



Dispersal, philopatry, and the role of fission-fusion dynamics in bottlenose dolphins

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ABSTRACT

In this quantitative study of locational and social dispersal at the individual level, we show that bottlenose dolphins (*Tursiops* sp.) continued to use their natal home ranges well into adulthood. Despite substantial home range overlap, mother–offspring associations decreased after weaning, particularly for sons. These data provide strong evidence for bisexual locational philopatry and mother–son avoidance in bottlenose dolphins. While bisexual locational philopatry offers the benefits of familiar social networks and foraging habitats, the costs of philopatry may be mitigated by reduced mother–offspring association, in which the risk of mother–daughter resource competition and mother–son mating is reduced. Our study highlights the advantages of high fission–fusion dynamics and longitudinal studies, and emphasizes the need for clarity when describing dispersal in this and other species.

Key words: bottlenose dolphin, *Tursiops* sp., association, juvenile, philopatry, locational dispersal, mother–offspring, ranging, site fidelity, social dispersal.

Dispersal is a key life history process that affects population demography, spatial distribution, and genetic structure, as well as individual fitness (Greenwood 1980, Johnson and Gaines 1990, Clobert *et al.* 2001, Bowler and Benton 2005). However, despite its importance, dispersal is not well understood in many systems, especially among marine mammals. In addition to the logistical difficulties of studying marine mammals, studies of cetacean dispersal are further complicated by their often highly complex social systems, in which movement away from familiar conspecifics (social dispersal) does not necessarily equate to movement away from a familiar site (locational dispersal) (Isbell and Van Vuren 1996). To better understand the intricate relationship between ranging and association in cetaceans and other socially complex species, we examined the locational and social dispersal of wild bottlenose dolphins in Shark Bay, Australia.

Although defined in a number of ways, dispersal is basically the movement of an individual from one site and/or group to another site/group where it breeds (Howard 1960, Greenwood 1980, Clobert *et al.* 2001). In contrast, philopatry means remaining in a site/group to breed, or not dispersing (Pusey and Packer 1987, Shields 1987). Sex-biased dispersal occurs when one sex characteristically disperses at a greater rate and/or further than the other (Greenwood 1980, Pusey 1987,

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Lawson Handley and Perrin 2007). In general, mammals exhibit male-biased dispersal (Greenwood 1980), although there are many exceptions (Greenwood 1980, Pusey and Packer 1987, Clutton-Brock 1989, Isbell and Van Vuren 1996). While little is known about cetacean dispersal, cetaceans are thought to display a diversity of dispersal patterns, including male-biased dispersal (sperm whales, *Physeter macrocephalus*: Best 1979, Rice 1989, Lyrholm *et al.* 1999, Engelhaupt *et al.* 2009; beluga whales, *Delphinapterus leucas*: O'Corry-Crowe *et al.* 1997; Dall's porpoises, *Phocoenoides dalli*: Escorza-Treviño and Dizon 2000; bottlenose dolphins, *Tursiops aduncus*: Möller and Beheregary 2004; and dusky dolphins, *Lagenorhynchus obscurus*: Cassens *et al.* 2005) and bisexual locational and social philopatry, in which neither sex leaves its natal group or area (*e.g.*, resident killer whale, *Orcinus orca*: Bigg *et al.* 1990, Baird 2000). However, no study of cetaceans to date has quantified both locational and social dispersal of individuals from birth to adulthood.

Shark Bay bottlenose dolphins (*Tursiops* sp.) are thought to be year-round residents of Shark Bay, Australia (Smolker *et al.* 1992), in which individually identified dolphins of both sexes have been observed repeatedly in the bay for up to 35 yr. Based on this, Shark Bay dolphins are considered to be bisexually philopatric, a dispersal pattern also seen in other coastal dolphin populations such as in Sarasota Bay, Florida (Connor *et al.* 2000). Shark Bay dolphin social structure appears to consist of overlapping social networks that extend throughout the bay (Smolker *et al.* 1992, Connor and Mann 2006), with groups changing temporally, spatially, and compositionally (*i.e.*, high fission-fusion dynamics: Aureli *et al.* 2008) in an open community (Smolker *et al.* 1992). While mother-calf relationships are extremely strong for at least the first three years of life, these associations drop substantially in the two years after weaning (Mann *et al.* 2000). Sex-specific juvenile association patterns are not yet fully understood, but based on adult association patterns, males are presumed to drastically reduce associations with their mothers and increase associations with other males after weaning, while females are thought to associate more frequently with their mothers than do males (Smolker *et al.* 1992, Connor *et al.* 2000, Mann *et al.* 2000, Gibson and Mann 2008*b*). Specifically, adult males form alliances, in which males form strong bonds with other males and cooperate to consort females (Connor *et al.* 1992*a, b*, 1999, 2010). Females are more socially variable than males (Smolker *et al.* 1992, Mann *et al.* 2000) and preferentially associate with other females, including maternal kin (Smolker *et al.* 1992, Connor *et al.* 2000, Gibson and Mann 2008*b*, Frère *et al.* 2010*b*). Similar sex-specific adult association patterns have been found at other *Tursiops* research sites (*e.g.*, Sarasota Bay, Florida: Wells *et al.* 1987, Wells 1991, and Port Stephens, Australia: Möller *et al.* 2001, 2006), although there are exceptions (*e.g.*, Doubtful Sound, New Zealand: Lusseau *et al.* 2003).

Given the social and ranging patterns of Shark Bay dolphins, we examined sex differences in site fidelity and mother-offspring association. We hypothesized that both sexes would maintain their natal ranges as adults, and in doing so could retain the social and resource benefits of locational philopatry. At the same time, we hypothesized that mother-offspring avoidance after weaning, especially by sons, could reduce the costs of locational philopatry. Specifically, mother-son avoidance could reduce inbreeding, and mother-daughter avoidance could reduce resource competition. By exploring fine-scale ranging and mother-offspring association, our study is the first on cetaceans to simultaneously examine mother-offspring social and locational dispersal at the individual level. Although previous studies on bottlenose dolphins in Shark Bay, Australia and Sarasota, Florida, have suggested that males and females are sighted consistently and breed within their natal ranges (Connor *et al.*

2000, Krützen *et al.* 2004a), examination of individual ranging and mother-offspring associations after weaning have not been reported at either site. Additionally, examining species with extreme social complexity, including high fission-fusion dynamics, calls for quantitative analysis of dispersal patterns for a better understanding of the social system.

MATERIALS AND METHODS

STUDY SITE

Shark Bay (25°47'S, 113°43'E) is a UNESCO World Heritage Site in Western Australia and is characterized by high environmental heterogeneity (Sargeant *et al.* 2007). In the eastern gulf of Shark Bay, over 1,500 bottlenose dolphins (*Tursiops* sp.) have been studied since 1984.

DATA COLLECTION

Data were collected using focal follows and surveys (see Mann 1999, Mann and Watson-Capps 2005, Gibson and Mann 2009). From these data, we used association and ranging data for individuals that met all sampling restrictions.

Sample Restrictions

Individuals were included in the sample if: (1) calves/juveniles/adults were not directly related to any other calves/juveniles/adults by matriline (no two had the same mother and no offspring-mother-grandmothers were included in the same analysis), (2) they were not provisioned (Mann and Kemps 2003), (3) data within each analysis and within individual spanned at least two years for each developmental period examined, and (4) mother and offspring were both alive at the same time for all observations and analyses. As not all individuals that met these requirements in one analysis necessarily met these requirements for another, the individuals included in each analysis differed depending on the comparison.

Sex and Age Determination

We examined male and female dolphins during the calf, juvenile, and adult periods. For the purposes of this study, we referred to the time from birth to weaning age as the calf period (see Mann *et al.* 2000), the time from weaning age to age 10 as the juvenile period, and ages 10–20 as adulthood. Birth year was known for all offspring. We used age 10 as a conservative age of sexual maturity for both males (Wells *et al.* 1987, Schroeder 1990) and females (age of first parturition: Mann *et al.* 2000), and no subject (male or female) in our sample was known to have offspring before age 10. Sexes were known from the presence of a dependent calf, views of the ventral genital area, and/or DNA analysis (Smolker *et al.* 1992, Krützen *et al.* 2004a).

RANGING

Ranging Comparisons

We examined site fidelity in Shark Bay dolphins using the percentage of home range overlap and the distance between home range centroids (mean latitude and longitude). We examined whether calves significantly changed their home range

location after weaning, whether juvenile ranging patterns persisted into adulthood, and whether mothers and their offspring range in the same areas after offspring weaning by comparing these measures in terms of: (1) the calf and juvenile period, (2) the juvenile and adult period, and (3) mother and juvenile offspring.

Data Restrictions

We restricted ranging data to one sighting of an individual per day (regardless of the number of times an individual was sighted within that day) to ensure temporal independence between each point. For all home range analyses, location points were restricted to an area in which search effort was most intensive (80% of the total area searched across 5 yr; 225 km²: Mann *et al.* 2008), although we routinely sample a much larger surrounding area. Subjects were sighted outside of the main study area a $\bar{x} \pm \text{SE}$ of 5.1 ± 0.7 times since 1988. Of the 56 individuals examined across all ranging analyses, 28 were sighted less than two times outside of the study area, suggesting that we captured a large portion of the ranging for individuals analyzed in this study. Home ranges constructed from these location points were clipped to exclude land.

Home Range Size

Kernel density estimators (KDEs: Worton 1989, Seaman and Powell 1996, Powell 2000) were used to calculate home ranges from which percent overlap was estimated. We used fixed kernel densities (Gaussian distribution) with a least-squares cross validation smoothing parameter (Seaman and Powell 1996) and calculated 95% probability contours (Powell 2000). All projections were in World Geodetic System 1984, Universal Transverse Mercator, zone 49S (Home Range Tools, Hawth's Tools, XTools Pro, and Spatial Analyst Extensions; ArcGIS v. 9.2: Environmental Systems Research Institute, Inc., Redlands, CA).

For all ranging analyses, we included individuals with at least 20 points per developmental period. We standardized the number of points used within individual to control for a potential correlation between home range size and the number of points used to estimate home range size (Seaman *et al.* 1999), although preliminary analyses suggested that there was no such correlation in our data. For example, an individual with 25 calf points and 36 juvenile points would be standardized to include 25 calf points and 25 of 36 juvenile points, randomly subsampled. While this threshold may have affected the precision with which we estimated range size (Seaman *et al.* 1999, Girard *et al.* 2002), we confirmed our main result that natal ranges were included in juvenile and adult ranging through visual examination of ranging data projected onto maps, which clearly showed interspersed location points and overlapping ranging (Fig. 1). Additionally, although we used a 20 observation point threshold to maximize the number of individuals included in each analysis, this threshold for home range size estimation was higher than those used in other cetacean studies of individual ranges (*e.g.*, Ingram and Rogan 2002, Silva *et al.* 2008), and we usually had many more than 20 points per individual (up to 248 points). Due to the limitations of the search area and sample sizes, absolute home range sizes must be considered with caution, although this is unlikely to affect our main examination of philopatry/dispersal.

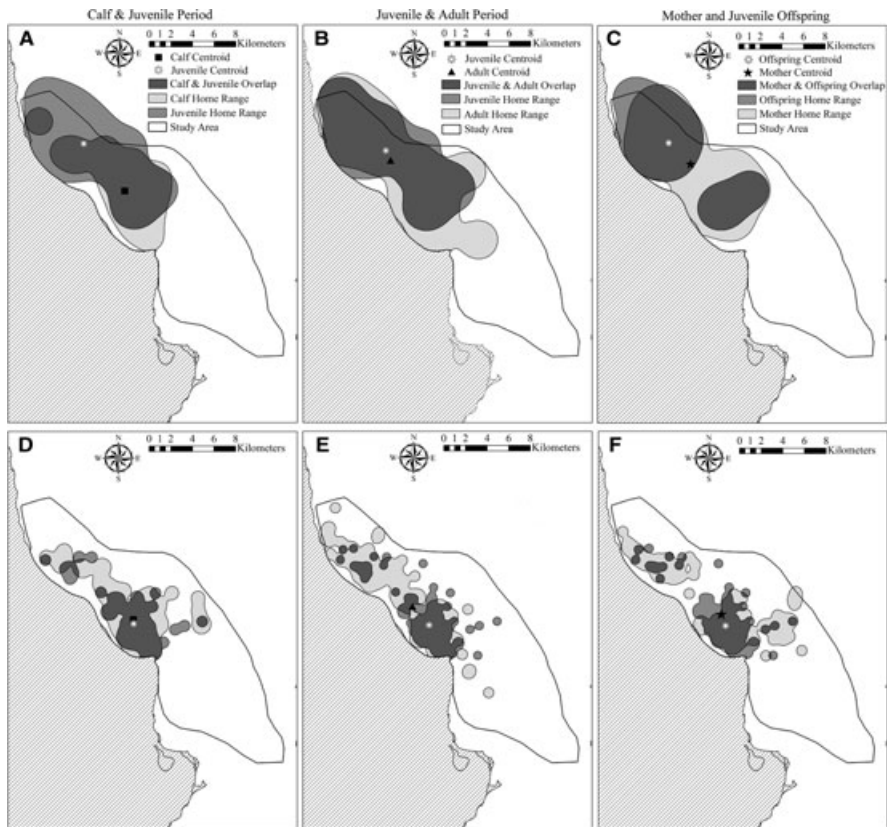


Figure 1. Examination of mother and offspring home ranges. Examination of individuals LIT (female; A–C) and URC (male; D–F) home ranges, home range overlap, and centroids for the calf and juvenile period (a, d), juvenile and adult period (B, E), and mother and offspring during the offspring’s juvenile period (C, F). Juvenile ranges differ slightly in each case because the number of points used to generate each range differed (standardized within developmental period and within individual). Study area was the area of high search effort to which all location points were restricted (225 km²). Only location points were restricted, so home ranges generated from these points could extend outside of the study area, but landmasses were excluded.

The sex ratio of the individuals included in each analysis was not affected by the 20 point threshold. When examining the calf–juvenile periods, the sex ratio of those included in the analysis ($n = 11$ females and 6 males) was not different from those excluded from the analysis ($n = 33$ females and 24 males; $\chi^2_1 = 0.25$, $P = 0.616$). This was also the case in terms of the juvenile–adult period ($\chi^2_1 = 0.24$, $P = 0.627$), in which we included 11 females and 8 males, but excluded 15 females and 8 males. Individuals were excluded from ranging analyses mostly due to (1) low monitoring of the population in the 1980s and early 1990s, (2) low sightings of individuals (*e.g.*, their core range was outside our main study area), (3) mortality before age 12 (for juvenile–adult comparisons), (4) age under 12 (for juvenile–adult comparisons), or

(5) direct matrilineal relatedness (two individuals shared the same mother or were offspring-mother-grandmother; see Sample Restrictions).

Home Range Overlap and Centroids

Percent overlap was calculated for each of the three comparisons: (1) calf-juvenile overlap divided by the total calf home range, (2) juvenile-adult overlap divided by the total juvenile home range size, and (3) mother-offspring overlap divided by the total mother home range. These comparisons allowed us to examine the percentage of natal home range retained as a juvenile, the percentage of the juvenile range retained into adulthood, and the percentage of the mother's home range that is shared by her juvenile offspring, respectively.

Centroids were calculated to estimate the "center" of each individual's home range (mean latitude and longitude for each developmental period), and then the distance between centroids was measured in kilometers. We used one-way ANOVAs with offspring sex as an explanatory variable and home range overlap or centroid distance as the response variable.

ASSOCIATIONS

We examined whether (1) there were sex differences in association between mother and her offspring (hereafter referred to as the mother-offspring association) between the calf and juvenile period, (2) there were sex differences in mother-offspring association between the juvenile and adult period, (3) a juvenile's closest associate had been a calf associate, (4) juveniles and adults showed sex differences in the strength of association with its closest associate, and (5) the closest associates of juveniles or adults were of the same sex.

Half-Weight Coefficients of Association

We calculated half-weight coefficients of association (COAs) to measure the frequency at which two individuals associate using SOCPROG 2.4 (Whitehead 2009). Half-weight COAs are least biased when pairs are more likely to be sighted apart than while together (Cairns and Schwager 1987). In this case, sighting within a group (defined using the 10 m chain rule: Smolker *et al.* 1992) was a proxy for association.

Data Restrictions

We restricted association data to the last sighting per day of a mother, offspring, or mother and offspring together to ensure temporal independence. For examinations of mother-offspring associations, only mother-offspring pairs with at least 20 points per developmental period were included in analyses. All points available (≥ 20 points) for each pair within each developmental period were used (no standardization), as preliminary analyses did not detect any systematic increase in COA with an increasing number of points used. Changes in mother-offspring association between calf and juvenile periods were easily detected using this threshold, although in most cases, we estimated COAs using far more than 20 points per mother-offspring pair (up to 441 points).

While our study used an observation threshold based on the number of times a mother-offspring pair was seen (together or apart), other examinations of cetacean association often use thresholds based on the number of times an *individual* was seen. Even so, our sample size per individual (*e.g.*, calf-juvenile comparison using all available points: $\bar{x} \pm \text{SE} = 61.8 \pm 5.8$ points per individual per developmental period) exceeded the 2–10 sightings per individual used in most studies of cetaceans.

Calf and Juvenile Period Comparison

Mother-offspring associations—To examine whether mother-offspring associations differed by sex during the calf and juvenile period, we used a mixed-model ANOVA, in which developmental period (calf and juvenile) and offspring sex were fixed explanatory variables, mother-offspring pair was a random explanatory variable, and half-weight COA was the response variable.

Natal associate retained into the juvenile period—To examine whether juveniles continued to associate with individuals from their natal (calf) network, we calculated pairwise half-weight COAs between offspring and all its associates during the calf and juvenile period. Offspring were then scored using either a 0 or 1 according to whether or not their closest juvenile associate (highest COA) had also been an associate during the calf period. Associate presence during the calf period was scored as a 1, and absence was scored as a 0. If a juvenile offspring had more than one closest associate (equally high COAs), it was scored based on the proportion of these associates that were also found as an associate during the calf period. For example, if a juvenile offspring had two closest associates, the juvenile received a score of 0, 0.5, or 1 based on whether none of the associates, one of the associates, or both associates were found in the natal network, respectively. All scores were then summed and divided by the number of offspring tested (percentage).

Juvenile and Adult Period Comparison

Mother-offspring associations—To examine whether mother-offspring associations persisted after sexual maturity, half-weight COAs were calculated between offspring and their mothers during juvenile and adult periods, and analyzed using a mixed-model ANOVA. The developmental period and sex were fixed explanatory variables, mother-offspring pair was a random explanatory variable, and COA was the response variable.

Juvenile and adult's closest association—To examine sex differences in association between offspring and their closest associate during the juvenile and adult period, pairwise half-weight COAs were calculated between the offspring and all other associates during the juvenile and adult period. COAs from the highest ranking associate (largest COA) were used as the response variable in an ANOVA with offspring sex and developmental period (juvenile and adult) as fixed explanatory variables.

To examine whether juveniles/adults associated with individuals of the same sex, we scored offspring based on whether their highest ranking associate was of the same sex, opposite sex, or unknown sex. In some instances, offspring had multiple highest ranking associates (equally high COAs), in which case it was scored based on the proportion of associates that were of the same, opposite, or unknown sex. For example, a female with 2 males and 3 females as highest ranking associates would

be scored as having 0.4 opposite sex associates and 0.6 same sex associates. All scores were then summed within sex and within developmental periods and divided by the number of offspring tested (percentage).

RESULTS

RANGING

Calf-Juvenile Comparison

A $\bar{x} \pm \text{SE}$ of 54.0 ± 5.8 points (range = 24–131 points) per individual per developmental period was used to calculate home range sizes. Calf home range sizes were $50 \pm 11 \text{ km}^2$ for females and $34 \pm 7 \text{ km}^2$ for males. Juvenile home range sizes were $54 \pm 9 \text{ km}^2$ for females and $39 \pm 8 \text{ km}^2$ for males.

Overlap was not significantly related to offspring sex ($n = 11$ females and 6 males, $F_{1,15} = 0.07$, $P = 0.792$), and the amount of overlap between the calf and juvenile period was large ($\bar{x} \pm \text{SE} = 68\% \pm 5\%$, range = 32%–100%), suggesting that offspring of both sexes may have retained large amounts of their natal ranges into the juvenile period.

Distance between calf and juvenile centroids showed a significant offspring sex effect ($n = 17$, $F_{1,15} = 6.02$, $P = 0.027$), in which female centroid distances ($\bar{x} \pm \text{SE} = 2.36 \pm 0.58 \text{ km}$, range = 1–6 km) were greater than male distances ($\bar{x} \pm \text{SE} = 0.33 \pm 0.33 \text{ km}$, range = 0–2 km), although the maximum that any individual moved was 6 km.

Juvenile-Adult Comparison

A $\bar{x} \pm \text{SE}$ of 71.3 ± 8.7 points (range = 20–190 points) per individual per developmental period was used to calculate home range sizes. Juvenile home range sizes calculated for individuals used in this analysis were $46 \pm 8 \text{ km}^2$ for females and $49 \pm 14 \text{ km}^2$ for males. Adult home range sizes were $54 \pm 11 \text{ km}^2$ for females and $59 \pm 11 \text{ km}^2$ for males.

Home range overlap did not meet assumptions of homogeneity of variance and was therefore log-transformed (Levene's: $P > 0.05$). Sex was not significantly related to log-transformed overlap ($n = 11$ females and 8 males, $F_{1,17} = 1.06$, $P = 0.318$) and overlap between juvenile and adult ranges was large (untransformed $\bar{x} \pm \text{SE} = 70\% \pm 5\%$, range = 22%–100%), suggesting that both sexes may have retained a large amount of their juvenile range into adulthood.

Distance between centroids was also log-transformed to meet assumptions of homogeneity of variance (Levene's: $P > 0.05$). Distance between the juvenile and adult centroids was not significantly related to sex ($n = 19$, $F_{1,17} = 2.02$, $P = 0.174$), and was relatively small (untransformed $\bar{x} \pm \text{SE} = 1.16 \pm 0.19 \text{ km}$, range = 0–3 km), suggesting that juvenile and adult range centers may not have been far apart in either sex.

Mother-Juvenile Comparison

A $\bar{x} \pm \text{SE}$ of 60.43 ± 7.8 points (range = 21–248 points) per individual per developmental period was used to calculate home range size. Juvenile offspring home range sizes were $41 \pm 6 \text{ km}^2$ for females and $59 \pm 12 \text{ km}^2$ for males.

Maternal home range sizes were $48 \pm 7 \text{ km}^2$ for females and $59 \pm 11 \text{ km}^2$ for males.

Neither overlap ($n = 13$ females and 10 males, $F_{1,21} = 0.26$, $P = 0.616$) nor distance between mother and juvenile offspring centroids ($n = 23$, $F_{1,21} = 0.39$, $P = 0.537$) were significantly related to offspring sex. Overlap between mother and juvenile offspring was large ($\bar{x} \pm \text{SE} = 65\% \pm 5\%$, range = 28%–98%), while distance between centroids was small ($\bar{x} \pm \text{SE} = 1.65 \pm 0.35 \text{ km}$, range = 0–6 km). This suggests that, regardless of offspring sex, mothers shared large amounts of their range with juvenile offspring, and that range centers between mother and juvenile offspring were not far from one another.

Visual examination of home ranges confirmed suggestions that offspring maintained a large proportion of their natal range as juveniles, offspring maintained a large proportion of their juvenile ranges as young adults, and offspring shared a large portion of their ranges with their mothers after weaning (Fig. 1).

ASSOCIATIONS

Calf Period and Juvenile Period Comparison

Mother-offspring associations—A $\bar{x} \pm \text{SE}$ of 86.02 ± 12.4 points (range = 21–441) per mother-offspring pair per developmental period was used to calculate half-weight COAs. COAs did not meet assumptions of homogeneity of variance (Levene's: $P > 0.05$), so these data were log-transformed. Log-transformed COAs varied by developmental period ($n = 14$ females and 10 males, $F_{1,22} = 13.98$, $P = 0.001$), but not by sex or sex*developmental period ($F_{1,22} = 0.29$, $P = 0.597$ and $F_{1,22} = 0.30$, $P = 0.591$, respectively). Specifically, both male and female offspring associations with their mothers decreased after weaning (untransformed calf COA $\bar{x} \pm \text{SE} = 0.926 \pm 0.055$, range = 0.73–1.00 to juvenile COA $\bar{x} \pm \text{SE} = 0.207 \pm 0.033$, range = 0.00–0.59; Fig. 2).

To ensure that this association pattern persisted for individuals that specifically remained in their natal ranges, we repeated the analysis using the same individuals as those used in the ranging analyses. However, several mother-offspring pairs did not meet the 20 point minimum, so we standardized the number of points used within mother-offspring pairs for each developmental period ($\bar{x} \pm \text{SE} = 48.9 \pm 6.3$ points, range = 5–157 points per mother-offspring pair). COAs were arcsine-transformed to meet assumptions of homogeneity of variance (Levene's: $P > 0.05$). In this case, both sex ($n = 13$ females and 10 males, $F_{1,21} = 4.72$, $P = 0.0414$) and developmental period ($F_{1,21} = 447.81$, $P < 0.0001$) but not sex*developmental period ($F_{1,21} = 2.03$, $P = 0.162$) affected arcsine-transformed mother-offspring association. When mother-calf pairs with less than 20 points were excluded, only developmental period was significant ($n = 9$ females and 5 males, $F_{1,12} = 283.40$, $P < 0.0001$), while sex ($F_{1,12} < 0.001$, $P = 0.954$) and sex*developmental period ($F_{1,12} = 1.74$, $P = 0.212$) were not. Together, these results suggest that despite extensive home range overlap with their mothers, both males and females decreased associations with their mothers after weaning.

Calf associates retained into the juvenile period—Overall, 90.6% of juvenile offspring had an associate during the calf period that was later their closest associate during the juvenile period (87.5% of 10 males and 92.9% of 14 females).

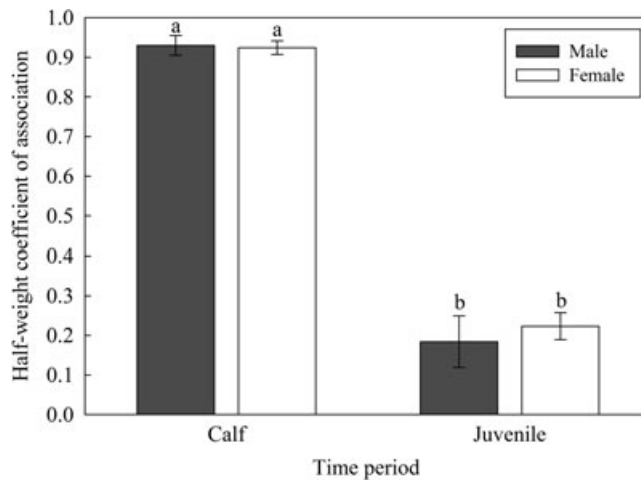


Figure 2. Calf and juvenile period comparison: Half-weight coefficients of mother-offspring association. Untransformed $\bar{x} \pm SE$ COAs between mother and offspring during the offspring's calf and juvenile periods are shown. Significant difference between developmental periods ($n = 24$, $F_{1,22} = 13.98$, $P = 0.001$) is denoted by different letters (a and b).

Juvenile Period and Adult Period Comparison

Mother-offspring associations—A $\bar{x} \pm SE$ of 126.7 ± 17.5 points (range = 22–441) per mother-offspring pair per developmental period was used to calculate half-weight COAs. We found that sex ($n = 11$ females and 7 males, $F_{1,16} = 5.29$, $P = 0.035$) but not developmental period or sex*developmental period ($F_{1,16} = 1.23$, $P = 0.284$ and $F_{1,16} = 0.09$, $P = 0.766$, respectively) had an effect on mother-offspring COAs, suggesting that females ($\bar{x} \pm SE = 0.204 \pm 0.027$, range = 0.00–0.44) associate more frequently with their mothers after weaning compared to males ($\bar{x} \pm SE = 0.08 \pm 0.027$, range = 0.00–0.34) during both the juvenile and adult period (Fig. 3). This sex effect was not detected during the juvenile period of the calf–juvenile comparison, which included two males that maintained extremely high associations with their mothers after weaning (0.50 and 0.53). However, these two males were the last surviving offspring of their mothers, which disappeared when the males were adults. It is not uncommon in Shark Bay dolphins for mothers to tolerate the continued association of their last-born offspring.

Juvenile and adult's closest associations—We found that sex ($n = 18$, $F_{1,16} = 17.32$, $P = 0.0007$), but not developmental period or sex*developmental period ($F_{1,16} = 1.88$, $P = 0.189$ and $F_{1,16} = 0.86$, $P = 0.367$, respectively), was significantly related to half-weight COAs between juveniles/adults and their closest associates. This suggests that males ($\bar{x} \pm SE = 0.707 \pm 0.041$, range = 0.39–0.92) associate more frequently with their closest associates compared to females ($\bar{x} \pm SE = 0.454 \pm 0.034$, range = 0.17–0.74) during both the juvenile and adult period (Fig. 4). Most COAs between juveniles/adults and their closest associates were greater than COAs between mother and offspring after weaning, suggesting that the decreased mother-offspring association exhibited after weaning is not the result of an overall decrease in association with all others.

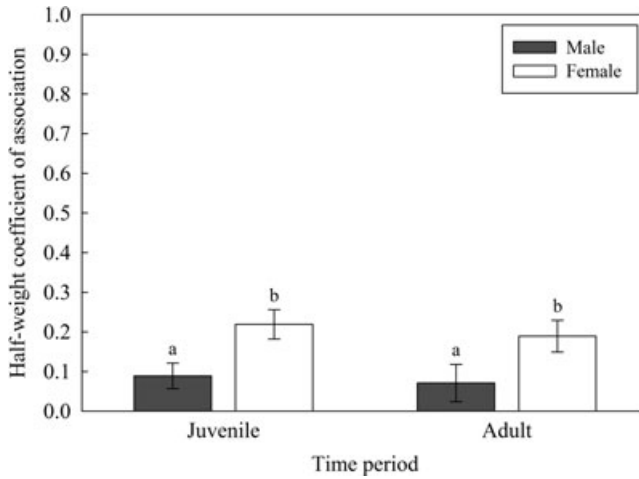


Figure 3. Juvenile and adult period comparison: Half-weight coefficients of mother-offspring association. $\bar{X} \pm SE$ COAs between mother and offspring during the offspring's juvenile and adult periods are shown. Significant sex difference ($n = 18, F_{1,16} = 5.29, P = 0.035$) is denoted by different letters (a and b).

We found that 70.9% of juvenile females had closest associates of the same sex, 15.5% of the opposite sex, and 13.6% of unknown sex, whereas 63.6% of adult females had closest associates of the same sex, 27.3% of the opposite sex, and 9.1% of unknown sex. For both juvenile and adult males, 85.7% had closest associates

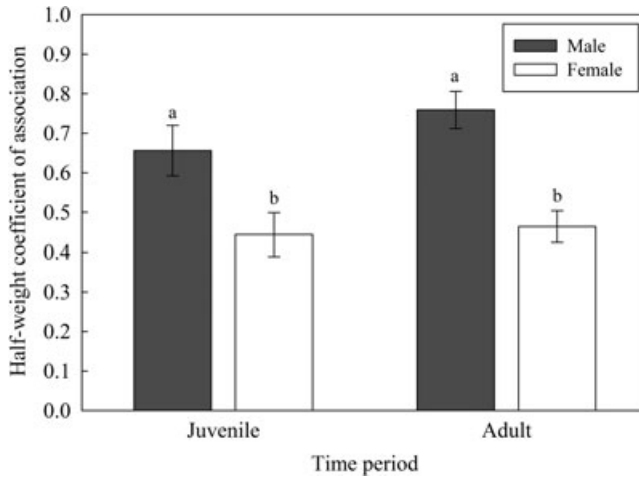


Figure 4. Juvenile and adult period comparison: Half-weight coefficients of offspring-closest associate association. $\bar{X} \pm SE$ COAs between offspring and the offspring's closest associate are shown during the offspring's juvenile and adult periods. Significant sex difference ($n = 18, F_{1,16} = 17.32, P = 0.0007$) is denoted by different letters (a and b).

of the same sex, 14.3% of the opposite sex, and 0% of unknown sex. Thus, most juveniles/adults were of the same sex as their highest ranked associate(s).

DISCUSSION

We found strong evidence for bisexual locational philopatry and decreased mother-offspring association post-weaning among Shark Bay dolphins. Dolphins of both sexes maintained much of their natal ranges well into adulthood (22%–100% overlap), and maintained home ranges that largely overlapped with that of their mothers (28%–98% overlap). Despite this, mother-offspring association was markedly reduced during the juvenile period and adulthood, especially for sons. In several cases, sons were never observed with their mothers as adults. Although a decrease in mother-offspring association post-weaning was documented previously (Mann *et al.* 2000), this decrease was only shown for the first two years after weaning, not the entire juvenile period or adult period. We found that the decline in mother-offspring association after weaning was not caused by locational dispersal, or to an overall decrease in association with conspecifics. Additionally, juveniles appeared to exhibit adult association patterns (see Smolker *et al.* 1992); most juveniles/adults were of the same sex as their closest associate(s), and juvenile/adult males had higher COAs with their closest associates compared to females. In fact, male COAs during the juvenile period (0.39–0.86) were within the ranges reported between adult male alliance members (Connor *et al.* 1999). Finally, the majority of offspring had natal associates which later became their closest juvenile associates. Thus, overall, Shark Bay dolphins exhibit a degree of social and locational philopatry. We suggest that both types of philopatry are facilitated by high fission-fusion dynamics, which allow Shark Bay dolphins to experience the benefits of familiar habitats and associates, while reducing costs of mother-son inbreeding and mother-daughter resource competition.

In addition to maintaining a portion of their natal home range after weaning, male and female ranges overlapped extensively, consistent with the idea of an “overlapping mosaic of ranges” previously used to describe Shark Bay dolphin ranging, and predicted in a society characterized by fission-fusion dynamics (Connor *et al.* 2000). While it could also be argued that dispersers would be difficult to detect within our study area, we have not observed juveniles moving *into* the study area, as would be expected if juvenile locational dispersal was widespread. Additionally, though not part of the study area analyzed here, outlying areas of eastern Shark Bay were sampled 5–10 times per year, and individuals that disappeared from the main study area were not seen in these outlying areas. Thus, although our study has limitations, we suggest that bisexual locational philopatry is the predominant dispersal pattern within the population.

PHILOPATRY AND DISASSOCIATION

The pattern of bisexual locational philopatry and reduced mother-offspring association observed in Shark Bay dolphins may be explained by a number of factors. Specifically, locational philopatry is thought to confer fitness benefits in terms of familiarity with associates and resources (*e.g.*, red-winged black birds, *Agelaius phoeniceus*: Beletsky and Orians 1989; cliff swallows, *Petrochelidon pyrrhonota*: Brown *et al.* 2008). At the same time, decreased mother-son association may reduce

the likelihood of close inbreeding, while decreased mother-daughter association may be in response to spatial resource competition.

Familiarity with natal networks may be particularly important to males, which form strong adult alliances (Connor *et al.* 1992*a, b*, 1999, 2010). As calves, males show stronger associations with same-sex calves compared to females during separations from their mothers (Stanton *et al.* 2011), suggesting that male calves are already establishing long-term bonds. By remaining in their natal range, males may have more opportunities to develop alliance partnerships with familiar males, which are also likely to be closely related due to locational philopatry (Waser and Jones 1983). In this study, 87.5% of males examined had natal associates that were retained as their top juvenile associates. Consistent with this, Krützen *et al.* (2003) demonstrated that males in first-order stable alliances were more closely related to one another than expected by chance. Both familiarity and relatedness with associates may translate into stronger male-male bonds and consequently fitness benefits; males in alliances have high reproductive success, and those not in alliances obtain only occasional paternities (Krützen *et al.* 2004*a*). Another consequence of alliance formation is that investment into strong male bonds during development may preclude frequent associations with other conspecifics, including their mothers. That is, males may have less time available to associate with their mothers because they are busy socializing and strengthening alliance partnerships, or mothers might avoid their sons in order to avoid being herded by their sons' alliance partners (Gibson and Mann 2008*b*). Unfortunately, the ontogeny of alliance formation is not yet well understood, so further study is needed to evaluate these arguments.

Female dolphins may also benefit from remaining in an area with familiar natal associates, especially with matrilineal kin (*e.g.*, baboons, *Papio cynocephalus*: Silk *et al.* 2003, 2009). In support of this, adult female dolphins often associate with matrilineal kin as adults (Smolker *et al.* 1992, Frère *et al.* 2010*b*), and 90.6% of females tested in this study maintained a natal associate as their closest juvenile associate. Despite these matrilineal/familial associations, alliances (stable coalitions) commonly found in female philopatric species (*e.g.*, spotted hyena, *Crocuta crocuta*, and many cercopithecines: Smith *et al.* 2010) have not been detected among female bottlenose dolphins.

Given Shark Bay's high environmental heterogeneity, resource familiarity is likely to be important for dolphin foraging success. Females, which invest substantially in their offspring (Mann *et al.* 2000) and whose reproductive success is more likely affected by access to resources (Trivers 1972), are likely to depend on resource familiarity more so than males. Additionally, while both sexes exhibit habitat-specific foraging tactics (Sargeant *et al.* 2007), females are more likely to specialize in the same foraging tactics as their mothers and thus might compete more directly with members of their matriline (Mann and Sargeant 2003, Sargeant *et al.* 2005, Mann *et al.* 2008, Sargeant and Mann 2009). Resource competition with female kin may help explain why daughters, despite higher association with their mothers after weaning compared to males, shifted centroid distances more than sons between the calf and juvenile periods.

However, this is not to dismiss the importance that familiarity with resources may have to the foraging of males. For example, chimpanzee (*Pan troglodytes*) males tended to use their mother's core area when foraging alone, away from their allies, suggesting a potential trade-off between the advantages of foraging in familiar habitats and maintaining important social bonds (Murray *et al.* 2008). Additionally, while less common than in females, at least some males adopt a rare form of tool-use

with sponges, a foraging tactic that is highly habitat specific and learned from their mothers (Mann *et al.* 2008).

Despite the benefits of locational philopatry, inbreeding is a potential cost, especially for females (Frère *et al.* 2010a). Therefore, mothers are predicted to avoid mating with their sons (although sons may also avoid their mothers). Consistent with this, mother-son associations decreased by age 10, the approximate age of sexual maturity and when some strong male-male bonds begin to or are already formed (Wells 1991, Connor *et al.* 1999, Owen *et al.* 2002). However, Shark Bay dolphins are still more inbred than expected under random mating, especially given dolphin mobility (Frère *et al.* 2010a). Potential factors contributing to inbreeding include strong bisexual locational philopatry, which results in substantially overlapping home ranges between kin (Waser and Jones 1983; *e.g.*, this study). Thus, male alliances that overlap with female kin have a higher likelihood of inbreeding. Male alliances in Shark Bay are also coercive (Connor *et al.* 1996, Scott *et al.* 2005), which is likely to limit female choice. Additionally, males may not face the same costs of inbreeding as females, and it has been suggested that male inbreeding can be favored under a larger range of circumstances than female inbreeding (Waser *et al.* 1986). Finally, inbreeding in the population may be driven by matings other than between mother and son, such as between siblings or father and daughter (Krützen *et al.* 2004a, Frère *et al.* 2010a).

Although mother-daughter associations were more frequent than mother-son associations after weaning, mother-daughter associations still decreased substantially after weaning, which we attribute primarily to resource competition. This avoidance of direct resource competition between mother and daughter appears to conflict with relatively high mother-daughter associations, but fission-fusion dynamics and low locomotion costs (Williams 1992) may allow females to vary their associations depending on context. Specifically, females may temporally separate socializing from foraging. Although they may avoid others while foraging, they can easily join together during rest, travel, or social activities. Consistent with this, females usually forage alone (Mann and Sargeant 2003; Gibson and Mann 2008a, b), but also maintain associations with matrilineal kin (Smolker *et al.* 1992, Frère *et al.* 2010b, this study), such as with maternal sisters. Even as calves, females spend more time foraging than males while separated from their mothers (Gibson and Mann 2008a). Furthermore, female offspring may shift their foraging areas away from their mothers (*e.g.*, larger female shift in centroids during the juvenile period than male), or *vice versa*, to avoid competition, while still overlapping in overall range to maintain natal and/or matrilineal networks.

DISPERSAL IN RELATIONSHIP TO POPULATION STRUCTURE

Genetic studies of Shark Bay dolphins suggest that dispersal is male biased (Krützen *et al.* 2004b), which seems to contradict our suggestion that Shark Bay dolphins exhibit bisexual locational philopatry. We suggest that the observed pattern can be achieved in the presence of locational philopatry through expanded male ranges, whether they are maintained year round or are expanded seasonally during breeding excursions by males (*e.g.*, coatis, *Nasua narica*: Gompper *et al.* 1998, and bannertail kangaroo rats, *Dipodomys spectabilis*: Winters and Waser 2003). Additionally, adult males might engage in temporary excursions to increase their access to mates. This is supported by anecdotal observations, in which alliances herd females from adjacent areas into the main study area, sometimes for several weeks. By

bringing females back to familiar areas, males may avoid confrontation or risk of a female being stolen by other alliances (Connor *et al.* 1992*b*).

SOCIAL DISPERSAL IN SPECIES EXHIBITING HIGH FISSION-FUSION DYNAMICS

While current descriptions of social (group) dispersal are sufficient for examining systems with stable groups (*e.g.*, gibbons, *Hylobates* spp.: reviewed by Leighton 1987) or closed communities (*e.g.*, chimpanzees, *Pan troglodytes*, and spider monkeys, *Ateles paniscus*: Symington 1990), these general terms require further definition when examining species exhibiting high fission-fusion dynamics in an open society, such as Shark Bay bottlenose dolphins. Without a delineated “natal group,” social dispersal is not easily defined. Thus, studies examining social dispersal should specify which individuals (*e.g.*, mother, maternal network, *etc.*) are being left or joined and the degree to which dispersal occurs (*e.g.*, proportion of network change or changes in the strength of network ties). In this study, for example, we examined offspring social dispersal from mothers specifically and the retention of natal associates into the juvenile period, although changes in natal networks are likely to be much more complex than what can be shown here (see also Stanton *et al.* 2011).

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