogeneity of variance (as visualized in Figure 3), and a Shapiro Wilcox test confirmed the data as non-normal where P<0.05. Socializing data and resting data also had both assumptions violated (as visualized in Figures 4 and 5 respectively), and Shapiro Wilko tests indicated the data non-normal where P<0.05. Travelling data met the assumptions (as visualized in Figure 6), and the Shapiro Wilcox test confirmed the data as normally distributed where P>0.05. Next, a Kruskal-Wallis test was conducted on activity budgets: foraging, socializing, and resting. This test checks for any significance among the data groups where P<0.05, without indicating which specific groups bear the significance. Each of the three activities indicated significance where P<0.05 following the Kruskal-Wallis test. As travelling data was parametric, a one-way ANOVA test was performed to also determine if the overall effect of the predictor is significant when P<0.05. The ANOVA summary indicated travelling data held significance. Either the ANOVA or the Kruskal-Wallis test was conducted, instead of a t-test or Wilcox Mann Whitney test, because the dataset consists of 2+groups not 1 group and the samples are not related but independent. All four activity budgets indicated significance among the data pairs, and thus underwent a pairwise.wilcox post-hoc test and consequent Bonferroni P-value correction method. The post-hoc test compared each activity’s medians through multiple comparison testing, whereupon the Bonferroni correction was required to indicate a 95% confidence in rejecting the null hypothesis without a false positive, and reveal which pairs bore significance when P>0.05 (Table 2). A conclusive boxplot was created for each of the four activities to visualize and read the significant trends of dolphin behaviour from the data (Figures 7, 8, 9 10). The boxplots were labelled according to the pairs’ similarity and dissimilarity.

Statistical Testing with R: Social Network

An undirected and weighted social network was built through R to visually explore influences of sex and tool use on *T. aduncus’* social network structure. First, package ASNIPE allowed for reorganizing the data into an unweighted adjacency matrix, whereupon weight = edge thickness proportional to the association index (proportion of interaction between individuals, where 0 = no interaction, and 1 = strong social bond). The SNA package introduced commands for statistical calculation of node-level network metrics to observe which individuals are more or less socially connected and influential within the network. Strength metric calculates gregariousness by how many direct connections an individual has (number of edges connected to a node). Eigenvector metric calculates potential influence of an individual by how well it is connected and how well its neighbors are connected. Strength and Eigenvector centralities were calculated for each individual and then created into objects to each undergo a GLM as in the methodology previously described and detailed in Figure 2. The strength and Eigenvector metrics violated the assumptions as non-normally distributed data (visualized in Figures 11 and 12 respectively). Both metrics underwent a Kruskal-Wallis test and indicated a significant overall effect of the categorical predictor, thus subsequently undergoing a pairwise.wilcox post-hoc test and Bonferroni correction. Significance between pairs was displayed again via labelled boxplots (Figures 13 and 14 respectively). Package IGRPAH allowed for building the social network from the adjacency matrix. The network was defined as undirected and weighted. During plotting, different node colours and shapes distinguished females vs. males (F=pink, M=blue), and spongers vs. non-spongers (S=square, NS=circle) respectively. The strength metric indicated better connected individuals in the network by producing larger nodes relative to higher strength values. To deeper understand the network’s clustering and homophily an assortativity test was carried out (Gera, 2019), separately on sex and tool use after transforming the variables to numerical objects, revealing through a positive coefficient which nodes were more similar or dissimilar (Farine, 2017).

**Results**

Refer to Table 1 for full record of activity and social metric medians, means, and to Table 2 for post-hoc+ Bonferroni corrected P-values. In testing foraging activity, there were statistically significant differences between the group medians (Kruskal-Wallis, X2 = 46.823, df=3, P < 0.0001, N=120). A pairwise.wilcox post hoc test with Bonferroni correction showed the pairs significantly different from each other were SF + NSF, NSM + SF, SM + SF, and SM + NSM where P<0.05 (Figure 7). Female spongers were the most significant foragers. Remaining pairs among all activities are insignificant where P>0.05.In testing socializing activity, there were statistically significant differences between the group medians (Kruskal-Wallis, X2 = 50.288, df=3, P<0.0001, N=120). A pairwise.wilcox post hoc test with Bonferroni correction showed the pairs significantly different from each other were SF+NSF, NSM+NSF, SM+NSF, NSM+SF, SM+SF, and SM+NSM where P<0.05 (Figure 8). Male groups were most significant. In testing the travelling activity, there were statistically significant differences between the group means following the one-way ANOVA during socializing activities (ANOVA, F3,98= 7.938, p<0.0001, N=120). A pairwise.wilcox post hoc test with Bonferroni correction showed the pairs significantly different from each other were SF+NSF and NSM+SF where P<0.05 (Figure 9). In testing resting activity, there were statistically significant differences between the group medians (Kruskal-Wallis, X2 = 21.195, df=3, P<0.0001, N=120). A pairwise.wilcox post hoc test with Bonferroni correction showed the pairs significantly different from each other were SF+NSF, NSM+SF, and SM+NSM where P<0.05 (Figure 10). In testing the strength metric, there were statistically significant differences between the group medians (Kruskal-Wallis, X2 = 42.132, df=3, P<0.0001, N=120). A pairwise.wilcox post hoc test with Bonferroni correction showed all the pairs were significantly different from each other except SM+NSM where was P>0.05 (Figure 13). In testing the eigenvector metric, there were statistically significant differences between the group medians (Kruskal-Wallis, X2 = 37.079, df=3, P<0.0001, N=120). A pairwise.wilcox post hoc test with Bonferroni correction showed the pairs significantly different from each other were SM+NSF, SM+SF, and SM+NSM where P<0.05 (Figure 14). Addressing the social network (Figure 15), assortativity of tool-use was a positive coefficient of 0.651, and assortativity of sex was also a positive coefficient at 0.118. This indicates strong homophily between spongers and non-spongers, and present, but weaker homophily among male and female groups. The square and circular nodes were distributed approximately 50/50 across the plot, indicating strong homophily among spongers and non-sponger groups. In contrast, the pink and blue nodes were distributed across the plot in small clusters indicating some homophily among groups of females or males, but considerate interspersing in the sample population. The social network thus highlights the influential role that sex and tool-use play among social network structures, by displaying homophilic distribution patterns among the males and females, and spongers and non-spongers.

**Conclusion**

Spongers spend the most significant proportion of time foraging as derived from Figure 7, moreover it is female spongers who are most influential, as they are known to pass the niche technique on to female young. Females additionally spend the largest proportion of time on travel, a possible indicator of the lengths of foraging journeys, Figure 9 furthermore indicates no trend among males regarding travel. In contrast, as male dolphins depend on alliances to secure reproductive success, they are the most frequent socializers. Figure 8, highlights this behaviour as non-sponger males socialize the most, followed by sponger-males, non-sponger females, and sponger females dedicating zero time to socializing over foraging. In figures 9 and 10, spongers spend less time resting or traveling then non-spongers, likely as they are socializing and strengthening social bonds as depicted in the social network. For future studies, it would be worthwhile increasing the sample size from 120, as once the attributes sex and tool were combined, there were fewer individuals in the groups SF, NSF, SM, NSM and the pairwise test lose power of significance.

**Figures and Tables**

**Chart, histogram

Description automatically generated**Figure 1. Four histograms of the raw data displaying the skews of frequency by the proportion of time spent on each of the four activities: foraging, resting, travelling, and socializing. The means are indicated by the red line. Socializing resting are strongly skewed, foraging is slightly skewed, and travelling appears normally distributed.

**Diagram

Description automatically generated**

Figure 2. Flow diagram relaying the statistical methods procedure conducted in R. Key steps including checking assumptions for each activity budget, parametric/ non-parametric tests, Post-hoc, and P-value correction tests.

**Chart

Description automatically generated**

Figure 3. Checking GLM assumptions for foraging with a histogram and QQplot testing normality of residuals and a fitted model testing homogeneity of variance. Both assumptions are violated.

**Chart

Description automatically generated**

Figure 4. Checking GLM assumptions for socializing with a histogram and QQplot testing normality of residuals and a fitted model testing homogeneity of variance. Both assumptions are violated.

**Chart

Description automatically generated with low confidence**

Figure 5. Checking GLM assumptions for traveling with a histogram and QQplot testing normality of residuals and a fitted model testing homogeneity of variance. Both assumptions are met.

**Chart

Description automatically generated**

Figure 6. Checking GLM assumptions for resting with a histogram and QQplot testing normality of residuals and a fitted model testing homogeneity of variance. Both assumptions are violated.

**Chart, box and whisker chart

Description automatically generated**

Figure 7. Boxplot for foraging data with indicated medians. Labelled with the same letter to indicate similarity (no significance in pairs P>0.05) and different letters to indicate dissimilarity (significance among pairs P<0.05).

**Chart, box and whisker chart

Description automatically generated**

Figure 8. Boxplot for socializing data with indicated medians. Labelled with the same letter to indicate similarity (no significance in pairs P>0.05) and different letters to indicate dissimilarity (significance among pairs P<0.05).

**Chart, box and whisker chart

Description automatically generated**

Figure 9. Boxplot for travelling data with indicated medians. Labelled with the same letter to indicate similarity (no significance in pairs P>0.05) and different letters to indicate dissimilarity (significance among pairs P<0.05).

**Chart, box and whisker chart

Description automatically generated**

Figure 10. Boxplot for resting data with indicated medians. Labelled with the same letter to indicate similarity (no significance in pairs P>0.05) and different letters to indicate dissimilarity (significance among pairs P<0.05).

**Chart, histogram

Description automatically generated**

Figure 11. Checking GLM assumptions for the strength centrality metric with a histogram and QQplot testing normality of residuals and a fitted model testing homogeneity of variance. Both assumptions are violated.

**Chart

Description automatically generated**

Figure 12. Checking GLM assumptions for Eigenvector metric with a histogram and QQplot testing normality of residuals and a fitted model testing homogeneity of variance. Both assumptions are violated.

**Chart, box and whisker chart

Description automatically generated**

Figure 13. Boxplot for strength centrality metric data with indicated medians. Labelled with the same letter to indicate similarity (no significance in pairs P>0.05) and different letters to indicate dissimilarity (significance among pairs P<0.05).

**Chart, box and whisker chart

Description automatically generated**

Figure 14. Boxplot for Eigenvector centrality data with indicated medians. Labelled with the same letter to indicate similarity (no significance in pairs P>0.05) and different letters to indicate dissimilarity (significance among pairs P<0.05).

**A picture containing sky, text, map, several

Description automatically generated**

Figure 15. Undirected and weight social structure network of *T. aduncus* built with R. Edge width indicates weight. Where pink= females, blue= males, squares = spongers, and circles = non=spongers. Assortativity coefficient 0.65 for tool-use attribute reflected in near 50/50 homophily among sponger and non-sponger groupings. Assortativity coefficient 0.12 for sex attribute reflected by weaker homophily (groups present but small) and interspersed individuals of either male or female sex. Node strength and individual influence indicated by node size. Stronger social bonds among male nodes, while females are more individually dispersed.

Table 1. Medians for combined attributes (sex and tool) on non-parametric forage, socialize, and rest activity budgets. Medians calculated for social network metric centralities: strength and Eigenvector. Means calculated for combined attributes (sex and tool) on parametric travel activity budget. **Table

Description automatically generated**

Table 2. Post-hoc+ Bonferroni corrected P-values for all activity budgets: foraging, socializing, travelling, and resting, as well as, social node metrics centralities: strength and Eigenvector.**Table

Description automatically generated**

**References**

Bizzozzero, M. R., et al. “Tool Use and Social Homophily among Male Bottlenose Dolphins.” *Proceedings of the Royal Society B: Biological Sciences*, vol. 286, no. 1904, 12 June 2019, p. 20190898.

Connor, Richard C., et al. “Complex Social Structure, Alliance Stability and Mating Access in a Bottlenose Dolphin ‘Super-Alliance.’” *Proceedings of the Royal Society of London. Series B: Biological Sciences*, vol. 268, no. 1464, 7 Feb. 2001, pp. 263–267.

Farine, Damien. “A Guide to Null Models for Animal Social Network Analysis.” *Methods in Ecology and Evolution*, vol. 8, no. 10, 18 Mar. 2017, pp. 1309–1320.

Gera, Ralucca. *Homophily (or Assortativity)*. Naval Postgraduate School, 2019.

Kopps, Anna M., et al. “Characterizing the Socially Transmitted Foraging Tactic ‘Sponging’ by Bottlenose Dolphins (Tursiopssp.) in the Western Gulf of Shark Bay, Western Australia.” *Marine Mammal Science*, vol. 30, no. 3, 10 Dec. 2013, pp. 847–863.

Mann, Janet, et al. “Social Networks Reveal Cultural Behaviour in Tool-Using Dolphins.” *Nature Communications*, vol. 3, no. 1, Jan. 2012.

---. “Why Do Dolphins Carry Sponges?” *PLoS ONE*, vol. 3, no. 12, 10 Dec. 2008, p. e3868.

Tinghitella, Robin M., et al. “On the Role of Male Competition in Speciation: A Review and Research Agenda.” *Behavioral Ecology*, vol. 29, no. 4, 3 July 2018, pp. 783–797.

Yamaguchi, Ryo, and Yoh Iwasa. “First Passage Time to Allopatric Speciation.” *Interface Focus*, vol. 3, no. 6, 6 Dec. 2013, p. 20130026.