

Mating in a bisexually philopatric society: bottlenose dolphin females associate with adult males but not adult sons during estrous

Megan M. Wallen¹  · Ewa Krzyszczyk¹ · Janet Mann^{1,2}

Received: 31 May 2017 / Revised: 5 September 2017 / Accepted: 11 September 2017 / Published online: 26 September 2017
© Springer-Verlag GmbH Germany 2017

Abstract

In fission-fusion societies, group size and composition change dynamically, reflecting social preferences and pressures. Most notably during reproduction, intersexual group dynamics reflect a balance between female choice for optimal mates and male competition for mating access. In systems where males and females remain in their natal area for life (bisexual philopatry), females can reduce the risk of incest by avoiding mating or associating with male kin. Shark Bay bottlenose dolphins (*Tursiops aduncus*) live in fission-fusion societies that enable them to exercise age, sex, and kin association biases. To determine how the balance between female choice and male competition is achieved, we examined adult female association with juvenile and adult males, including sons during female receptive periods, using 30 years of longitudinal data. Adult females demonstrated an increase in adult male association just prior to known conceptions, while juvenile male association consistently remained low. A decline in male association post-conception suggests that one or both sexes detect pregnancy early on. When we examined female association with juvenile and adult sons, a distinct pattern emerged. Adult females preferentially associated with sons

compared to non-sons of the same age class post-weaning. Strikingly, females rarely associated with their adult sons when cycling. Our results suggest that (1) adult males either out-compete juvenile males in gaining access to fertile females or females prefer adult to juvenile males and (2) females mitigate the risk of close inbreeding by reducing association with sons when cycling.

Significance statement

No study has investigated behavioral strategies for reducing close inbreeding in bisexually philopatric, fluid mammal societies outside of humans. Using over 30 years of longitudinal data, we document how association dynamics change with female reproductive state. Post-weaning, mothers and sons associate, but almost never during conceptive periods. Adult male–female association is frequent during estrous, with a sharp decline after conception. Our study provides evidence for long-term kin recognition and detection of both estrous and early pregnancy among wild bottlenose dolphins. These findings have implications for the evolution of bisexual philopatry, fission-fusion dynamics, and infanticide—or lack thereof—in mammals.

Communicated by L. M. Moller

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00265-017-2380-7>) contains supplementary material, which is available to authorized users.

✉ Megan M. Wallen
mmw89@georgetown.edu

¹ Department of Biology, Georgetown University, 406 Reiss Science Bldg., Washington D.C., WA 20057-1229, USA

² Department of Psychology, Georgetown University, Washington D.C., WA, USA

Keywords Bisexual philopatry · Estrous · Inbreeding · Juvenile · Pregnancy · *Tursiops*

Introduction

Intersexual association patterns are expected to vary with female reproductive status. With substantial investment in each offspring, mammalian females are expected to discriminate against suboptimal mates, including subadult males and close relatives. Subadult males are by definition fertile, but have not yet reached full body size (Barrows 2011) and are considered

subprime because they have lower physiological reproductive potential (Amann and Schanbacher 1983; Pagel and Harvey 2002), subordinate status (Cox and Le Boeuf 1977; Sandel et al. 2017), and lower competitive abilities than adult males (Dobson 1982; Banes et al. 2015; Ciuti and Apollonio 2016). Close kin are also suboptimal mating partners because mating between close relatives results in reduced fitness or inbreeding depression (Charlesworth and Charlesworth 1987; Keller and Waller 2002). Most mammalian societies have mechanisms that reduce the probability of mating with a close relative, including male-biased dispersal (Clutton-Brock and Lukas 2012), or more rarely, female-biased dispersal (e.g., chimpanzees, *Pan troglodytes*; Pusey and Packer 1987), such that potential mating partners are not likely to be close relatives (Pusey and Wolf 1996). Inbreeding can also be avoided in stable societies through kin recognition (Mateo 2004) via prior association familiarity or mechanisms of phenotype matching (e.g., detection of MHC dissimilarity: Brown and Eklund 1994; Penn 2002).

In fission-fusion social organizations, grouping patterns are temporally and compositionally variable as subgroups dynamically change size and composition (Aureli et al. 2008). The social fluidity of fission-fusion species therefore provides a useful framework in which to consider female tradeoffs of association patterns during conceptive periods. This is particularly true in species such as bottlenose dolphins (*Tursiops truncatus* and *T. aduncus*), which are characterized by a high degree of fission-fusion dynamics. In this study, we investigate context-dependent association patterns that emerge as a result of social fluidity.

Bisexually philopatric species present an unusual case in the animal kingdom in which both sexes remain in their natal area after reaching sexual maturity. Here, animals have the added complexity of searching for mating opportunities while reducing the consequences of close inbreeding (Frère et al. 2010a). In such species, mechanisms of kin recognition or avoidance are imperative for appropriate mate selection. For example, both sexes of fish-eating killer whales (*Orcinus orca*; Baird and Whitehead 2000; Wright et al. 2016), and long-finned pilot whales (*Globicephala melas*; Amos et al. 1993; Ottensmeyer and Whitehead 2003) stay in their natal pod for life, but genetic evidence indicates that mating occurs outside of their primary social group (Amos et al. 1993; Pilot et al. 2010). Kin recognition is obvious because the group membership is highly stable. By contrast, in the bottlenose dolphin, group membership is highly dynamic and may change on a minute-by-minute basis. Here, bisexual philopatry takes a different form, where sons and daughters maintain locational philopatry but daughters maintain higher matrilineal social philopatry (Tsai and Mann 2013). Thus, we expect intersexual associations to reflect a balance between female association with prime (i.e., unrelated adult) males and reduced association with closely related males during conceptive periods.

An added driver of intersexual association dynamics is the threat of infanticide by unrelated males. In polygynous and promiscuous mating systems, where the threat of infanticide is prominent, mating continues during pregnancy, presumably to confuse paternity and thereby reduce the risk of infanticide (van Schaik et al. 2004; Lukas and Huchard 2014). Under such circumstances, females may tolerate or encourage male presence or matings even though conception is unlikely.

In this study, we investigate how female bottlenose dolphins navigate the conflicting demands of mate selection while reducing the risk of inbreeding with close relatives in Shark Bay, Western Australia. In this fission-fusion society, foraging is primarily a solitary activity (Mann and Sargeant 2003; Sargeant et al. 2007; Sargeant and Mann 2009), but groups form during socializing, traveling, resting, and some types of foraging (Heithaus and Dill 2002; Gero et al. 2005). During the breeding season and presumably during female cycling periods, males cooperate within and between stable alliances to consort with females for mating access and often coerce consortships with conspicuous aggression (Connor et al. 1992a, b, 1996). Indeed, Scott et al. (2005) found higher levels of female-directed intersexual aggression in cycling compared to non-cycling females.

Previous work in Shark Bay has shown that association patterns reflect female reproductive state, with intersexual dyadic association being highest when females are cycling compared to when they are pregnant (Smolker et al. 1992). Importantly, despite the opportunity for frequent contact with conspecifics, male-female association is virtually always low: adult females spend less than 20% of their time with adult males outside of cycling periods (Wallen et al. 2016), and male-female dyads almost never preferred associations (Smolker et al. 1992). Additionally, mothers with dependent calves associate with juvenile and adult males less than expected based on their availability (Gibson and Mann 2008b).

Further, Shark Bay adult female dolphins preferentially associate with kin compared to non-kin (Frère et al. 2010b). However, upon weaning, mother-offspring association—particularly mother-son association—declines dramatically despite the lack of geographic or social dispersal in this population (Tsai and Mann 2013). Social avoidance post-weaning may be one mechanism by which mothers and sons reduce the risk of inbreeding. Reduced mother-son association may also indicate the time when males reach physiological or behavioral (e.g., alliance formation and competitive ability) sexual maturity.

Here, we seek to understand female association patterns with respect to reproductive status, male age, and relatedness. Specifically, we hypothesize that females optimize mate choice directly or indirectly by associating preferentially with adult males and reducing association with juvenile males and sons near conception. Consistent with this hypothesis, we predict that adult female association is (i)

highest with adult (prime) males around conception and (ii) lowest with juvenile (subprime) males around conception, given their subordinate status. Further, if infanticide presents a real risk to females as proposed previously (Connor et al. 1996), then females will frequently associate with adult males post-conception, during early pregnancy. If adult male-female association is strongly dictated by conception date, this would suggest that males can detect fertile periods with a high degree of accuracy, which would undermine the infanticide hypothesis for bottlenose dolphins (Lukas and Huchard 2014). Secondly, we hypothesize that females reduce the chances of close inbreeding by avoiding association with sons during her fertile periods. Due to the costs of inbreeding, already demonstrated in this population (Frère et al. 2010a), we predict that mothers will associate less with their weaned sons (iii) as they transition from the juvenile to the adult stage, (iv) in comparison to unrelated males, and (v) during cycling (fertile) periods. We also predict that mothers will be more tolerant of her son's presence in specific contexts, such as larger groups and non-socializing groups when she can avoid incestuous matings. Specifically, we predict that (vi) group size will be larger with adult sons compared to juvenile sons, such that the group provides a social buffer between the mother and her son, and (vii) group activity state will primarily be resting or traveling (non-social contexts) when females are with their adult sons compared to with their juvenile sons. It is also likely that larger group size with adult sons might be driven by near constant association between adult males and their alliance partners, while juvenile males have not yet established such bonds (Connor et al. 2000).

Methods

Study site

Shark Bay, Western Australia (25°47'S, 113°43'E) is home to a resident population of bottlenose dolphins (*T. aduncus*) that has been studied continuously since 1984. Researchers have collected behavioral, ecological, genetic, and demographic data on > 1600 individuals within the 300-km² study area in the eastern gulf. In particular, adult females and their calves have been intensively tracked, enabling detailed study of female association patterns over time. Matrilineal relationships are known through observed association of the calf with the mother early in life. Individuals are uniquely identified by the shape and damage to the dorsal fin using photo ID, as well as other obvious bodily markings such as tooth rakes and shark bites (Whitehead et al. 2000). Sexes are determined by views of the genital area, consistent presence of a dependent calf (Smolker et al. 1992; Mann et al. 2000), and genetics

(Krützen et al. 2004). Birth years are known for most individuals born since the mid-1980s and are otherwise estimated based on ventral speckling and size information (Krzyszczczyk and Mann 2012). Given the individual nature of this study involving focal animals in the field, it was not possible to record data blind.

Data collection—life history

For this study, adult females were included if they had at least one calf with a highly accurate birthdate (± 3 days) and were observed at least once within 8 months of conception ($N = 65$ adult females, 104 calves). Only calves whose birthdate assignment was accurate to the day (± 3 days) were used to determine conception. Calves can be aged precisely by both physiological and behavioral characteristics (fetal folds, floppy dorsal fin, curled tail flukes, cork-like surfacings), in addition to sightings of the mother just before and just after the birth (Mann and Smuts 1999). Conception date was assigned based on the 12-month gestation period documented for captive *T. truncatus* and *T. aduncus*. (Schroeder 1990; Lacave et al. 2004).

To investigate how associations with sons and unrelated males change during the receptive period, we classified males as juveniles (subprime) or adults (prime). The juvenile period is defined as the period between the weaning age until the age of 10. Weaning age was determined by taking the midpoint between the last sighting of a calf in infant position or spending more than 80% of the time with the mother and when this association decreased to less than 50% (Mann et al. 2000). Weaning ages ranged from 2.45 to 7.24 (mean \pm SE = 4.04 \pm 0.10).

Though little is known about age at sexual maturity for *T. aduncus* (Kemper et al. 2014), we define the adult period from the age of 10 onwards: in Shark Bay, the earliest pregnancy occurs at age 10 (JM unpublished data), and male bottlenose dolphins in captivity are almost always sexually mature by age 10 based on testosterone levels (Wells et al. 1987; Brook et al. 2000; Yuen 2007) even if asymptotic growth has not been reached (Read et al. 1993).

Data collection—association measured by surveys

Female association data were calculated from 1211 unique surveys conducted from 1989 to 2015 ($N = 65$ adult females, 104 conceptions). Only the last survey per female per day was selected to reduce temporal autocorrelation. Surveys are brief, five-minute “snapshots” of group behavior and composition collected by scan sampling (Altmann 1974; Mann 1999). Predominant group behavior was defined as the activity of $\geq 50\%$ of group members during the first 5 min of the survey. Activities included foraging, resting, socializing, and traveling (see Karniski et al. 2015 for an ethogram). Dolphins were considered to be associating (group members) if they were

within 10 m of any dolphin in the group during the survey (Smolker et al. 1992).

To investigate how female association changed around receptivity, we considered all survey data in which a female was observed 4 months before conception (when the female was cycling) versus 4 months after conception (when the female was pregnant). Four months was selected to encapsulate periods prior to females becoming attractive, and after conception when female attractiveness is expected to wane.

If there are several adult females in a large group with several males, we cannot be certain which female (if any) is driving male interest. To check this bias, we restricted our surveys to those where only one conceptive female was present. Our results stayed the same, so the original data are presented.

The following association metrics were calculated separately for each female to account for individual differences in gregariousness; females may have different baseline levels of association with males regardless of reproductive state. We first calculated the average number of males each female was found associating with across all surveys in which she was observed, such that each individual female was assigned her own *male average* across all surveys. The number of males in each survey during the pre- and post-conceptive time periods was then subtracted from each female's *male average* to obtain her *male difference*, which is the number of males present in a female's survey relative to that female's *male average*. Therefore, any values greater than 0 indicate higher than average association, while any values less than 0 indicate lower than average association. We calculated a *male difference* for adult male association and juvenile male association separately.

To test how mother-son association varies by reproductive status, we included mothers that were known to be alive while their sons were juveniles ($N = 59$ mothers, 78 sons) and/or adults ($N = 40$ mothers, 44 sons). Each mother and son had to have 15 surveys or more (total) during the offspring's respective juvenile or adult time period. We compared mother-son association to mother-unrelated male association, both at the juvenile and adult stages. Unrelated male association was calculated as the number of surveys (excluding those with sons) with juvenile or adult males, divided by the number of available juvenile or adult males in our entire study population during that time period, to get the average number of surveys per unrelated male. Because the age at which males become fertile is not well defined (between 8 and 13 years depending on species (*T. aduncus* or *T. truncatus*) and whether captive or not—see Read et al. 1993; Kemper et al. 2014), we further classified sons by year of age and calculated the proportion of mother-son pairs that

were seen associating at least once within each son age-year class. Finally, we compared group size and group activity when mothers were with their juvenile sons to when they were with their adult sons.

Data analysis

We used permutation tests to compare the proportion of surveys in which a female associated with juvenile (subprime) and adult (prime) males in the pre- and post-conception windows. To assess juvenile and adult male association from pre- to post-conception on a continuous scale, we used linear mixed effect models with day from conception as a fixed effect and the mother's ID as a random effect. Models for juvenile and adult males were run separately as association was on vastly different scales (mean *juvenile male average*: 0.34; mean *adult male average*: 1.34). Exploratory analysis indicated that a quadratic function was a better fit for adult male association, while linear was the best fit for juvenile male association. We calculated R^2 for goodness of fit for mixed effect models following Xu (2003).

To determine the breakpoint at which female association patterns with adult males changed, we ran a piecewise linear regression using fixed effects only (R package 'segmented'; Muggeo 2003, 2008). We first specified the single continuous variable (day from conception) on which to determine a segmented relationship, and provided a start value for the breakpoint estimation based on a visual examination of where the relationship changes from a positive slope to a negative slope. This method uses maximum likelihood to calculate the distance between each segment and converges when the distance is 0, making the model nearly continuous. We tested the null hypothesis that the difference in slope on either side of the breakpoint is zero.

To investigate how kinship may influence association, we first used permutation tests to compare female-son to female-unrelated male association, separately at the son's juvenile and adult stages. We then refined age class by year and ran a logistic regression to calculate the probability of a weaned son being seen with his mother given his age, using age in years as a fixed effect and the mother's ID as a random effect. To compare group size when mothers were with their juvenile versus adult sons, we ran a generalized linear mixed effect model with a Poisson distribution. The son's age class (juvenile or adult) was included as a fixed effect and the mother's ID was included as a random effect. To compare group activity (proportion of surveys) when mothers were with their juvenile versus adult sons, we conducted a paired permutation test. All statistical analyses were run in R version 3.3.1 (R Core Team 2016).

Results

Female-male association patterns around conception

Adult females associate with adult males more than juvenile males both before and after conception (pre-conception: $t = -7.47$, $df = 1816$, $P < 0.0001$; post-conception: $t = -4.33$, $df = 757$, $P < 0.0001$).

Female association with adult males showed a negative quadratic relationship across the conception window, with highest association just prior to and at conception (Table 1; Figs. 1a, 2). The polynomial quadratic model fits significantly better than the linear model excluding the quadratic term ($\chi^2 = 32.65$, $P < 0.0001$). To determine the time at which adult male association peaks prior to known conception date, we fit a linear model (this time excluding random factors) and ran a piecewise regression to determine the most likely break point at which the relationship between day from conception and male association changes. At -13.74 (SE ± 7.7) days prior to conception (red dashed line, Fig. 1), the relationship changes from a positive slope ($+0.017$) to a negative, but nearly equivalent in magnitude, slope (-0.016).

Association with juvenile males, while consistently lower than adult males, showed a linear decline across the 8 months from pre- to post-conception (Table 2; Fig. 1b).

Mother-son association patterns

There was a steady decline in the proportion of mothers and sons that associate from weaning through adulthood (Fig. 3). Additionally, the predicted probability of a mother being seen with her weaned son, given his age, decreased nearly to zero by the time her son reaches age 20 (Fig. 4). However, mother-son association post-weaning was higher than we expected during the juvenile period. Females associated *more* with their juvenile sons than they did with any given unrelated juvenile male ($Z = -3.81$, $P < 0.0001$). However, once their sons reached adulthood, mothers associated with adult sons just as much as unrelated adult males ($Z = -0.16$, $P > 0.1$). Despite these trends, 32% of mother-son pairs were never sighted together during the son's juvenile period, even though both were sighted frequently during that time. By contrast, 64% of mother-son pairs were never sighted together during the son's adult period, even though both were sighted frequently during that time.

Table 1 Parameter estimates for fixed effects in the quadratic regression model for adult male association

	Estimate \pm SE	<i>t</i>	<i>P</i>	<i>R</i> ²
Intercept	0.8759 \pm 0.1591	5.506	< 0.0001	0.25
Day from conception	-1.9615 \pm 2.8189	-0.696	0.487	
(Day from conception) ²	-18.5091 \pm 2.5905	-7.145	< 0.0001***	

P-values in italics with asterisks indicate significance at alpha = 0.05 ($P < 0.01$ **, $P < 0.0001$ ***)

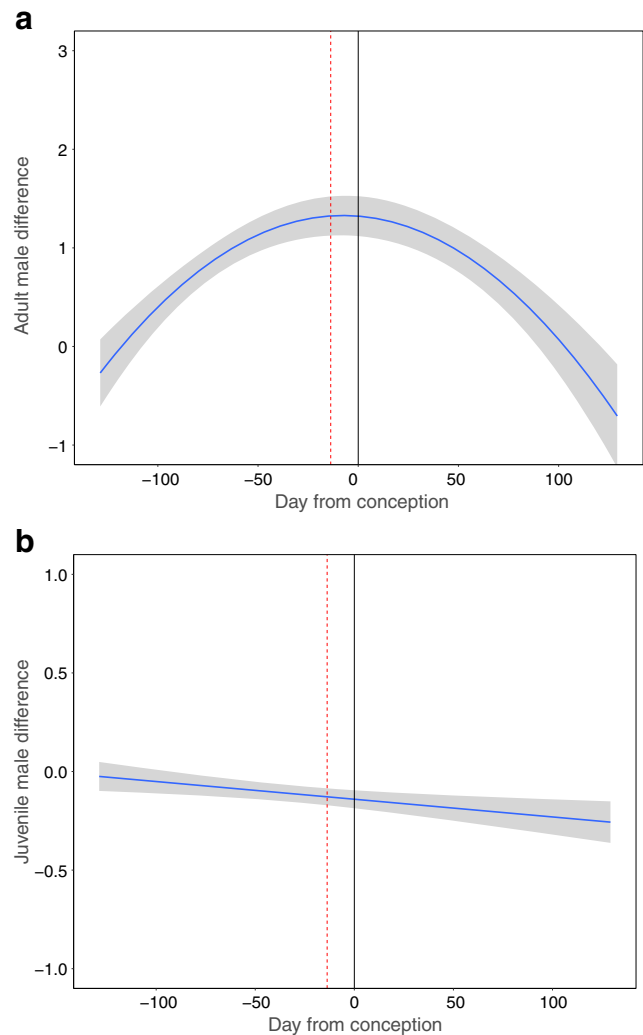


Fig. 1 Representation of the fitted models with 95% confidence intervals for the predicted number of **a** adult males and **b** juvenile males associating with females by day from conception. The solid vertical black line at 0 indicates estimated conception date. The dashed red line indicates the statistical breakpoint at which adult male association starts to decline (-13.74 days). Raw data are provided in the [Electronic supplementary material](#)

A more striking pattern emerges when taking into account the mother's reproductive state. When females were cycling, there was no significant difference in association with juvenile sons versus unrelated juvenile males ($Z = -1.5621$, $P > 0.1$; Fig. 5). However, cycling females were rarely seen with adult sons compared to unrelated adult males ($Z = 1.7812$, $P < 0.05$; Fig. 5). In fact, only

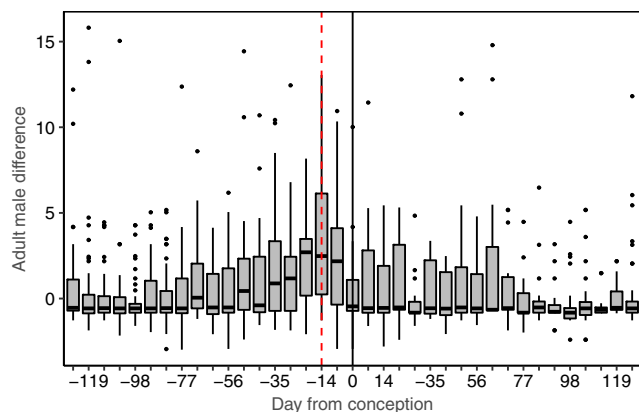


Fig. 2 Box and whisker plot showing the median number of adult males associating with females by day from conception, where the upper and lower hinges represent the first (Q1) and third (Q3) quartiles, and outliers beyond the whiskers represent values greater than $Q3 + 1.5 \cdot IQR$ or less than $Q1 - 1.5 \cdot IQR$ (with $IQR = Q3 - Q1$). The solid vertical black line at 0 indicates predicted conception date. The dashed red line indicates the breakpoint at which adult male association starts to decline (-13.74 days). Raw data are provided in the [Electronic supplementary material](#)

one adult son was observed in the same group as his mother within 4 weeks of conception.

Finally, group size was significantly larger when females were with their adult sons compared to when they were with their juvenile sons ($Z = -4.94$, $df = 447$, $P < 0.0001$). The predominant group activity when females were with their adult sons was primarily traveling (40%, $SE \pm 9\%$) or resting (32%, $SE \pm 8\%$). Traveling rates were higher with adult sons ($40 \pm 9\%$) than juvenile sons ($19 \pm 3\%$, $P < 0.05$) while resting rates were higher with juvenile sons ($51 \pm 5\%$) than with adult sons ($31 \pm 7\%$, $P < 0.05$). Female social budgets were equally low ($P > 0.1$) when they were with juvenile sons ($8 \pm 2\%$) and adult sons ($13 \pm 6\%$), as were foraging budgets (juvenile: $17 \pm 3\%$, adult: $14 \pm 4\%$, $P > 0.1$).

Discussion

In this study, we demonstrate how female-male associations vary by reproductive status, relatedness, and male age. As expected, females associate with adult males pre-conception far more than they do with juvenile males (Smolker et al. 1992). Interestingly, the peak in adult female-adult male association occurred 14 days prior to the estimated conception date and association persisted briefly post-conception (Fig. 1),

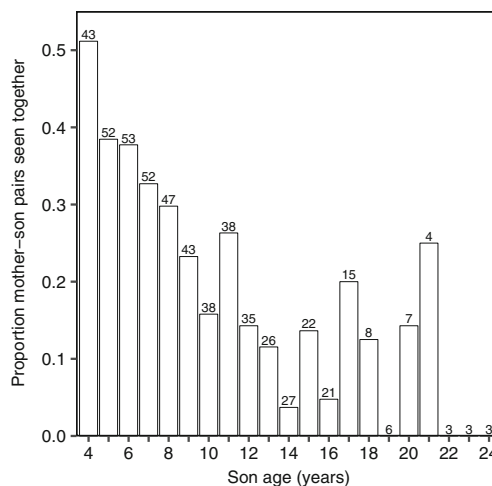


Fig. 3 Proportion of mother-son pairs seen together by son's age in years post-weaning with sample sizes above bars

suggesting that there is an optimal time for males to remain with females to ensure conception and paternity, and this drops off once pregnancy is detected by conspecifics. Further, some have hypothesized a 54-week gestation period, slightly longer than the estimated 52 weeks (O'Brien and Robeck 2012), and our association patterns are consistent with that hypothesis.

Although bottlenose dolphins are polyoestrous, going through 3–4 estrus cycles of approximately 21–42 days each within a cycling season (Schroeder 1990; Robeck et al. 2005; O'Brien and Robeck 2012), we detected only one peak in above-average male association within the 4 months prior to a known conception. We suggest that male interest would be unlikely to wane between consecutive estrus cycles, even if anovulatory (e.g., elephants, Hildebrandt et al. 2011), because the cost of missing an ovulation would be high. Further, surveys are conducted periodically, are weather-dependent, and the likelihood of sampling the same individuals every consecutive day is very low, which may preclude detection of narrow, local association peaks prior to the term conception.

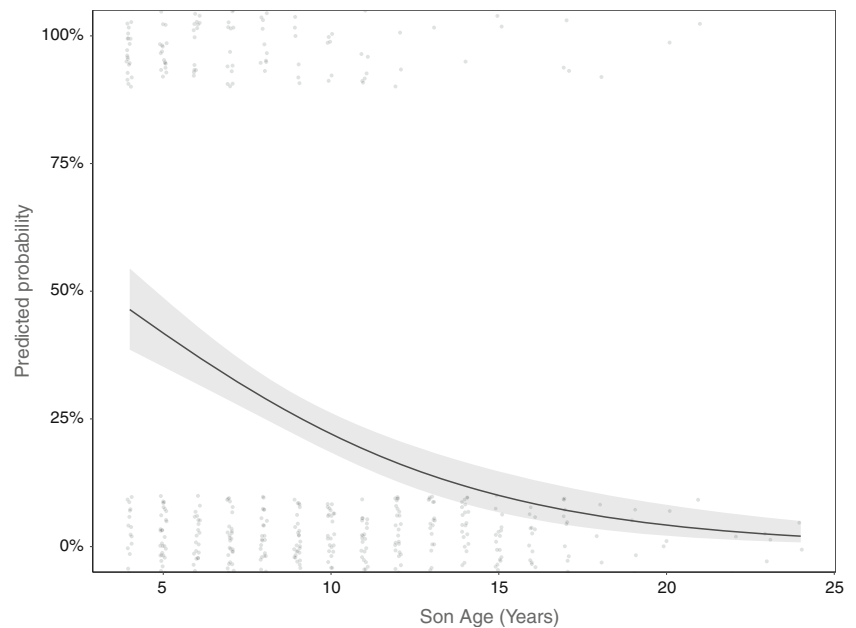
From pre- to post-conception, the average number of juvenile males present with adult females decreased significantly but to a small degree (Fig. 1b), while only adult males showed a sizeable peak in association at, or prior to, conception (Fig. 1a). We suggest two, non-mutually exclusive hypotheses to explain this temporal pattern. First, we hypothesize that both juvenile and adult males can detect female pregnancy (or, more accurately, the cessation of ovulation), and thus interest

Table 2 Parameter estimates for fixed effects in the linear regression model for juvenile male association

	Estimate \pm SE	<i>t</i>	<i>P</i>	<i>R</i> ²
Intercept	- 0.1404 \pm 0.03459	- 4.058	< 0.0001	0.13
Day from conception	- 8.963E04 \pm 3.389E04	- 2.645	0.00829**	

P values bolded with asterisks indicate significance at alpha = 0.05 ($P < 0.01$ ** , $P < 0.0001$ ***)

Fig. 4 Predicted probabilities with 95% confidence interval of mother-son pairs being sighted together post-weaning (fixed effect), conditioned on the random effect (Son ID), given son's age



wanes following conception. Males of several non-human primate species use color signals to detect pregnancy (Rowell and Chalmers 1970; Altmann 1973; Loy 1974; Dunbar and Dunbar 1974; Gerald et al. 2009; Setchell et al. 2006). While in some species young males may not yet be able to detect female fertility (e.g., leaf monkeys, *Trachypithecus* spp., Lu et al. 2012), our results are concordant with the hypothesis that males adjust their behavior after a female becomes pregnant. Some studies have recorded female fertility detection in dolphins by the presence of specific estrus behaviors based on captive dolphin (*T. truncatus*) observations (Muraco and Kuczaj 2015) or pheromones released in urine (Muraco 2015), but to date, no study has documented the mechanism by which pregnancy is detected by conspecifics in bottlenose dolphins.

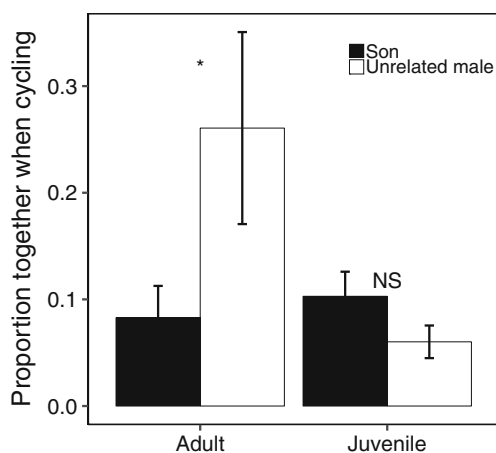


Fig. 5 Mean proportion of time that females were with adult or juvenile sons or unrelated males during her known cycling periods. Error bars represent standard errors Z

Our second hypothesis to explain the temporal pattern of association between conceptive females and males is that females either (a) tolerate adult males only or (b) elicit sexual advances towards adult males near ovulation. This may explain the higher than average adult male association prior to pregnancy, but consistently decreasing juvenile male presence prior to conception. This is in contrast to other work, where female reproductive state did not influence intersexual association frequency (e.g., Guinea baboons, *Papio papio*, Goffe et al. 2016). Our results also help explain why juvenile males are not likely to be fathers, in contrast to other species where young males regularly copulate with or even father offspring (e.g., chimpanzees, Watts 2015; savanna baboons, Alberts et al. 2003), albeit rarely. Additionally, adult male alliances would readily outcompete juveniles for access to female dolphins. Ultimately, females appear to associate very little with juvenile males.

We cannot differentiate which sex is driving the observed patterns so it is equally important to consider male trade-offs. Adult males are better equipped to outcompete juvenile males to gain access to fertile females because they are physically larger and have stable alliance partners, whereas juvenile males typically have not yet formed strong social bonds. Adult males may also be intolerant of juvenile males or even direct aggression towards them. A previous study found that male calves that associate more with juvenile males had reduced survival (Stanton and Mann 2012), suggesting male competition during early stages of development. Young males may simply be avoiding adult males, despite the presence of a fertile female.

Given that adult males, and possibly juvenile males, may detect pregnancy as evidenced by reduced association with

females post-conception, female dolphins would not be able to confuse paternity by mating with males post-conception. That said, infanticide might be important at other sites, given several documented cases of infanticide in dolphins (*T. truncatus*) (Patterson et al. 1998; Dunn et al. 2002; Kaplan et al. 2009; Robinson 2014; Perrtree et al. 2016). In addition, despite over 30 years of intensive study, aggression by adult males towards young infants is absent or rare. Therefore, we argue that infanticide risk is not a driver in Shark Bay dolphin behavior because individuals are philopatric, year-round residents that maintain long-term social bonds important for fitness (Krützen et al. 2004; Frère et al. 2010c; Stanton and Mann 2012). It is notable that at another long-term study site, Sarasota, Florida, where both sexes are residential, infanticide has not been reported (Wells 2014). Additionally, the chances of achieving a paternity following infant death are relatively low because successful mating requires the cooperation of alliance partners (Krützen et al. 2004). Upon loss of offspring, it takes weeks to months for the female to resume cycling, and the chance of that male fathering the next offspring might be small (Mann et al. 2000).

Many females are consorted by multiple alliances during a single breeding year. The length of attractive periods is generally 7 days or less, though consortships can last several weeks (Connor et al. 1996) up to several months (Connor and Krützen 2015), and mating probably occurs with more than one (if not all) alliance members during that time. So, while paternity confusion via mating within and across alliances may occur during the pre-conception period, pregnancy probably cannot be concealed, as supported by the drop in male association upon conception. While some coerced consortships have been recorded during non-fertile periods (pre- and post-partum), these appeared to be an anomalous case restricted to one aggressive provisioned male alliance with almost unlimited access to food (Connor et al. 1996).

Female choice is difficult to document in Shark Bay dolphins, where alliances harass females and coerce consortships during fertile periods. Mate choice is likely to be constrained in sexually coercive systems (e.g., chimpanzees; Muller et al. 2011). In Shark Bay dolphins, females are known to “bolt” to escape a male alliance, and it is fairly obvious that these females are trying to get away from aggressive males, as opposed to testing their physical vigor (Connor et al. 1996). An alternative explanation is that female tolerance of adult males is a mechanism of conflict management, seen in many primate species (Cords and Mann 2014), as male aggression is known to be higher towards cycling than non-cycling females (Scott et al. 2005; Watson-Capps 2005).

In our study of female associations with juvenile and adult males near conception, all surveys with sons were excluded. We took a closer look at mother-son relationships to determine whether social mechanisms for close inbreeding avoidance were present (Clutton-Brock and Lukas 2012), despite

inbreeding values greater than expected by random mating in this population (Frère et al. 2010a). Mothers associate with their weaned sons less than their weaned daughters (Tsai and Mann 2013), which echoes a more general pattern that females associate less with males than with other females (Wallen et al. 2016). Interestingly, mothers associated with their weaned juvenile sons more than any given unrelated male of comparable age. We suggest that at young ages, males do not yet present a threat of inbreeding as they are still allocating energy towards growth and have not yet established stable alliances. Females can avoid mating attempts by young sons, and male fertility is probably low in the juvenile period. Mothers also might continue to provide social or ecological benefits to juvenile sons, extending her maternal influence post-weaning (Gibson and Mann 2008a, b) either through information sharing, social support, or protection from older or more aggressive males (Stanton and Mann 2012). Broken down by year, mothers gradually associated less with their weaned sons throughout from the juvenile to adult period, and generally adult males only rarely associated with their mothers. However, association did not drop off to zero with older male ages. Only cycling females associated less with adult sons than with unrelated adult males. We cannot determine whether the mechanism is by mutual avoidance between mothers and adult sons, or whether competition between alliances for fertile females prevents sons from access to their mothers.

Though mothers and their adult sons reduced association only during cycling periods, association was not absent. Mothers tended to associate with adult sons in large groups when other individuals might form a buffer between them, possibly because females tolerate their adult sons when other individuals (including her close associates) are nearby. Further, groups were rarely socializing when mothers and sons were together, suggesting that association is tolerated in non-mating contexts (e.g., large resting groups). It might also be that groups are larger because adult males are in alliances which will necessarily magnify group size. To date, sons have not been observed mounting their mothers post-weaning although they do so often as calves (Mann 2006). Given that dispersal is highly variable in *Tursiops* (Wilson et al. 1997; Möller and Beheregaray 2004; McHugh et al. 2011; Nuutila et al. 2017), and that dolphins appear to tolerate some level of inbreeding (Frère et al. 2010b), sex-biased dispersal is likely explained by drivers other than inbreeding avoidance (Moore and Ali 1984; Szulkin et al. 2013).

We caution that survey association data introduces a potential ‘gambit of the group’ bias, where individuals in the same survey may not necessarily be social partners. However, results stayed the same when we restricted our surveys to those where only one conceptive female was present. In the future, direct interactions and association measures from individual focal follows may provide more complete picture on the

causes and/or function of male-female associations across different reproductive states.

Another caveat to this study is that kin association as measured is almost certainly an underestimate. While mother-dependent offspring relationships are known (Mann et al. 2000), there are likely many undetected kin relationships among adults that were dependent calves before the project started in 1982. Genetic sampling has enabled additional kin relationships to be discovered (Krützen et al. 2004), but there are likely some mother-offspring pairs that were analyzed as mother-unrelated male pairs (i.e., false negatives).

Collection of physiological data via non-invasive methods has become increasingly important for understanding health and vulnerability of wild populations (Cooke et al. 2014). Techniques in reproductive endocrinology have allowed for the non-invasive study of physiology, most notably from urine (Preis et al. 2011) or fecal (Millsbaugh and Washburn 2004) metabolite analysis, though there are many unresolved issues (Goymann 2012). In wild cetacean populations, methods for detecting reproductive state are typically invasive. Blubber can be collected with a remote biopsy system, but is a crude measure of pregnancy, not the timing of ovulation (Perez et al. 2011), or tissue and sonograms can be collected from captured and/or temporarily restrained animals (Wells 1991; Bergfelt et al. 2013). Fecal and urine samples can be collected from captive marine mammals (Robeck et al. 1993; Biancani et al. 2009; Amaral 2010), and more recently, scat collection is possible with wild cetaceans using detection dogs (e.g., right whales, *Eubalaena glacialis*; Rolland et al. 2005; killer whales, Ayres et al. 2012). Non-invasive detection of reproductive state in smaller delphinids remains a challenge.

For human observers without easy access to physiological indicators, behavior and association patterns may serve as accurate indicators of female reproductive state in wild populations. In the case of bottlenose dolphins, fertile periods can be determined post hoc based on pregnancy and birth of a calf, but might also be obvious based on male attention, behavior, and association. Mounting behaviors, while common among immature dolphins, are rarely observed between adults of the opposite sex (Mann 2006), but likely correspond to periods of estrus. Lactation is conspicuous in dolphins because the presence of a dependent calf in infant position indicates nursing offspring (Mann et al. 2000) and mammary glands are visibly swollen up until the time of weaning. However, bottlenose dolphins have overlapping reproductive states and become attractive to males prior to weaning dependent offspring (Mann et al. 2000). Pregnancy cannot be easily detected until the later stages based on female girth (J.M. personal observation), unless the animal is captured and restrained for blood testing or ultrasonographic analysis (Wells and Scott 1990; Wells et al. 2004). If there is fetal loss, especially early fetal loss, then the pregnancy—and corresponding fertile periods—might not be known.

Association patterns as demonstrated in this study may be a useful tool to model known conceptions, at least in species with predictable temporal sexual segregation such as the bottlenose dolphin. Empirical association records may be useful for informing computational models to predict reproductive events that go undetected via observational methods, such as pregnancies lost *in utero*, or ovulations that were not followed by a conception. Future work should investigate the predictive power of intersexual associations with known pregnancies, as a model for determining missed ovulations or conceptions.

Acknowledgements We thank current and past members of the Shark Bay Dolphin Project, and numerous field assistants, for their efforts in data collection used for this project. In particular, we would like to acknowledge Ann-Marie Jacoby, Sara Eshleman, Jillian Wisse, Desirae Cambrelen, and Theodora Efthymiou. We are grateful to the Western Australia Department of Parks and Wildlife (DPaW) and the Monkey Mia Dolphin Resort for their logistical support in the field. We thank DPaW for contributing a portion of the life history data. We also thank two anonymous reviewers for their input on an earlier version of this manuscript. The study was funded by National Science Foundation grants 0941487, 0918308, 0316800, National Geographic Society Committee for Research and Exploration, ONR BAA 10230702, and Georgetown University.

Compliance with ethical standards This work was approved by the Georgetown University Animal Care and Use Committee, permits #07–041, #10–023, #13–069, Western Australia Department of Parks and Wildlife permit #SF007418, #SF007975, #SF006897, #SF007457, #SF009311, #SF008076, #SF009876, and The University of Western Australia animal ethics permit #600–37. All procedures performed in this study were in accordance with the ethical standards of the aforementioned institutions and agencies. The study was funded by National Science Foundation grants 0941487, 0918308, 0316800, National Geographic Society Committee for Research and Exploration, ONR BAA 10230702, and Georgetown University.

Conflict of interest The authors declare that they have no conflict of interest.

References

- Alberts SC, Watts HE, Altmann J (2003) Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. *Anim Behav* 65:821–840
- Altmann SA (1973) The pregnancy sign in savannah baboons. *J Zoo Anim Med* 4:8–12
- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227–266
- Amann RP, Schanbacher BD (1983) Physiology of male reproduction. *J Anim Sci* 57:380–403
- Amaral RS (2010) Use of alternative matrices to monitor steroid hormones in aquatic mammals: a review. *Aquat Mamm* 36:162
- Amos B, Schlötterer C, Tautz D (1993) Social structure of pilot whales revealed by analytical DNA profiling. *Science* 260:670–672
- Aureli F, Schaffner CM, Boesch C et al (2008) Fission-fusion dynamics. *Curr Anthropol* 49:627–654
- Ayres KL, Booth RK, Hempelmann JA, Koski KL, Emmons CK, Baird RW, Balcomb-Bartok K, Hanson MB, Ford MJ, Wasser SK (2012)

- Distinguishing the impacts of inadequate prey and vessel traffic on an endangered killer whale (*Orcinus orca*) population. *PLoS One* 7: e36842
- Baird RW, Whitehead H (2000) Social organization of mammal-eating killer whales: group stability and dispersal patterns. *Can J Zool* 78: 2096–2105
- Banes GL, Galdikas BM, Vigilant L (2015) Male orang-utan bimaturism and reproductive success at Camp Leakey in Tanjung Puting National Park, Indonesia. *Behav Ecol Sociobiol* 69:1785–1794
- Barrows EM (2011) Animal behavior desk reference: a dictionary of animal behavior, ecology, and evolution. CRC press, Ann Arbor
- Bergfelt DR, Steinetz BG, Reif JS, Schaefer AM, Bossart GD, Mazzoil MS, Zolman E, Fair PA (2013) Evaluation of single-sample analysis of progesterone in combination with relaxin for diagnosis of pregnancy in wild bottlenose dolphins (*Tursiops truncatus*). *Aquat Mamm* 39:187–195
- Biancani B, Da Dalt L, Lacave G, Romagnoli S, Gabai G (2009) Measuring fecal progestogens as a tool to monitor reproductive activity in captive female bottlenose dolphins (*Tursiops truncatus*). *Theriogenology* 72:1282–1292
- Brook FM, Kinoshita R, Brown B, Metreweli C (2000) Ultrasonographic imaging of the testis and epididymis of the bottlenose dolphin, *Tursiops truncatus aduncus*. *J Reprod Fertil* 119:233–240
- Brown JL, Eklund A (1994) Kin recognition and the major histocompatibility complex: an integrative review. *Am Nat* 143:435–461
- Charlesworth D, Charlesworth B (1987) Inbreeding depression and its evolutionary consequences. *Annu Rev Ecol Syst* 18:237–268
- Ciuti S, Apollonio M (2016) Reproductive timing in a lekking mammal: male fallow deer getting ready for female estrus. *Behav Ecol* 27: 1522–1532
- Clutton-Brock TH, Lukas D (2012) The evolution of social philopatry and dispersal in female mammals. *Mol Ecol* 21:472–492
- Connor RC, Krützen M (2015) Male dolphin alliances in Shark Bay: changing perspectives in a 30-year study. *Anim Behav* 103:223–235
- Connor RC, Smolker RA, Richards AF (1992a) Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *P Natl Acad Sci USA* 89:987–990
- Connor RC, Smolker RA, Richards AF (1992b) Dolphin alliances and coalitions. In: Harcourt AH, de Waal FBM (eds) *Coalitions and alliances in humans and other animals*. Oxford University Press, New York, pp 415–443
- Connor RC, Richards A, Smolker R, Mann J (1996) Patterns of female attractiveness in Indian Ocean bottlenose dolphins. *Behaviour* 133: 37–69
- Connor RC, Wells RS, Mann J, Read AJ (2000) The bottlenose dolphin. *Cetacean Societies*, p 91–125
- Cooke SJ, Blumstein DT, Buchholz R, Caro T, Fernández-Juricic E, Franklin CE, Wikelski M (2014) Physiology, behavior, and conservation. *Physiol Biochem Zool* 87:1–14
- Cords M, Mann J (2014) Social conflict management in primates: is there a case for dolphins? In: Yamagiwa J, Karczmarski L (eds) *Primates and cetaceans*. Springer, Inuyama, pp 207–212
- Core Team R (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna <https://www.R-project.org/>
- Cox CR, Le Boeuf BJ (1977) Female incitation of male competition: a mechanism in sexual selection. *Am Nat* 111:317–335
- Dobson FS (1982) Competition for mates and predominant juvenile male dispersal in mammals. *Anim Behav* 30:1183–1192
- Dunbar RIM, Dunbar P (1974) The reproductive cycle of the gelada baboon. *Anim Behav* 22:203–210
- Dunn DG, Barco SG, Pabst DA, McLellan WA (2002) Evidence for infanticide in bottlenose dolphins of the western North Atlantic. *J Wildlife Dis* 38:505–510
- Frère CH, Krützen M, Kopps A, Ward P, Mann J, Sherwin WB (2010a) Inbreeding tolerance and fitness costs in wild bottlenose dolphins. *Proc R Soc Lond B* 277:2667–2673
- Frère CH, Krützen M, Mann J, Connor RC, Bejder L, Sherwin WB (2010b) Social and genetic interactions drive fitness variation in a free-living dolphin population. *P Natl Acad Sci USA* 107:19949–19954
- Frère CH, Krützen M, Mann J, Watson-Capps JJ, Tsai YJ, Patterson EM, Connor RC, Bejder L, Sherwin WB (2010c) Home range overlap, matrilineal and biparental kinship drive female associations in bottlenose dolphins. *Anim Behav* 80:481–486
- Gerald MS, Waitt C, Little AC (2009) Pregnancy coloration in macaques may act as a warning signal to reduce antagonism by conspecifics. *Behav Process* 80:7–11
- Gero S, Bejder L, Whitehead H, Mann J, Connor RC (2005) Behaviourally specific preferred associations in bottlenose dolphins, *Tursiops* spp. *Can J Zool* 83:1566–1573
- Gibson QA, Mann J (2008a) Early social development in wild bottlenose dolphins: sex differences, individual variation and maternal influence. *Anim Behav* 76:375–387
- Gibson QA, Mann J (2008b) The size, composition and function of wild bottlenose dolphin (*Tursiops* sp.) mother–calf groups in Shark Bay, Australia. *Anim Behav* 76:389–405
- Goffe AS, Zinner D, Fischer J (2016) Sex and friendship in a multilevel society: behavioural patterns and associations between female and male Guinea baboons. *Behav Ecol Sociobiol* 70:323–336
- Goymann W (2012) On the use of non-invasive hormone research in uncontrolled, natural environments: the problem with sex, diet, metabolic rate and the individual. *Methods Ecol Evol* 3:757–765
- Heithaus M, Dill L (2002) Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology* 83:480–491
- Hildebrandt TB, Lueders I, Hermes R, Goeritz F, Saragusty J (2011) Reproductive cycle of the elephant. *Anim Reprod Sci* 124:176–183
- Kaplan J, Lentell BJ, Lange W (2009) Possible evidence for infanticide among bottlenose dolphins (*Tursiops truncatus*) off St. Augustine, Florida. *Mar Mamm Sci* 25:970–975
- Karniski C, Patterson EM, Krzyszczyk E, Foroughirad V, Stanton MA, Mann J (2015) A comparison of survey and focal follow methods for estimating individual activity budgets of cetaceans. *Mar Mamm Sci* 31:839–852
- Keller L, Waller D (2002) Inbreeding effects in wild populations. *Trends Ecol Evol* 17:230–241
- Kemper CM, Trentin E, Tomo I (2014) Sexual maturity in male Indo-Pacific bottlenose dolphins (*Tursiops aduncus*): evidence for regressed/pathological adults. *J Mammal* 95:357–368
- Krützen M, Barré LM, Connor RC, Mann J, Sherwin WB (2004) ‘O father: where art thou?’—paternity assessment in an open fission–fusion society of wild bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia. *Mol Ecol* 13:1975–1990
- Krzyszczyk E, Mann J (2012) Why become speckled? Ontogeny and function of speckling in Shark Bay bottlenose dolphins (*Tursiops* sp.). *Mar Mamm Sci* 28(2):295–307
- Lacave G, Eggemont M, Verslycke T, Brook F, Salbany A, Roque L, Kinoshita R (2004) Prediction from ultrasonographic measurements of the expected delivery date in two species of bottlenosed dolphin (*Tursiops truncatus* and *Tursiops aduncus*). *Vet Rec* 154:228–233
- Loy J (1974) Changes in facial color associated with pregnancy in patas monkeys. *Folia Primatol* 22:251–257
- Lu A, Beehner JC, Czekala NM, Borries C (2012) Juggling priorities: female mating tactics in Phayre’s leaf monkeys. *Am J Primatol* 74: 471–481
- Lukas D, Huchard E (2014) The evolution of infanticide by males in mammalian societies. *Science* 346:841–844
- Mann J (1999) Behavioral sampling methods for cetaceans: a review and critique. *Mar Mamm Sci* 15:102–122

- Mann J (2006) Establishing trust: socio-sexual behaviour and the development of male-male bonds among Indian Ocean bottlenose dolphins. In: Sommer V, Vasey PL (eds) Homosexual behaviour in animals: an evolutionary perspective. Cambridge University press, pp 107–130
- Mann J, Sargeant B (2003) Like mother, like calf: the ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (*Tursiops* sp.) In: Fragaszy D, Perry S (eds) The biology of traditions. Cambridge University Press, Cambridge, pp 236–266
- Mann J, Smuts B (1999) Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour* 136:529–566
- Mann J, Connor RC, Barré LM, Heithaus MR (2000) Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. *Behav Ecol* 11:210–219
- Mateo JM (2004) Recognition systems and biological organization: the perception component of social recognition. *Ann Zool Fenn* 41: 729–745
- McHugh KA, Allen JB, Barleycorn AA, Wells RS (2011) Natal philopatry, ranging behavior, and habitat selection of juvenile bottlenose dolphins in Sarasota Bay, Florida. *J Mammal* 92:1298–1313
- Millsbaugh JJ, Washburn BE (2004) Use of fecal glucocorticoid metabolite measures in conservation biology research: considerations for application and interpretation. *Gen Comp Endocrinol* 138:189–199
- Möller LM, Beheregaray LB (2004) Genetic evidence for sex-biased dispersal in resident bottlenose dolphins (*Tursiops aduncus*). *Mol Ecol* 13:1607–1612
- Moore J, Ali R (1984) Are dispersal and inbreeding avoidance related? *Anim Behav* 32:94–112
- Muggeo VM (2003) Estimating regression models with unknown breakpoints. *Stat Med* 22:3055–3071
- Muggeo VM (2008) Segmented: an R package to fit regression models with broken-line relationships. *R News* 8:20–25
- Muller MN, Thompson ME, Kahlenberg SM, Wrangham RW (2011) Sexual coercion by male chimpanzees shows that female choice may be more apparent than real. *Behav Ecol Sociobiol* 65:921–933
- Muraco HS (2015) Reproductive biology of the female bottlenose dolphin (*Tursiops truncatus*). Dissertation, Mississippi State University
- Muraco H, Kuczaj SA (2015) Conceptive estrus behavior in three bottlenose dolphins (*Tursiops truncatus*). *Anim Behav Cogn* 2:30–48
- Nuutila HK, Courteney-Jones W, Baulch S, Simon M, Evans PG (2017) Don't forget the porpoise: acoustic monitoring reveals fine scale temporal variation between bottlenose dolphin and harbour porpoise in Cardigan Bay SAC. *Mar Biol* 164:50
- O'Brien JK, Robeck TR (2012) The relationship of maternal characteristics and circulating progesterone concentrations with reproductive outcome in the bottlenose dolphin (*Tursiops truncatus*) after artificial insemination, with and without ovulation induction, and natural breeding. *Theriogenology* 78:469–482
- Ottensmeyer CA, Whitehead H (2003) Behavioural evidence for social units in long-finned pilot whales. *Can J Zool* 81:1327–1338
- Pagel MD, Harvey PH (2002) Evolution of the juvenile period in mammals. In: Pereira ME, Fairbanks LA (eds) Juvenile primates: life history, development, and behavior. University of Chicago Press, Chicago, pp 28–37
- Patterson IAP, Reid RJ, Wilson B, Grellier K, Ross HM, Thompson PM (1998) Evidence for infanticide in bottlenose dolphins: an explanation for violent interactions with harbour porpoises? *Proc R Soc Lond B* 265:1167–1170
- Penn DJ (2002) The scent of genetic compatibility: sexual selection and the major histocompatibility complex. *Ethology* 108:1–21
- Perez S, Garcia-Lopez A, De Stephanis R, Gimenez J, Garcia-Tiscar S, Verborgh P, Mancera JM, Martinez-Rodriguez G (2011) Use of blubber levels of progesterone to determine pregnancy in free-ranging live cetaceans. *Mar Biol* 158:1677–1680
- Perrtree RM, Sayigh LS, Williford A, Bocconcelli A, Curran MC, Cox TM (2016) First observed wild birth and acoustic record of a possible infanticide attempt on a common bottlenose dolphin (*Tursiops truncatus*). *Mar Mamm Sci* 32:376–385
- Pilot M, Dahlheim ME, Hoelzel AR (2010) Social cohesion among kin, gene flow without dispersal and the evolution of population genetic structure in the killer whale (*Orcinus orca*). *J Evol Biol* 23:20–31
- Preis A, Mugisha L, Hauser B, Weltring A, Deschner T (2011) Androgen and androgen metabolite levels in serum and urine of east African chimpanzees (*Pan troglodytes schweinfurthii*): comparison of EIA and LC-MS analyses. *Gen Comp Endocrinol* 174:335–343
- Pusey AE, Packer C (1987) Dispersal and philopatry. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate Societies. University of Chicago Press, Chicago, pp 250–266
- Pusey A, Wolf M (1996) Inbreeding avoidance in animals. *Trends Ecol Evol* 11:201–206
- Read AJ, Wells RS, Hohn AA, Scott MD (1993) Patterns of growth in wild bottlenose dolphins, *Tursiops truncatus*. *J Zool* 231:107–123
- Robeck TR, Schneyer AL, McBain JF, Dalton LM, Walsh MT, Czekala NM, Kraemer DC (1993) Analysis of urinary immunoreactive steroid metabolites and gonadotropins for characterization of the estrous cycle, breeding period, and seasonal estrous activity of captive killer whales (*Orcinus orca*). *Zoo Biol* 12:173–187
- Robeck TR, Steinman KJ, Yoshioka M, Jensen E, O'Brien JK, Katsumata E, Gili C, McBain JF, Sweeney J, Monfort SL (2005) Estrous cycle characterisation and artificial insemination using frozen-thawed spermatozoa in the bottlenose dolphin (*Tursiops truncatus*). *Reproduction* 129:659–674
- Robinson KP (2014) Agonistic intraspecific behavior in free-ranging bottlenose dolphins: calf-directed aggression and infanticidal tendencies by adult males. *Mar Mamm Sci* 30:381–388
- Rolland RM, Hunt KE, Kraus SD, Wasser SK (2005) Assessing reproductive status of right whales (*Eubalaena glacialis*) using fecal hormone metabolites. *Gen Comp Endocrinol* 142:308–317
- Rowell TE, Chalmers NR (1970) Reproductive cycles of the mangabey *Cercocebus albigena*. *Folia Primatol* 12:264–272
- Sandel AA, Reddy RB, Mitani JC (2017) Adolescent male chimpanzees do not form a dominance hierarchy with their peers. *Primates* 58:39–49
- Sargeant BL, Mann J (2009) Developmental evidence for foraging traditions in wild bottlenose dolphins. *Anim Behav* 78:715–721
- Sargeant BL, Wirsing AJ, Heithaus MR, Mann J (2007) Can environmental heterogeneity explain individual foraging variation in wild bottlenose dolphins (*Tursiops* sp.)? *Behav Ecol Sociobiol* 61:679–688
- Schroeder PJ (1990) Breeding bottlenose dolphins in captivity. In: Leatherwood S, Reeves RR (eds) The bottlenose dolphin. Academic Press, New York, pp 435–446
- Scott E, Mann J, Watson-Capps JJ (2005) Aggression in bottlenose dolphins: evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behaviour. *Behaviour* 142:21–44
- Setchell JM, Wickings EJ, Knapp LA (2006) Signal content of red facial coloration in female mandrills (*Mandrillus sphinx*). *Proc R Soc Lond B* 273:2395–2400
- Smolker RA, Richards AF, Connor RC, Pepper JW (1992) Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour* 123:38–69
- Stanton MA, Mann J (2012) Early social networks predict survival in wild bottlenose dolphins. *PLoS One* 7:e47508
- Szulkin M, Stopher KV, Pemberton JM, Reid JM (2013) Inbreeding avoidance, tolerance, or preference in animals? *Trends Ecol Evol* 28:205–211
- Tsai YJ, Mann J (2013) Dispersal, philopatry, and the role of fission-fusion dynamics in bottlenose dolphins. *Mar Mamm Sci* 29:261–279
- van Schaik CP, Pradhan GR, van Noordwijk MA (2004) Mating conflict in primates: infanticide, sexual harassment and female sexuality. In:

- Kappeler PM, van Schaik CP (eds) Sexual selection in primates: new and comparative perspectives. Cambridge University Press, Cambridge, pp 131–150
- Wallen MM, Patterson EM, Krzyszczyk E, Mann J (2016) The ecological costs to females in a system with allied sexual coercion. *Anim Behav* 115:227–236
- Watson-Capps JJ (2005) Female mating behavior in the context of sexual coercion and female ranging behavior of bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia. Dissertation, Georgetown University
- Watts DP (2015) Mating behavior of adolescent male chimpanzees (*Pan troglodytes*) at Ngogo, Kibale National Park, Uganda. *Primates* 56: 163–172
- Wells RS (1991) The role of long-term study in understanding the social structure of a bottlenose dolphin community. In: Pryor K, Norris KS (eds) *Dolphin societies: discoveries and puzzles*. University of California Press, Berkeley, pp 199–225
- Wells RS (2014) Social structure and life history of common bottlenose dolphins near Sarasota Bay, Florida: insights from four decades and five generations. In: Yamigawa J, Karczmarski L (eds) *Primates and cetaceans: field research and conservation of complex mammalian societies*. Springer Press, Tokyo, pp 149–172
- Wells RS, Scott MD (1990) Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. In: Hammond PS, Mizroch SA, Donovan GP (eds) *Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters*. Report of the international whaling commission, special issue 12, Cambridge, pp 407–415
- Wells RS, Scott MD, Irvine AB (1987) The social structure of free-ranging bottlenose dolphins. In: Genoways HH (ed) *Current Mammalogy*. Springer US, pp 247–305
- Wells RS, Rhinehart HL, Hansen LJ, Sweeney JC, Townsend FI, Stone R, Casper DR, Scott MD, Hohn AA, Rowles TK (2004) Bottlenose dolphins as marine ecosystem sentinels: developing a health monitoring system. *EcoHealth* 1:246–254
- Whitehead H, Christal J, Tyack PL (2000) Studying cetacean social structure in space and time. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds) *Cetacean Societies*. University of Chicago Press, Chicago, pp 65–87
- Wilson B, Thompson PM, Hammond PS (1997) Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *J Appl Ecol* 34:1365–1374
- Wright BM, Stredulinsky EH, Ellis GM, Ford JKB (2016) Kin-directed food sharing promotes lifetime natal philopatry of both sexes in a population of 2 fish-eating killer whales (*Orcinus orca*). *Anim Behav* 115:81–95
- Xu R (2003) Measuring explained variation in linear mixed effects models. *Stat Med* 22:3527–3541
- Yuen WHQ (2007) An assessment of reproductive development of the male Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, in captivity. Dissertation, The Hong Kong Polytechnic University

Data availability statement

The datasets analyzed during the current study are available from the corresponding author on reasonable request.