



Original Article

Juvenile social dynamics reflect adult reproductive strategies in bottlenose dolphins

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The juvenile period is a challenging life-history stage, especially in species with a high degree of fission–fusion dynamics, such as bottlenose dolphins, where maternal protection is virtually absent. Here, we examined how juvenile male and female bottlenose dolphins navigate this vulnerable period. Specifically, we examined their grouping patterns, activity budget, network dynamics, and social associations in the absence of adults. We found that juveniles live in highly dynamic groups, with group composition changing every 10 min on average. Groups were generally segregated by sex, and segregation was driven by same-sex preference rather than opposite-sex avoidance. Juveniles formed strong associations with select individuals, especially kin and same-sex partners, and both sexes formed cliques with their preferred partners. Sex-specific strategies in the juvenile period reflected adult reproductive strategies, in which the exploration of potential social partners may be more important for males (which form long-term alliances in adulthood) than females (which preferentially associate with kin in adulthood). Females spent more time alone and were more focused on foraging than males, but still formed close same-sex associations, especially with kin. Males cast a wider social net than females, with strong same-sex associations and many male associates. Males engaged in more affiliative behavior than females. These results are consistent with the social bonds and skills hypothesis and suggest that delayed sexual maturity in species with relational social complexity may allow individuals to assess potential associates and explore a complex social landscape without the risks associated with sexual maturity (e.g., adult reproductive competition; inbreeding).

Keywords: fission–fusion, juvenile, sex differences, sex segregation, social development, social network.

INTRODUCTION

Early-life social development can have profound effects on adult behavior, survival, and reproduction (reviewed in Sánchez et al. 2001 and Brown and Laland 2003). For example, early-life social network metrics have been linked to survival and adult social status (McDonald 2007; Stanton and Mann 2012; Nuñez et al. 2014), whereas social isolation in early life has been linked to reduced offspring survival (Margulis et al. 2005). Individuals reared without access to key social partners (e.g., mothers, opposite-sex conspecifics,

and same-age conspecifics) may exhibit abnormal social behaviors as adults, such as atypical mate choice or social incompetence (in which animals respond inappropriately to available social cues, e.g., escalating social play to aggression; birds: Adkins-Regan and Krakauer 2000; mammals: Kempes et al. 2008; van Leeuwen et al. 2014; fish: Arnold and Taborsky 2010; Taborsky et al. 2012).

In addition to benefiting from developing social skills, individuals can also benefit from forming persistent associations with particular conspecifics (Silk 2002). These persistent associations have repeatedly been linked to survival and reproductive success in adult mammals (dolphins: Krützen et al. 2004; Frère et al. 2010; hyraxes: Barocas et al. 2011; ungulates: Cameron et al. 2009; Vander

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associates, they may still benefit from engaging in mixed-sex social interactions in all-juvenile groups when allied adult males are absent. During the juvenile period, both males and females have elevated tooth rake marks (Lee et al. 2019), suggesting that social interactions are not without some cost, though it is currently unknown whether these injuries primarily come from juvenile or adult males.

Finally, we expect juvenile social structure to reflect underlying association patterns (Hinde 1976). First, we anticipate that juvenile social groups will largely be segregated by sex due to a preference for same-sex associates. In addition, sex segregation may be driven by sex-biased activity budgets: females at all life stages make foraging a higher priority than males, whereas adult males spend more time in active social groups (Krzyszczuk et al. 2017; Galezo et al. 2018). Sex differences in activity preferences can result in sex segregation if mixed-sex groups become unstable (Conradt and Roper 2000; Galezo et al. 2018). Second, given the lack of allied male aggression in juveniles, we predict that juvenile females will not explicitly avoid juvenile males.

METHODS

Study site and data collection

The Shark Bay Dolphin Research Project has collected behavioral, demographic, genetic, and ecological data on a population of over 1700 wild Indo-Pacific bottlenose dolphins (*T. aduncus*) in Shark Bay, Western Australia (25°47'S, 113°43'E) since 1984. Shark Bay is a UNESCO World Heritage Site with extensive seagrass beds and a stable dolphin population (Manlik et al. 2016). This population is characterized by bisexual philopatry (Tsai and Mann 2013), which allows us to study both sexes from birth to adulthood.

We used both survey and focal follow data in our analyses. Surveys are opportunistic boat-based observations of a group of dolphins in which group composition and predominant activity are recorded via 5-min scan sampling (Karniski et al. 2015). Individual dolphins were identified via dorsal fin photo identification and/or other markings (Würsig and Jefferson 1990; Bichell et al. 2018). The ages of individuals were determined via known birth date (Mann et al. 2000), degree of ventral speckling (Krzyszczuk and Mann 2012), or body size (for young animals). For all juvenile subjects in this study, birth date was known. The sexes of individuals were determined by sightings of genitals, sighting of a dependent calf, and/or genetically (Mann et al. 2000; Krützen et al. 2002). We used a 10-m chain rule to determine group membership (Smolker et al. 1992).

Focal follows are systematic observations of a focal individual or mother-calf pair for a maximum duration determined a priori ranging from 30 min to 10 h. The behavioral state of the focal individual was recorded via 1-min point sampling, and discrete behavioral events were recorded continuously (see Supplementary Appendix for ethogram). The identities of all individuals in the focal group were recorded via 1-min point sampling, and any changes in group composition (new individuals joining or leaving the group) were recorded continuously.

We define juveniles as individuals who are weaned and under age 10. Weaning date is determined by two metrics, cessation of swimming in “infant position” (under the mother’s abdomen, tail; an indicator of nursing) and when association between mother and calf drops below 50% (Mann et al. 2000; Karniski et al. 2018). Weaning ages range from 2.5 to 8.5 years (Mann et al. 2000; Karniski et al. 2018). Age 10 is used as the upper bound of juvenescence as >99.9% of pregnancies are at age 10 or older (*T. aduncus*; Karniski et al. 2018; Mann 2019) and because males reach adult

testosterone concentrations around age 10 (*Tursiops truncatus*; Wells et al. 1987; Robeck et al. 1994).

Kinship between individuals was assigned either via an observed maternal pedigree or through calculation of a genetic relatedness coefficient. Genetic relatedness data were obtained using single nucleotide polymorphism (SNP) markers generated from RAD-sequencing as described in Foroughirad et al. 2019. A quality-filtered panel of 4235 SNPs was used to calculate relatedness coefficients using the dyadic maximum likelihood estimator (Milligan 2003) implemented in the COANCESTRY software (Wang 2011). For the purposes of this study, we defined kin as any individuals sharing a relationship with an expected relatedness coefficient ≥ 0.0625 , for example, half-first cousins. We base this cutoff on studies showing that affiliation (Foroughirad 2019) and other social behaviors (e.g., response to alarm calls; Rendall et al. 1996) can be biased toward this kin category compared with unrelated individuals.

Spatially explicit null model

To determine expected association values under the null hypothesis of no effect of sex on juvenile associations, we simulated data using a spatially explicit null model (Carter et al. 2009; Strickland et al. 2017). These models provide expected values of social behavior taking into account individual space use, temporal availability, average gregariousness, and observation biases that can occur from opportunistic and/or uneven sampling of the study site. The null model also allows us to adjust our expectations for the slightly skewed sex ratio resulting from high juvenile male mortality (Stanton and Mann 2012).

In the null model, we included all individuals of known sex that had at least 15 survey observations (mean \pm standard deviation [SD] = 56.3 ± 53.7) between weaning and 10 years of age as focals ($n = 140$, $n_{\text{females}} = 80$, $n_{\text{males}} = 60$). Any individual that had at least 15 total observations was included as a potential associate ($n = 603$). Fifteen observations are sufficient to accurately measure social network metrics in this population (Mann et al. 2012) and are sufficient to estimate individual home ranges: randomly sampling 15 observations from a larger subset of observations produces dyadic home-range overlap correlations greater than 0.75 on average compared with the full set of observations (Foroughirad et al. 2019). A total of 2900 survey days conducted between June 1988 and December 2017 were included.

Our simulation protocol followed the same general steps outlined in Strickland et al. (2017) with minor modifications. In brief:

1. A 100- \times 100-m grid was overlaid on the study site.
2. A home range was constructed for each individual by creating a kernel utilization distribution (see R package “adehabitatHR”; Calenge 2006) over the grid using one location per day.
3. A daily search area polygon was created by taking a minimum convex hull around the day’s sightings and the launch point and adding a 1 km buffer.
4. For each survey day, the search area polygon was intersected with the set of home ranges, and a set number of dolphins was selected from that area based on the number of real dolphins observed during the survey day.
5. The identity of dolphins selected was determined by randomly sampling from the set of available individuals, weighted by the proportion of each individual’s home range covered by the search area.
6. Each individual’s location was assigned by randomly sampling a grid cell from within the search area with a probability equal to the proportion of that individual’s home range on each grid cell.

7. The set of dolphin locations was then clustered into the number of groups actually observed using complete-linkage hierarchical clustering (Murtagh 1985).
8. Steps 4–7 were repeated for all 2900 surveys days.
9. Association indices (the weight of a connection between a focal and their associate) were calculated using the simple ratio index (Cairns and Schwager 1987). The simple ratio index is calculated as the number of times both individuals are sighted in the same group divided by the cumulative number of times each individual has been sighted in any group. We chose the simple ratio index because it has been shown to be an unbiased estimator of association rates from sampled data with group location error, particularly when true association rates are unavailable for calibration (Hoppitt and Farine 2018). For each pair, sightings used in the index were limited to when the focal was between weaning and age 10, and the alter was between ages 4 and 12. The alter age can be slightly older because the focal and alter would have still been calves and juveniles at the same time, so s/he would be part of the same cohort.
10. Ten network metrics were calculated within each focal's ego network (see R package "igraph"; Csardi and Nepusz 2006): degree, same-sex degree, opposite-sex degree, strength (cumulative weighted degree), same-sex strength, opposite-sex strength, opposite-sex strength (kin only), opposite-sex strength (nonkin only), local clustering coefficient, and proportion close kin associated with. Degree is the focal's number of unique associates aged 4–12. Strength is the sum of the focal's association indices with associates aged 4–12. Local clustering coefficient is the probability that the focal's associates (aged 4–12) are also associated with each other. Proportion close kin is the proportion of an ego's available close kin aged 4–12 (coefficient of relatedness ≥ 0.0625) that they ever associated with.

The simulation was repeated 1000 times. Each individual has "true" social metric values from observed data, as well as an expected distribution of values from the 1000 simulations.

To compare the observed social metrics of juveniles to their expected values, we compared the observed male and female means of each social metric with the distribution of expected male and female means using the significance testing rule described in Phipson and Smyth 2010:

$$P = \frac{b + 1}{m + 1}$$

where m is the number of permutations (here, 1000) and b is the number of permutations that are more extreme than the observed value. To account for multiple testing ($n = 10$ social network metrics calculated for each sex, total tests = 20), we applied Bonferroni corrections to the P -values and interpreted results using these adjusted P -values. A Bonferroni-corrected P -value of 0.01998 is the lowest value possible given the number of simulations used (1000) and represents a scenario in which the observed measurement falls outside of the simulated distribution.

To compare the strength of same-sex associations in males versus females, we subtracted expected same-sex strength from observed same-sex strength for each focal, then took the mean of the resulting 1000 differentials to produce a single mean differential for each focal. We then compared male and female mean differentials using a two-tailed two-sample exact permutation test using a Monte Carlo method (in R package "perm"; Fay and Shaw 2010). We used the same procedure to compare the degrees (number of

unique associates) and local clustering coefficients of males and females.

Finally, we compared the strength and quantity of same-sex versus opposite-sex associations. First, we used a general symmetry test to compare a focal's observed same-sex strength with their observed opposite-sex strength (see R package "coin"; Zeileis et al. 2008). We used the same procedure to compare a focal's observed same-sex degree with their observed opposite-sex degree.

Activity budget and behavioral events

To assess the activity budgets of single-sex versus mixed-sex groups, we analyzed the predominant activity during 264 all-juvenile surveys collected from 1990 to 2017. We included any surveys of two or more individuals in which all individuals sighted in the first 5 min of the survey were juveniles of known sex. We ran pairwise Fisher's exact tests with Bonferroni corrections for multiple testing to assess the relationship between the sex composition (all male, all female, or mixed sex) and the predominant activity of the group (forage, rest, social, travel, or other).

To compare time spent foraging and socializing in male ($n = 7$) and female ($n = 18$) focal juveniles, we analyzed point sample data from 140 focal follows on 25 unique individuals, totaling 283 h of observation. We only included focal individuals with at least 3 h of point sample data from the juvenile period collected from at least two unique focal follow sessions. To compare time spent socializing and time spent foraging by sex, we ran two-tailed two-sample exact permutation tests using a Monte Carlo method (in R package "perm"; Fay and Shaw 2010). Using the same focal follow data set, we also analyzed behavioral events: discrete behaviors that are recorded continuously during focal follows (see Supplementary Appendix for ethogram). To compare hourly rates of aggressive, affiliative, and sociosexual behavioral events by sex, we ran two-tailed two-sample exact permutation tests using the network algorithm method (see R package "perm"; Fay and Shaw 2010).

Quantifying sexual segregation

We quantified the degree of sexual segregation in juveniles using survey data. We only included surveys in which all individuals were juveniles or calves, and the sex of all juveniles was known ($n = 1576$ surveys, spanning 1989–2017). Although calves could be present in surveyed groups, they were not included when determining group sex composition. Only individuals sighted in the first 5 min of the survey were included in analyses. Two hundred fifteen unique juvenile individuals were represented in the data set (116 females and 99 males). To calculate the degree of sexual segregation, we used the sexual segregation and aggregation statistic (SSAS; Bonenfant et al. 2007):

$$SSAS = 1 - \frac{N}{XY} \sum_{i=1}^k \frac{X_i Y_i}{N_i}$$

where X = the total number of males, Y = the total number of females, N = the total number of animals, k = the number of groups, X_i = the number of males in the i th group, Y_i = the number of females in the i th group, and N_i = the total number of animals in the i th group.

We then generated an expected distribution of SSAS values by randomizing the sex composition of juvenile groups while preserving group sizes and overall sex ratio for 1000 permutations. An observed SSAS value greater than the expected distribution indicates significant segregation, whereas an observed value less than

the expected distribution indicates significant aggregation. A value that falls within the expected distribution indicates that individuals associate randomly with respect to sex.

Juvenile fission–fusion dynamics

To quantify the overall fission–fusion rate for juveniles, we calculated the total number of group composition changes (joins or leaves) per hour for all-juvenile focals with at least 30 min of focal follow data, then calculated an average across all individuals.

To determine if one sex was disproportionately driving sexual segregation by often leaving and rarely joining the opposite sex, we calculated Hinde's index values for juvenile male–female dyads in our population (Hinde and Atkinson 1970):

$$\text{Hinde's index} = \frac{\# \text{ times male joins female}}{\text{total joins between male and female}} - \frac{\# \text{ times male leaves female}}{\text{total leaves between male and female}}$$

A positive Hinde's index value indicates that the male in the dyad is responsible for maintaining proximity to the female, whereas a negative value indicates that the female is responsible for maintaining proximity to the male.

We identified all-juvenile dyads (same sex or mixed sex) for whom we observed at least five join–leave interactions that occurred when no adults were present in the group (as in Galezo et al. 2018; $n = 95$ dyads, 32 females, 21 males, 608 joins, 666 leaves). We then calculated the mean Hinde's index for all juvenile male–female dyads ($n = 34$ male–female dyads, 227 joins, 175 leaves). To generate an expected distribution of the mean Hinde's index given no effect of sex on fission–fusion dynamics, we randomized the sexes of all individuals ($n = 32$ females, 21 males) and calculated the mean Hinde's index for the new set of male–female dyads, and repeated this for 1000 permutations. An observed mean Hinde's index greater than the expected distribution indicates that males are largely responsible for maintaining proximity to females, whereas an observed value less than the expected distribution indicates that females are responsible for maintaining proximity to males. A value that falls within the expected distribution indicates that there is no sex bias in patterns of joins and leaves (see also Galezo et al. 2018).

RESULTS

Group size and composition

Averages are reported as mean \pm standard error (SE) unless otherwise specified. Of 84 females and 62 males with at least 15 survey sightings in the juvenile period, juvenile females were alone significantly more than males, with females alone in $15.2\% \pm 1.8\%$ of sightings and males alone in $9.5\% \pm 1.1\%$ of sightings on average (permutation t -test, $\zeta = -2.49$, $P = 0.0128$). Juvenile males were sighted in larger groups than females on average (permutation t -test, $\zeta = -2.21$, $P = 0.027$). Mean observed group size for individual juvenile females ranged from 2.11 to 10.1 (6.06 ± 0.21), and mean observed group size for individual juvenile males ranged from 3.93 to 11.3 (6.74 ± 0.20).

Of these animals, 25 females and 14 males had at least 15 survey sightings in all-juvenile groups. In all-juvenile groups ($n = 1495$ sightings), mean group size for individual females ranged from 1.0 to 2.29 (1.45 ± 0.08), and mean group size for individual males ranged from 1.38 to 2.7 (1.79 ± 0.10). Mean group size for individual females in all-juvenile groups was significantly lower than for

individual males (permutation t -test, $\zeta = -2.48$, $P = 0.013$). Most all-juvenile groups contained one individual, up to a maximum of seven individuals (Figure 1). As group size increased, mixed-sex groups became more common and all-female groups became less common (Figure 2).

Social network analysis

Of 26 117 focal–alter juvenile pairs, 40.8% (10 668) of pairs could be classified as kin or nonkin. Of these, 9.8% were kin and the remainder were nonkin. Both males and females associated with more of their close juvenile kin (coefficient of relatedness ≥ 0.0625) than expected ($P_{\text{male}} < 0.02$, $P_{\text{female}} < 0.02$; Figure 3e; Table 1).

Female juveniles had a mean \pm SD of 21.9 ± 9.3 unique associates ($n = 80$ females, range = 5–46), whereas juvenile males had a mean \pm SD of 27.0 ± 7.8 unique associates ($n = 60$ males, range = 9–49). Based on the spatially explicit null model, juveniles had fewer associates than expected ($P_{\text{female}} < 0.02$, $P_{\text{male}} < 0.02$; Table 1). In males, degree (number of unique associates) was, on average (mean \pm SE), 4.87 ± 1.68 associates lower than expected. In females, degree was, on average (mean \pm SE), 8.97 ± 1.46 associates lower than expected. Specifically, males matched the expected number of male associates ($P = 1$; Figure 3a; Table 1), but had fewer female associates than expected ($P < 0.02$; Figure 3b; Table 1). Female juveniles had both fewer male ($P < 0.02$; Figure 3b; Table 1) and fewer female ($P < 0.02$; Figure 3a; Table 1) associates than expected. There was no significant difference in how much observed degree differed from expected for males versus females (two-tailed two-sample permutation test, Monte Carlo method, $P = 0.076$). On average, 53.7% of females' associates and 51.3% of males' associates were same sex.

Male and female juveniles had higher association strengths than expected ($P_{\text{female}} < 0.02$, $P_{\text{male}} < 0.02$; Figure 3c; Table 1), regardless of the sex of their partner (same-sex strength: $P_{\text{female}} < 0.02$, $P_{\text{male}} < 0.02$; opposite-sex strength: $P_{\text{female}} < 0.02$, $P_{\text{male}} < 0.02$; Table 1). Association strengths with opposite-sex partners were higher than expected regardless of whether or not the

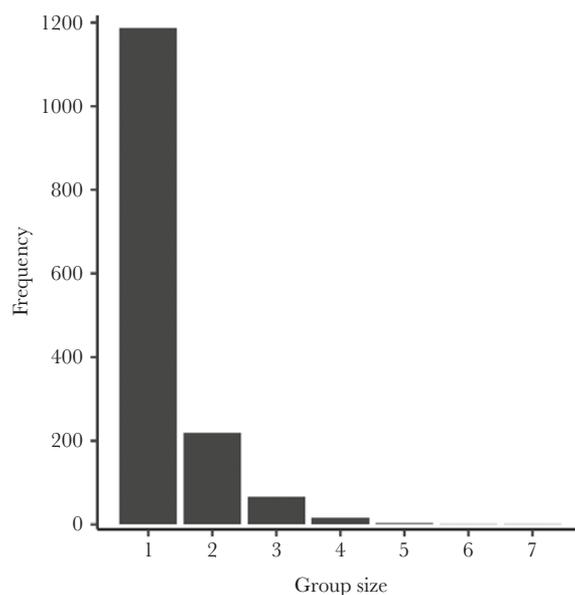


Figure 1 Histogram of group sizes of all-juvenile groups. Includes 1495 surveys collected from 1989 to 2017. Mean \pm SD group size was 1.29 ± 0.65 .

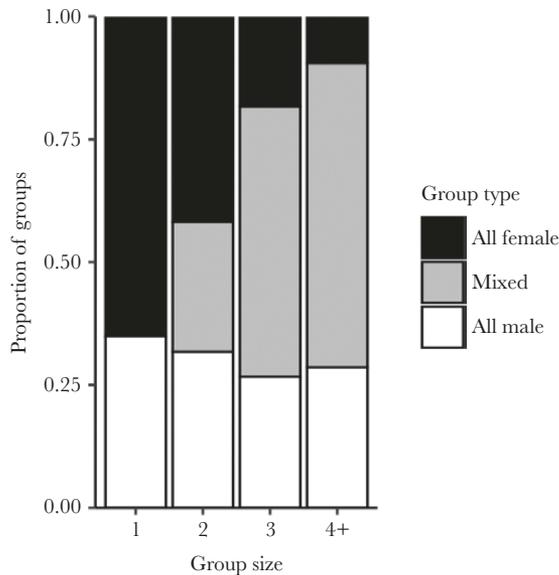


Figure 2
Group sex composition as a function of group size in all-juvenile groups. Includes 1495 surveys collected from 1989 to 2017.

focal and partner were closely related (opposite-sex strength, kin only: $P_{\text{female}} < 0.02$, $P_{\text{male}} < 0.02$; opposite-sex strength, nonkin only: $P_{\text{female}} < 0.02$, $P_{\text{male}} < 0.02$; Table 1). In males, kin made up 30.3% of opposite-sex association strength on average, whereas, in females, kin made up 21.7% of opposite-sex association strength.

Male and female juveniles had higher clustering coefficients than expected ($P_{\text{male}} < 0.02$, $P_{\text{female}} < 0.02$; Figure 3d; Table 1). In males, clustering coefficients were, on average (mean \pm SE), 0.120 ± 0.011 higher than the expected value. In females, clustering coefficients were, on average (mean \pm SE), 0.147 ± 0.016 higher than the expected value. There was no significant difference in how much observed clustering coefficients differed from expected for males versus females (two-tailed two-sample permutation test, Monte Carlo method, $P = 0.248$). In other words, the degree of “cliquishness” of a focal was independent of their sex.

Same-sex associations were more common than opposite-sex associations (general symmetry test, $P = 0.0008$). Females had an average (mean \pm SE) of 11.8 ± 0.54 same-sex associates and 10.1 ± 0.60 opposite-sex associates. Males had an average of 13.9 ± 0.60 same-sex associates and 13.2 ± 0.56 opposite-sex associates. Similarly, same-sex associations were stronger than opposite-sex associations (general symmetry test, $P = 1.2 \times 10^{-14}$). Females had an average same-sex association strength of 0.613 ± 0.038 compared with an average opposite-sex association strength of 0.390 ± 0.029 . Males had an average same-sex association strength of 0.871 ± 0.048 compared with an average opposite-sex association strength of 0.549 ± 0.032 .

Same-sex associations were stronger in males than in females (two-tailed two-sample permutation test, Monte Carlo method, $P = 0.002$). In males, same-sex association strengths were $54.8\% \pm 6.7\%$ (mean \pm SE) higher than expected on average. In females, same-sex association strengths were $23.5\% \pm 7.6\%$ higher than expected on average. See Supplementary Figure 1 for examples of male and female ego networks.

Activity budget and behavioral events

Juvenile females spent, on average, twice as much time foraging as juvenile males (mean proportion time \pm SE, females = 0.52 ± 0.06 , males = 0.25 ± 0.06 , two-tailed two-sample permutation test, Monte Carlo method, $P = 0.026$; Figure 4). Time spent socializing was not significantly different between males and females (mean proportion time \pm SE, females = 0.08 ± 0.02 , males = 0.13 ± 0.03 , two-tailed two-sample permutation test, Monte Carlo method, $P = 0.156$; Figure 4).

In all-juvenile groups of two or more individuals, all-male and mixed-sex groups had similar activity budgets (Fisher’s exact test with Bonferroni correction, $P > 0.05$), but both differed from all-female groups (Fisher’s exact tests with Bonferroni corrections, $P_{\text{all-male vs. all-female}} = 0.006$, $P_{\text{mixed-sex vs. all-female}} = 0.009$). All-male groups socialized and rested more than all-female groups and foraged and traveled less (Figure 5).

In juveniles, hourly rates of aggressive (median \pm interquartile range [IQR], males = 0.00 ± 0.62 , females = 0.09 ± 0.43) and sociosexual (median \pm IQR, males = 0.00 ± 0.57 , females = 0.00 ± 0.12) behavioral events were relatively low compared with rates of affiliative events (median \pm IQR, males = 8.5 ± 13.5 , females = 2.8 ± 3.3). Juvenile males had higher rates of affiliative events than juvenile females (two-tailed two-sample permutation test, $P = 0.002$), but there was no significant sex difference in the rate of aggressive events (two-tailed two-sample permutation test, $P = 0.64$) or sociosexual events (two-tailed two-sample permutation test, $P = 0.65$), possibly due to the very low rate of aggressive and sociosexual behaviors.

Sexual segregation and fission-fusion dynamics

The mean (\pm SE) fission–fusion rate of focal juveniles ($n = 53$) was 5.9 ± 0.56 joins/leaves per hour, representing a change in group composition every 10 min on average. All-juvenile groups in our population exhibited significant sexual segregation ($P < 0.001$; Figure 6). However, male–female juvenile pairs did not exhibit a sex bias in fission–fusion dynamics ($n = 34$ male–female dyads with more than five interactions, mean Hinde’s Index = 0.018 , SE = 0.053 , $P = 0.37$; Figure 7). Juvenile males joined juvenile females 164 times and left 98 times, and juvenile females joined juvenile males 138 times and left 109 times. Across all juvenile male–female pairs with at least five interactions, males were responsible for maintaining proximity to females in 56% of pairs, females were responsible for maintaining proximity to males in 38% of pairs, and 6% of pairs had Hinde’s index values of 0 (mutual maintenance of proximity).

DISCUSSION

The juvenile period is fraught with potential fitness costs as juveniles are still reproductively immature yet no longer enjoy the benefits of infancy (e.g., maternal protection and nutritional dependence). Despite this, prolonged juvenile periods are common, especially among taxa with marked relational social complexity, in which individuals maintain differentiated relationships (Joffe 1997; Bergman and Beehner 2015; Lukas and Clutton-Brock 2018). Here, we assessed the *social bonds and skills hypothesis*, which posits that delayed sexual maturity allows juveniles to explore the social landscape, begin forming strong associations with preferred social partners, and practice social skills before incurring the costs of reproductive competition (Joffe 1997; Fairbanks 2002). In the

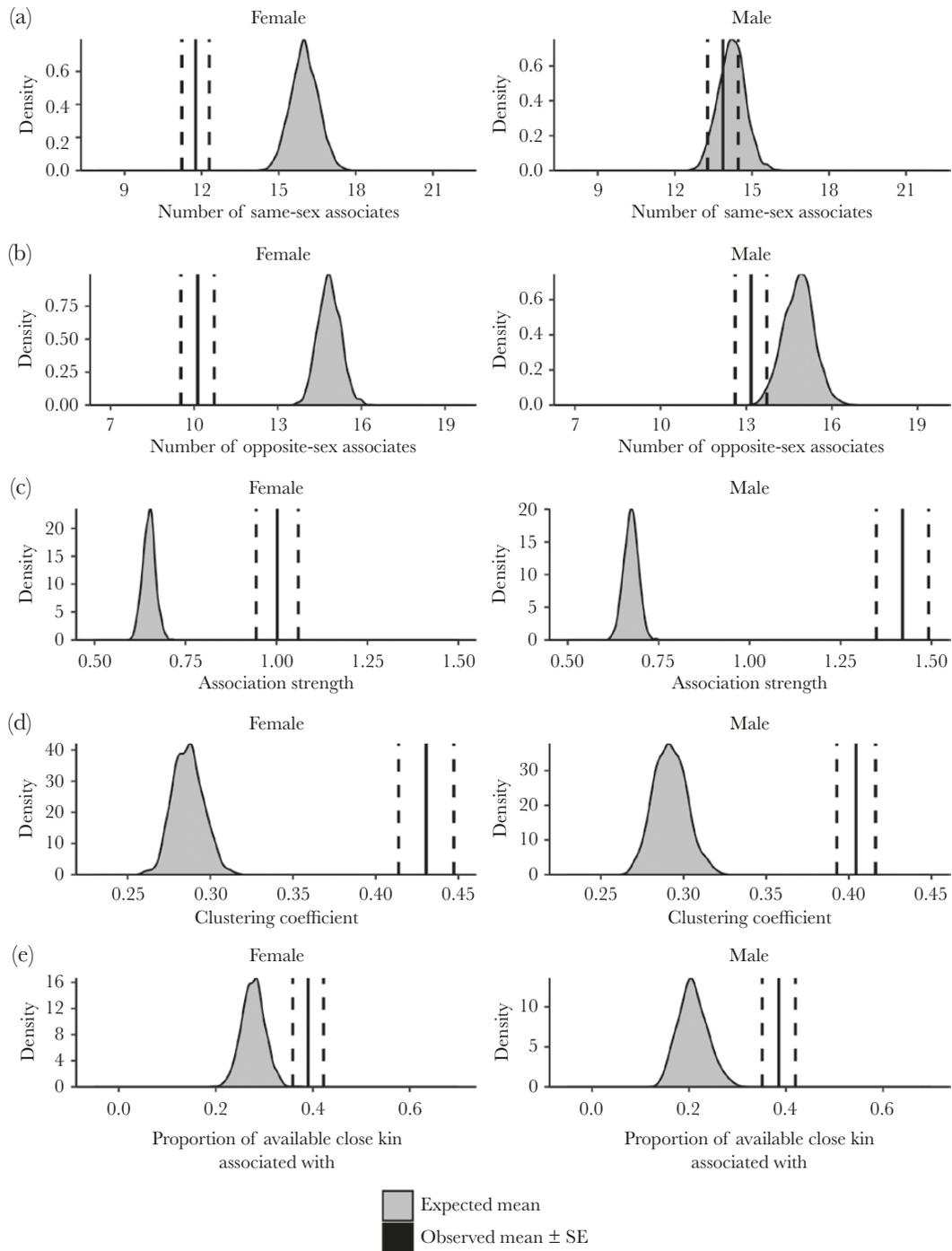


Figure 3

Social network metrics of juvenile individuals ($n = 80$ females, 60 males) compared with expected values from a spatially explicit null model. The spatially explicit null model randomly samples sets of individuals from within their respective home ranges and groups them by proximity such that their average group size in the simulation matches observed group sizes (Strickland et al. 2017). Social network metrics calculated from the null model represent expected values given individuals’ space use, temporal availability, and average gregariousness. Individuals’ social network metrics are grouped by sex to calculate the mean and SE. (a) Observed same-sex degree, or number of same-sex associates, is lower than expected for females ($P < 0.02$) but consistent with expected values for males ($P > 0.05$). (b) Observed opposite-sex degree (number of opposite-sex associates) is lower than expected for both males ($P < 0.02$) and females ($P < 0.02$). (c) Observed strength of associations are greater than expected for both males ($P < 0.02$) and females ($P < 0.02$). (d) Observed clustering coefficients are greater than expected for both males ($P < 0.02$) and females ($P < 0.02$). (e) Both males ($P < 0.02$) and females ($P < 0.02$) associate with more of their available close juvenile kin than expected (coefficient of relatedness ≥ 0.0625).

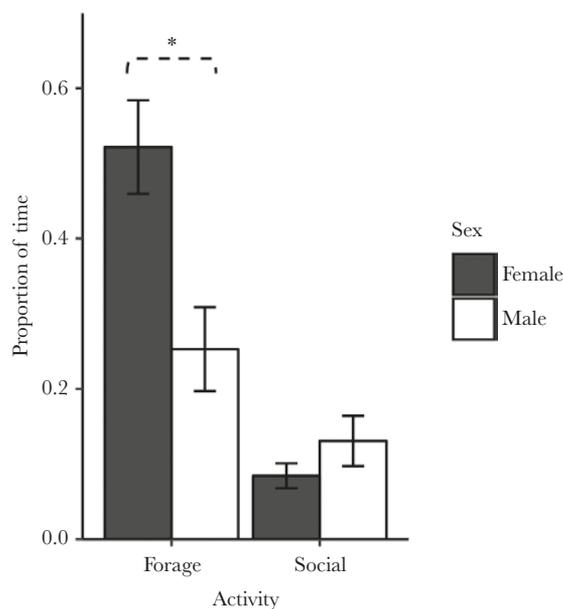
dolphin’s fission–fusion society, juveniles face additional challenges as they must navigate a constantly changing social environment, where group composition changes, on average, five or six times per hour (Galezo et al. 2018; this study) and adults are often absent.

Consistent with the *social bonds and skills hypothesis*, we did not find opposite-sex avoidance in juveniles, suggesting that juveniles elect to explore mixed-sex interactions when the risks associated with sexual maturity, such as inbreeding and sexual conflict, are absent.

Table 1

Spatially explicit null model results ($n = 60$ males, 80 females). P -values are Bonferroni corrected. Expected range represents the expected range of means based on the simulation results ($n = 1000$ permutations)

Social network metric	Sex	Observed mean	Expected range	P
Degree	Female	21.89	28.68–33.44	0.01998
Degree	Male	27.03	29.22–34.43	0.01998
Same-sex degree	Female	11.76	14.35–17.68	0.01998
Same-sex degree	Male	13.87	12.7–16	1.00000
Opposite-sex degree	Female	10.12	13.66–16.32	0.01998
Opposite-sex degree	Male	13.17	13.32–16.72	0.01998
Strength	Female	1.00	0.6–0.71	0.01998
Strength	Male	1.42	0.62–0.74	0.01998
Same-sex strength	Female	0.61	0.3–0.37	0.01998
Same-sex strength	Male	0.87	0.26–0.33	0.01998
Opposite-sex strength	Female	0.39	0.29–0.36	0.01998
Opposite-sex strength	Male	0.55	0.27–0.35	0.01998
Opposite-sex strength (kin only)	Female	0.05	0.02–0.03	0.01998
Opposite-sex strength (kin only)	Male	0.10	0.01–0.03	0.01998
Opposite-sex strength (nonkin only)	Female	0.18	0.12–0.16	0.01998
Opposite-sex strength (nonkin only)	Male	0.23	0.1–0.16	0.01998
Clustering coefficient	Female	0.43	0.26–0.32	0.01998
Clustering coefficient	Male	0.40	0.26–0.32	0.01998
Proportion of close kin associated with	Female	0.39	0.2–0.37	0.01998
Proportion of close kin associated with	Male	0.39	0.13–0.31	0.01998

**Figure 4**

Activity budgets of juvenile males and females. Values represent the mean \pm SE for each sex. Includes point sample data from 140 focal follows on 25 juvenile individuals ($n = 7$ males, 18 females), totaling 283 h of observation. All focal individuals had at least 3 h of point sample data collected from two or more focal follow sessions during the juvenile period. Sex differences in time spent foraging and socializing were compared with a two-tailed two-sample exact permutation test using the Monte Carlo method. Significance stars indicate a significance level of $P < 0.05$.

This contrasts with the adult period, where females avoid males (Galezo et al. 2018). Similarly, juvenile social interactions showed strikingly little aggression: affiliative behaviors were two orders of magnitude more frequent than aggressive or sociosexual interactions. These results suggest that the juvenile period offers both sexes the opportunity to evaluate potential mates without the risks of inbreeding, poor mate choice, or injury associated with adult

male alliances (Scott et al. 2005; Wallen et al. 2017), although elevated tooth rake scarring during the juvenile period suggests that mild injuries occur during socializing (Lee et al. 2019). Whether or not juvenile dolphins actually evaluate conspecifics as potential future mates is currently unknown, but evidence in birds does suggest that early-life exposure to potential mates can profoundly affect adult mate choice (Adkins-Regan and Krakauer 2000). In addition, even if juvenile females have the opportunity to evaluate juvenile males, whether or not female dolphins can exercise mate choice as adults in the face of sexual coercion is currently unknown (but see Bisazza et al. 2001 for work in fish).

Although juveniles may be free to explore interactions that would be risky in adulthood, juveniles should still benefit from prioritizing associations with conspecifics that will provide them the greatest utility (Joffe 1997; Fairbanks 2002). In this population, mixed-sex associations may be a poor investment of time and energy given the lack of mixed-sex bonds in adults (Smolker et al. 1992; Mann et al. 2012). Consistent with this expectation, juveniles had stronger and more abundant same-sex than mixed-sex associations. This same-sex preference in juveniles is likely to be the driving factor behind juvenile sex segregation, given no evidence of opposite-sex avoidance. This contrasts with adults, in which sex segregation is largely driven by female avoidance of males (Galezo et al. 2018). These results highlight the value of examining dyadic-level interactions when characterizing social structure as identical features of social structure (e.g., sex segregation) can be driven by entirely different underlying processes (e.g., preference vs. avoidance). In addition, these results indicate that social pressures specific to adults (e.g., reproductive competition) can be key drivers of subadult social structure and behavior, consistent with findings in other mammals (Mendoza-Granados and Sommer 1995; Maestripieri and Ross 2004; Mazikowski et al. 2018).

More generally, both male and female juveniles were selective in forming preferred social partners: males and females associated with fewer individuals than expected given spatial overlap, but the strength of these associations was higher than expected. It is unsurprising that juveniles take a “quality over quantity” approach

in their association patterns as stronger associations may provide the greatest fitness benefits (e.g., mammals: Silk et al. 2009; Kern and Radford 2016; fish: Heathcote et al. 2017; birds: Woods et al. 2018). At least some of these relationships were initiated during

the calf period and strengthened postweaning (Tsai and Mann 2013). Importantly, we controlled for spatial overlap in our model: strong same-sex associations in juveniles are true preferences, not a product of proximity.

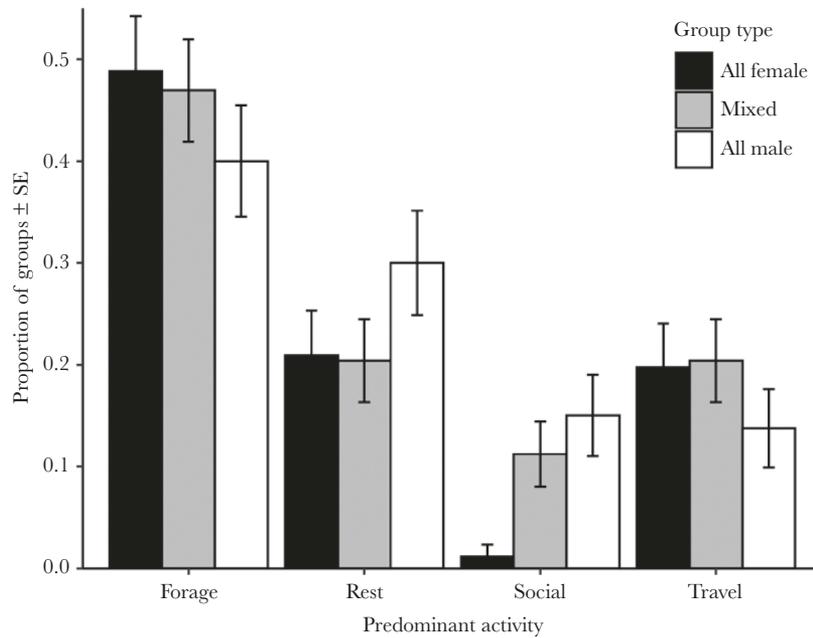


Figure 5

Predominant group activity as a function of group sex composition in all-juvenile groups of two or more individuals. Includes data from 264 surveys collected from 1990 to 2017. We only included surveys in which all individuals were juveniles of known sex. Activity budgets of all-male and mixed-sex groups did not differ significantly, but both differed from all-female groups (Fisher’s exact tests with Bonferroni corrections, $P_{\text{all-male vs. all-female}} = 0.003$, $P_{\text{mixed-sex vs. all-female}} = 0.015$).

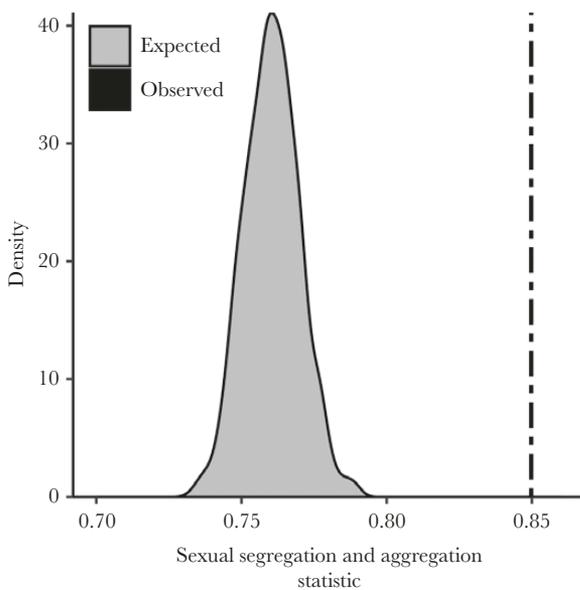


Figure 6

SSAS of all-juvenile surveyed groups. We only included surveys ($n = 1576$, spanning 1989–2017) in which all individuals were juveniles or calves, and the sex of all juveniles was known. The observed SSAS value lies above the expected distribution, indicating that juvenile groups are significantly sexually segregated ($P < 0.001$). The expected distribution was generated by permuting group sighting data to randomize sex composition while preserving group sizes and overall sex ratio for 1000 permutations.

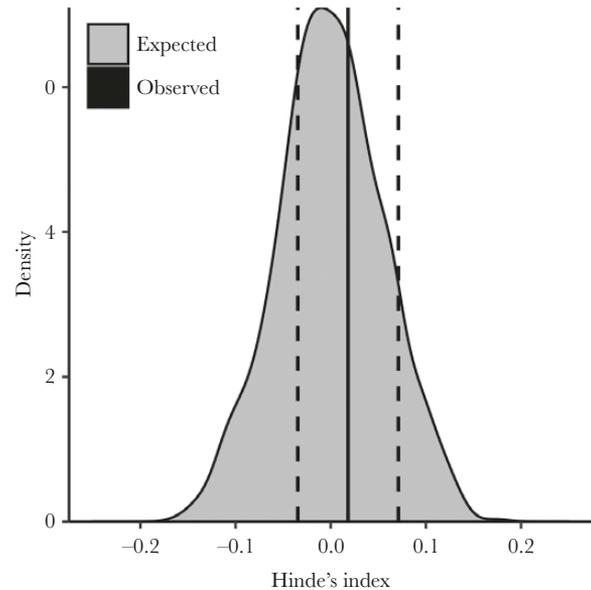


Figure 7

Mean \pm SE Hinde’s Index value of 34 male–female juvenile pairs versus the expected distribution. Each pair had to have at least five join or leave interactions to be included in analysis. Only join and leave events that occurred when no adults were present in the group were included. The expected distribution was generated by randomizing the sexes of all individuals and recalculating the mean Hinde’s Index for 1000 permutations.

Although both sexes are generally selective in their associations, the emergence of sex differences in other aspects of social behavior reflects sex-specific adult reproductive strategies. First, we found that juvenile males, but not females, had as many same-sex associates as expected given spatiotemporal overlap, suggesting that males are not yet exercising selectivity and may benefit more from broader assessment of potential social partners. Male calves also preferentially associate with other male calves (but not juvenile males), suggesting that this exploration of age-cohort members in males starts early in life (Stanton et al. 2011; Stanton and Mann 2012). Similarly, we found that juvenile males formed stronger same-sex associations than females. These results are unsurprising given the importance of alliance formation to adult male reproductive success, in which males in alliances attain more than 80% of paternities (Krützen et al. 2004). Recent findings suggest that males' close associates from ages 8 to 14 are likely to become future alliance partners (Gerber et al. 2019). Thus, for males, the early formation of social relationships with other males is likely critical to adult reproductive success.

Second, we found that social activity was more common in all-male and mixed-sex groups than all-female groups and that males engaged in more discrete affiliative social behaviors than females. This is consistent with findings in other mammals (primates: Maestriperi and Ross 2004; Paukner and Suomi 2008; Yanagi and Berman 2017; rodents: Olioff and Stewart 1978; Nunes et al. 1999; cetaceans: Zoidis et al. 2014; canids: Pal 2010; but see Pedersen et al. 1990; Kulik et al. 2015). In this population, mixed-sex and all-male groups may allow juvenile males to practice physical-contact social skills associated with initiating and maintaining consortships (e.g., displays, agonisms, or affiliative behaviors) to assess their value before forming an alliance, which can last for more than 20 years (Connor and Krützen 2015). Similarly, mixed-sex groups may allow females to practice physical social skills that help them cope with unwanted male attention (e.g., evasive behaviors or affiliative behaviors that diffuse conflict). These results support the notion that adult reproductive competition can be a major driver of subadult socialization patterns.

In contrast to males, female strategy was driven more by foraging ecology. Juvenile females foraged six times as much as they socialized (averaging 54% and 9%, respectively), whereas juvenile males foraged twice as much as they socialized (29% and 16%, respectively). Juvenile females allocate effort to growth and foraging skill to meet the demands of maternal care in the future (Patterson et al. 2015). Adult females devote a large portion of their activity budget to foraging (Galezo et al. 2018) due to the energetic demands of pregnancy and lactation (Clutton-Brock 1991), especially given a long period of calf dependency: calves are weaned on average at age 4 but may nurse for up to 8.5 years (Mann et al. 2000; Karniski et al. 2018). Juvenile females may form clustered social networks if daughters adopt similar foraging tactics as their mothers or due to preferential association with maternal kin (Mann and Sargeant 2003; Frère et al. 2010; Mann et al. 2012). Indeed, low rates of socializing in all-female groups suggest that the formation of relationships between females is less dependent on physical-contact social skills and more dependent on factors such as kinship, shared foraging specialty, and shared reproductive state (e.g., Frère et al. 2010; Mann et al. 2012). The emergence of sex differences in social preferences and activity budget that mirror diverging adult reproductive strategies, even in the absence of adults, suggests that juvenile social behavior is largely shaped by the upcoming demands of adulthood.

Although males more than females rely upon physical social skills to assess and cultivate same-sex relationships, “nonphysical” social skills are likely crucial for both sexes in a fission–fusion society. Juveniles are challenged with choices on which groups to avoid or join (and in what contexts), identifying third-party interactions, and generally learning to identify individuals and form differentiated relationships. Indeed, the juvenile period has repeatedly been shown to be a critical time for the development of “social competence”—the ability to adjust social behavior given particular social contexts and/or available social information—in fish, birds, and mammals (de Waal and Johanowicz 1993; Bester-Meredith and Marler 2007; Kempes et al. 2008; Oliveira 2009; Arnold and Taborsky 2010; Taborsky et al. 2012; van Leeuwen et al. 2014). For example, findings in corvids, primates, and spotted hyenas have demonstrated that individuals adjust social behavior in accordance with third-party relationships (Bachmann and Kummer 1980; Silk 1999; Perry et al. 2004; Engh et al. 2005; Emery et al. 2007). In this population, identifying third-party interactions may be especially important to male decision-making in the context of multilevel alliances (alliances of alliances; Connor and Krützen 2015). Furthermore, some males change alliance membership (Connor and Krützen 2015), so familiarity with other males in the community might afford them some flexibility.

As a whole, our results indicate that juvenile behavior—from activity budgets to social relationships—is largely shaped by emerging sex-specific reproductive strategies, even in the absence of direct adult influence. In other words, juvenile phenotypes were largely predicted by selective pressures on adults. This work demonstrates that, despite the fitness costs of delayed sexual maturity, a period of social development uninhibited by risks associated with sexual maturity may be crucial to adult reproductive success, especially in species marked by relational social complexity. These findings add to a body of work highlighting the importance of early-life social experiences by demonstrating that strategic socializing in early life can prime individuals for reproductive success as adults.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

Appendix

Supplementary Figure 1. Representative ego networks for a) male and b) female juveniles. Red circular nodes are females and blue square nodes are males, with the ego represented in black. Edge thickness represents association index strength and node size is proportional to the number of connections within the ego network. Both males and females form clustered networks with strong same-sex associations, but males form stronger same-sex associations than females. On average, males have more associates than females, but this difference is consistent with what would be expected given spatial overlap between individuals' home ranges.

Supplemental Table 1. Ethogram.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Mann et al. 2020.

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