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Original Article

Sexual segregation in Indo-Pacific bottlenose dolphins is driven by female avoidance of males

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Sexual segregation is widespread in mammals, although the proximate causes are poorly understood in monomorphic species. Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), which exhibit a high degree of fission–fusion dynamics, offer a useful lens to examine the ecological and social drivers of sexual segregation. While ecological hypotheses suggest that sexual segregation is a by-product of sex-specific ecological preferences (e.g., related to habitat, foraging, or predator avoidance), the social hypothesis proffers that segregation results from same-sex preferences (e.g., due to cooperative benefits) and/or opposite-sex avoidance (e.g., due to competitive or exploitative interactions). Indo-Pacific bottlenose dolphin females range from nearly solitary to highly sociable. Males associate in alliances that cooperate to sequester individual females and exclude competing males. Given evidence for allied sexual coercion, our primary hypothesis was that sexual segregation is driven by female avoidance of aggressive males. However, given robust evidence for sex-biased foraging tactics, ecological factors likely also contribute. Using the Sexual Segregation and Aggregation Statistic with 17,468 sighting records spanning 31 years, we found strong sexual segregation. Unique to our work, we analyzed the direction of joins and leaves between males and females from focal observations ($N = 10{,}715$ fission–fusion events, 87 females, 111 males) to determine which sex drives sexual segregation. Females drove segregation by rarely joining and often leaving males. Although ecological factors likely reinforce sexual segregation, social factors predominate. This study demonstrates a sex-bias in fission–fusion dynamics in a socially complex wild mammal population and offers strong empirical support to the social hypothesis of sexual segregation.

Key words: **avoidance, fission–fusion, sexual conflict, sex differences, sexual segregation, social behavior.**

INTRODUCTION

Sexual segregation is the separation of males and females into different groups, whether by social segregation or differential use of habitats or area (Conradt 1998). The occurrence and degree of sexual segregation in a population is largely driven by the degree of sexual dimorphism and differences between the sexes in reproductive strategies, which in turn cause intersexual differences in predation risk, dietary requirements, social preferences, and activity budgets (Conradt and Roper 2000; Ruckstuhl and Neuhaus 2000). Sexual segregation is common in many group-living species (reviewed in Ruckstuhl and Neuhaus 2005; Wearmouth and Sims 2008), including ungulates (Main et al. 1996; Ruckstuhl and Neuhaus 2000), primates (Ruckstuhl and Neuhaus 2005), and cetaceans (Brown et al. 1995; Gowans et al. 2001; Martin and da Silva 2004; reviewed in Wearmouth and Sims 2008). Sexual segregation has also been described in bottlenose dolphins (*Tursiops truncatus* and *T. aduncus*) (Wells et al. 1987; Smolker et al. 1992; Fury et al. 2013; Wallen et al. 2016; but see Lusseau et al. 2003). In a small population of *T. aduncus* studied over a 3-year period, Fury et al. (2013) found that female and mixed-sex groups differ in habitat use and activity budget, and that a large proportion of mixed-sex social interactions involved aggressive behavior. This suggests that activity budgets and social factors may drive segregation. However, the drivers and degree of sexual segregation in bottlenose dolphins have never been formally tested using a metric that controls for variables such as group size and sex ratio (see Conradt 1998; Bonenfant et al. 2007), or by examining which sex drives segregation. Determining which sex drives segregation has been neglected in the sexual segregation literature as a whole, and can provide insights into the evolution of sociality and sexual segregation.

Sexual segregation is an important component of social organization in group-living species. Although group living offers a variety of potential benefits, such as reduced predation risk (Neill and Cullen 1974; Hill and Lee 1998) and communal defense of

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resources (Gray et al. 2002), group living is contingent on group stability. Group stability can be compromised when individuals differ in what ecological conditions or behaviors maximize their fitness, as social organization is driven by the behavior of individuals (Hinde 1976; Conradt and Roper 2000; Kappeler and van Schaik 2002). The fitness optima and reproductive strategies of males and females can differ for a variety of reasons (Parker 1979; Chapman et al. 2003), and these differences can lead to sexual segregation.

While sex-specific reproductive strategies, including sexual dimorphism, are ultimate factors driving sexual segregation, ecological factors (predation risk, diet, activity budget) and social preferences are important proximate explanations. In general, females' energetic demands are higher than males', and they are more sensitive to predation risk than males because of differential investment in offspring (Clutton-Brock and Parker 1992). In addition, intrasexual competition, typically contest competition, leads to greater male than female aggression (Clutton-Brock and Parker 1992) and sexual dimorphism, which can impact predation risk (e.g., Bildstein et al. 1989), activity budget (Ruckstuhl 1998), and diet (Demment and van Soest 1985). These factors are the basis for the major ecological and social hypotheses explaining the occurrence of sexual segregation: the *predation risk hypothesis,* the *forage selection hypothesis,* the *activity budget hypothesis*, and the *social hypothesis* (reviewed in Main et al. 1996; Ruckstuhl and Neuhaus 2000).

The *predation risk hypothesis* predicts that whichever sex is more vulnerable to predation, whether directly if smaller in size or indirectly through protection of offspring, may forgo optimal foraging locations to minimize predation risk on themselves and/or their offspring (Main et al. 1996; Bleich et al. 1997; Ruckstuhl and Neuhaus 2000). This can result in habitat segregation of the sexes based on relative predation risk. For example, in desert bighorn sheep (*Ovis canadensis*), females with calves preferentially select habitats with the fewest predators, despite the inferior nutritional quality of these habitats (Bleich et al. 1997). A similar pattern can be seen in female giraffe (*Giraffa camelopardalis*) and female rocky mountain mule deer (*Odocoileus hemionus*) (Young and Isbell 1991; Main and Coblentz 1996). In Trinidadian guppies (*Poecilia reticulata*), in which females have a larger maximum body size than males, males preferentially use low-predation risk shallow-water habitats while females remain in deep-water habitats (Croft et al. 2006).

Under the *forage selection hypothesis*, sex differences in energy requirements will lead to segregated habitat use based on food availability (Main et al. 1996; Ruckstuhl and Neuhaus 2000). Sex differences in dietary requirements may stem from sexual dimorphism or special requirements during lactation or gestation (Main et al. 1996; Ruckstuhl and Neuhaus 2000). For example, in African elephants (*Loxodonta africana*), females target higher quality food sources than males, likely due to the high energetic demands of reproduction (Shannon et al. 2006).

The *activity budget hypothesis* proposes that if the sexes have different activity budgets, same-sex groups will have a greater degree of passive activity synchronization, which promotes continued group cohesion (Conradt and Roper 2000; Ruckstuhl and Neuhaus 2000). This can result in habitat, spatial, or social segregation of the sexes. For example, female spider monkeys (*Ateles geoffroyi*) feed and rest more than males, while males spend more time travelling (Hartwell et al. 2014). These differing activity budgets lead to reduced stability of mixed-sex groups, resulting in sexual segregation (Hartwell et al. 2014). In feral goats (*Capra hircus*), differences between the sexes in time spent foraging lead to the disbanding of mixed-sex groups (Calhim et al. 2006). In Tibetan argali (*Ovis ammon*), segregation is largely driven by females spending more time displaying vigilance, while males spend more time resting and feeding (Singh et al. 2010). Monomorphic species are less likely to have sex differences in activity budget. For example, the African oryx (*Oryx gazelle*) exhibits sex segregation but no sex differences in activity budget (Ruckstuhl and Neuhaus 2009). This suggests that body size is an important factor explaining activity budget, though sex differences in activity budget can also manifest from antipredation tactics and energetic or dietary needs.

Finally, the *social hypothesis* proposes that segregation is the result of social affinity for same-sex groups and/or aversion between the 2 sexes (Wearmouth and Sims 2008). In other words, sexual segregation is driven by social behavior and preferences as opposed to being a by-product of ecologically driven differences in behavior. For example, male–male affinity might favor the development of fighting skills and dominance hierarchies (Main et al. 1996), and females might avoid males due to intersexual aggression driven by differences in optimum mating strategies between the sexes (Parker 2006). For example, female grizzly bears likely avoid males because males are infanticidal and aggressive towards competitors for food (Wielgus and Bunnell 1994). In red deer (*Cervus elaphus*), males threaten females trying to escape harems through kicks, vocalizations, or by threatening them with antlers (Clutton-Brock et al. 1982). In sperm whales (*Physeter macrocephalus*), female kin assist each other in calf care and protection (Gero et al. 2009). Female lions (*Panthera leo*) engage in communal nursing, care and defense of cubs from infanticidal males (Packer and Pusey 1983; Pusey and Packer 1994). In some species, male aggression can result in both female avoidance of males and female–female affiliation, especially if female groups can deter male aggression.

A critical way to test these hypotheses is to examine how group composition and size fluctuate through time based on changing ecological and social conditions, as in societies with a high degree of fission–fusion dynamics (Aureli et al. 2008). Species that exhibit both sexual segregation and a high degree of fission–fusion dynamics include spider monkeys (*Ateles* spp., Symington 1990; Hartwell et al. 2014), African elephants (*Loxodonta Africana*, Stokke and du Toit 2002; Wittemyer et al. 2005), and bottlenose dolphins (*Tursiops truncatus* and *T. aduncus*, Wilson 1995; Bearzi et al. 1997; Connor et al. 2000).

Both sexual segregation (Smolker et al. 1992; Wallen et al. 2016) and a high degree of fission–fusion dynamics (Connor et al. 2000) are characteristic of the Indo-Pacific bottlenose dolphins of Shark Bay, Australia, although the degree of sexual segregation has never been formally tested using a metric that controls for group size and sex ratio. In this population, same-sex bonds are common, while opposite-sex bonds are weak or absent (Smolker et al. 1992; Mann et al. 2012). Males form long-term alliances with other males in which they cooperate to aggressively sequester cycling females (Smolker et al. 1992), and associate in alliances even when not in consortships with females (Connor et al. 1992). Harassment by male alliances is costly to females (Scott et al. 2005; Wallen et al. 2016). Females are typically found alone or in all-female groups (Wallen et al. 2016), have strong bonds with their offspring, especially daughters (Mann et al. 2000; Tsai and Mann 2013), and form female-dominated networks (Smolker et al. 1992; Mann et al. 2012). Mother-calf groups typically include juvenile and adult females, but few juvenile or adult males (Gibson and Mann 2008). In general, females are more solitary than males, and males are more cliquish (Mann et al. 2012). Because of sexual coercion in this population, our primary hypothesis is that female avoidance of males drives sex segregation, consistent with the *social hypothesis*.

Risk of tiger shark (*Galeocerdo cuvier*) attack is high among Shark Bay bottlenose dolphins (Heithaus 2001). Although tiger sharks disproportionately use shallow habitats and are in high abundance in the warmer months (September through May), dolphin habitat use does not differ by sex when sharks are abundant (Heithaus and Dill 2002), indicating that predation does not drive habitat segregation, but social segregation may result from females with calves associating with one another for calf protection (Mann et al. 2000; Gibson and Mann 2008).

Although there are clear sex differences in foraging behavior (e.g., Sargeant et al. 2005; Mann et al. 2008, 2012; Mann and Patterson 2013), most foraging behavior is solitary (Mann and Sargeant 2003), so foraging would not drive same-sex affiliation by itself. In addition, the *forage selection hypothesis* proffers that foraging differences should result in habitat or spatial segregation, but there is complete overlap in habitats used by males and females, though females tend to specialize while males tend to use more habitats (Patterson 2012). Consequently, the *forage selection hypothesis* does not seem to be a driving force in sex segregation per se, although differences in foraging might impact activity budgets and therefore impact the degree to which males and females associate in groups. Additionally, females have higher energetic demands due to lactation, and are predicted to spend more time foraging alone than males. This may influence the degree to which females join and leave groups relative to males, but not which sex they affiliate with. That said, there is some evidence that females preferentially affiliate with other females that use the same foraging tactics, even when habitat use is controlled for (Mann et al. 2012). This suggests a cultural bias, more than one driven by sex.

Given overt sexual conflict, solitary foraging, and the lack of habitat segregation, our major hypothesis is that sex segregation is driven by social factors. Specifically, we predict that female avoidance of males is the primary driver of segregation. Very few studies have studied avoidance (Strickland et al. 2017), and here we directly assess avoidance by analyzing the direction of joins and leaves between males and females. Same-sex preferences likely also reinforce segregation. First, male–male preference is obviously driven by the benefits of male–male alliance formation, as few males achieve mating success unless they are in an alliance (Krützen et al. 2004), and they are likely vulnerable to attacks by other males when on their own. Similarly, female–female preference might be favored by mutual interests in information sharing, calf protection, and skill development (Gibson and Mann 2008). In fact, females with high calving success preferentially associate with each other (Frère et al. 2010).

To date, the *social hypothesis* for sex segregation has received little support, possibly because most studies have focused on sexually dimorphic species. Our study population is an ideal candidate to test the *social hypothesis* given the high rate of fission–fusion dynamics and *lack* of sexual dimorphism. By directly testing for a sex-bias in fission–fusion dynamics, we explicitly evaluate if one sex disproportionately drives sex segregation. It is likely that more than one factor favors sex segregation in a population, especially one marked by social complexity and high fission–fusion dynamics, so we also assess the *activity budget hypothesis* given evidence of sex-specific foraging strategies.

METHODS

Study site and data collection

The Shark Bay Dolphin Research Project (SBDRP) has collected demographic, behavioral, genetic, and ecological data from a population of over 1600 Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) from the eastern gulf of Shark Bay, Australia (25°47′S, 113°43′E) since 1984. The remote study site is a UNESCO World Heritage Site with low anthropogenic influence. Shark Bay dolphins do not exhibit obvious sexual dimorphism.

This study used 17,468 opportunistic boat-based surveys collected from 1985 to 2015. We define a survey as a sighting of a group of dolphins in which group composition and predominant group activity are determined through a 5-min scan sample (Karniski et al. 2015). Most surveys were 5 min in length. Anywhere from 1 to 25 surveys were conducted on a typical day of boat-based sampling. Sampling days ranged in duration from 1 to 12 h depending on weather conditions. Group membership was based on the 10 m chain rule, in which individuals within 10 m of one another were considered to be in the same group (Smolker et al. 1992). Individuals were identified via dorsal fin photo identification (Würsig and Jefferson 1990). The sex of each individual was determined by views of the genital area, presence of a dependent calf, and/or genetics (Mann et al. 2000; Krützen et al. 2002). Age was determined based on known birth date (Mann et al. 2000), physical size, or degree of ventral speckling (Krzyszczyk and Mann 2012). Adults were defined as all individuals older than age 10, as this is the age of earliest pregnancy (Mann et al. 2000; unpublished data). In the current analysis, 440 adults (228 females, 212 males) were included. Adults of unknown sex ($N = 25$) were excluded from analyses and groups with individuals of unknown sex were also excluded. We used survey data to quantify the degree of sexual segregation in the population and assess sex differences in activity budget.

This study also used 1031 focal follows on 257 individuals collected from 1988 to 2016, totaling 2485 h of observation. While surveys are “snapshots” of opportunistically sighted groups of dolphins, focal follows provide detailed quantitative behavioral data on a focal individual. Focal follows were initiated on individual dolphins, mostly adult females or mother–calf pairs from an a priori target list (depending on the specific research project). The behavioral activity state of the focal animal(s) was recorded through point sampling at minute intervals for a duration determined a priori. Follow length ranged from 30 min to 9.75 h. Group composition was recorded for each minute and changes in group composition (including directionality) were recorded continuously (Karniski et al. 2015). As we had few follows of adult males, we used surveys rather than focal follow data to examine sex differences in activity budget. Focal follows, which quantify the direction of and changes in group membership, were used to detect sex-biases in fission–fusion dynamics.

Quantifying sexual segregation

To quantify the degree of sexual segregation, we included all surveys that included at least one adult individual and in which the sex of all adults was known (N = 17,468 surveys). Only adults sighted in the first 5 min of the survey were counted when determining group sex composition (228 females, 212 males).

We applied the Sexual Segregation and Aggregation Statistic (SSAS) developed by Bonenfant et al. (2007) to determine if our population displayed sexual segregation. The SSAS is calculated as follows:

$$SSAS = \frac{\chi^2}{N} = 1 - \frac{N}{XY}\sum_{i=1}^{k}\frac{X_iY_i}{N_i}$$

Where N = the total number of individuals, X = the total number of males, Y = the total number of females, k = the total number of groups, N_i = the total number of individuals in the ith group, X_i = the number of males in the ith group, and Y_i = the total number of females in the ith group. The SSAS is derived from the χ^2 statistic and Conradt's segregation coefficient (Conradt 1998). An SSAS value of 0 indicates complete aggregation, while a value of 1 indicates complete segregation.

The significance of the observed SSAS value is determined by comparing the observed value to the expected SSAS distribution based on the assumption of random association between individuals, in accordance with the population sex ratio (Bonenfant et al. 2007). To establish an expected distribution of SSAS values, we permuted our data while preserving row and column totals in order to retain group sizes and overall sex ratio. We calculated SSAS values for 999 permutations to establish an expected range of SSAS values assuming random association between individuals. An observed SSAS value that falls above or below this expected distribution is indicative of either sexual segregation or aggregation, respectively. An observed SSAS value that falls within the expected distribution is consistent with random association (Bonenfant et al. 2007).

We calculated the SSAS for our 30-year dataset as a whole, as well as subdividing our data by month (999 permutations per month) to consider how sexual segregation varies seasonally.

Determining directionality

To determine directionality, we analyzed 4952 join events and 5763 leave events from 1031 unique focal follows on 257 individuals. An individual "joins" another individual by approaching within 10 m, and "leaves" by moving greater than 10 m away. Determination of who joins and who leaves was based on orientation and swimming direction. Joins and leaves that were mutual or where directionality could not be determined (e.g., in large foraging groups) were excluded from analysis. To determine if there was a sex-bias in fission–fusion dynamics, we assessed the joins and leaves between 839 male–female dyads, representing 87 females and 111 males. We only included male–female dyads that had at least 5 join/leave interactions (as in Matsumoto-Oda 1999). We calculated the Hinde's index for each unique male–female dyad to quantify the directionality of joins and leaves (Hinde and Atkinson 1970). For any male–female dyad, a positive Hinde's index indicates that the male is responsible for maintaining proximity to the female (by often joining and not leaving her), while a negative value indicates that the female is responsible for maintaining proximity to the male.

The mean Hinde's index of all 839 male–female dyads was compared to an expected distribution of values generated through 10,000 permutations, each randomizing the sexes of all individuals, to determine if there was a significant sex-bias in the directionality of joins and leaves. A Hinde's index value that falls within this expected distribution indicates that there is no sex-bias in fission–fusion dynamics. A value greater than the expected distribution indicates that males are generally responsible for maintaining proximity to females, while a value less than the expected distribution indicates that females are generally responsible for maintaining proximity to males.

We repeated this analysis after subdividing our data into 4 categories: joins and leaves that occurred when one male and one female were present (N = 17 dyads, 14 males, 14 females, 126 joins and leaves), when one male and multiple females were present (N = 105 dyads, 25 males, 33 females, 1491 joins and leaves), when multiple males and one female were present (N = 57 dyads, 34 males, 15 females, 520 joins and leaves), and when multiple males and multiple females were present (N = 518 dyads, 73 males, 61 females, 6006 joins and leaves). Again, we only included male–female dyads that had at least 5 join/leave interactions in the given category.

Some individuals were present in more than one male–female dyad. To assess the potential effects of pseudoreplication, we generated 300 subsamples by randomly selecting one dyad for each individual represented in multiple dyads. We repeated our analyses on the 300 subsamples and found that the results were identical to our initial results using all 839 male–female dyads.

We also calculated the fission–fusion rate (number of joins/leaves per hour) for all focal individuals, including join or leave events between all age-sex classes and events of known, unknown, or mutual direction. When calculating the population mean fission–fusion rate, we removed focal individuals with less than 30 min of focal follow data.

Activity budget analyses

We compared the activity budgets of lone males (N = 77) and lone females (N = 101) including only adults of known sex with 5 or more surveys (N = 2993 surveys total), using a one-tailed permutation t-test with Monte Carlo sampling (permutations = 999).

We also compared the activity budgets of all male (N = 2680) and all female (N = 6328) groups of 2 or more individuals in which the primary activity was foraging, socializing, or resting (N = 9008 surveys). Traveling was excluded because this activity tends to be under-represented in survey data (Karniski et al. 2015). Only adults of known sex were included when determining group size and sex composition (374 females, 364 males). We assessed the effects of group size and group sex composition (all male or all female) on group activity (foraging, resting or socializing) using multinomial logistic regression. We fit our multinomial logistic regression model using the *multinom* function of the *nnet* package in R Studio Version 0.99.876. Our data met the assumption of no multicollinearity. The reference categories were "foraging" and "all female" for group activity and group sex composition, respectively.

RESULTS

Group size, composition, and activity budget

The adult M:F sex ratio of our population is 0.97 (N = 1003). The majority of surveyed groups consisted of 1 adult individual, with larger groups containing up to 45 adult individuals (Figure 1). As expected, the proportion of mixed sex groups increases with group size (Figure 2).

The frequency of resting (r_τ = 0.83, $P < 0.001$) and socializing (r_τ = 0.94, $P < 0.0001$) behaviors increased with group size, and the frequency of foraging behavior (r_τ = −0.67, $P < 0.05$) decreased with group size (Figure 3).

Lone females foraged more than lone males (1-tailed permutation t-test, $P = 0.001$) and lone males rested more than lone females (1-tailed permutation t-test, $P = 0.003$). As group size increased, both sexes were more likely to socialize ($z = 25.7$, $P < 0.0001$) or rest ($z = 31.7$, $P < 0.0001$) rather than forage (Table 1, Figure 4). All-male groups were more likely to socialize ($z = 5.33$, $P < 0.0001$) and less likely to rest ($z = -6.66$, $P < 0.0001$) than all-female groups (Figure 4).

Sexual segregation and fission–fusion dynamics

Our population exhibited consistent and marked sexual segregation regardless of season (Figure 5). As might be expected,

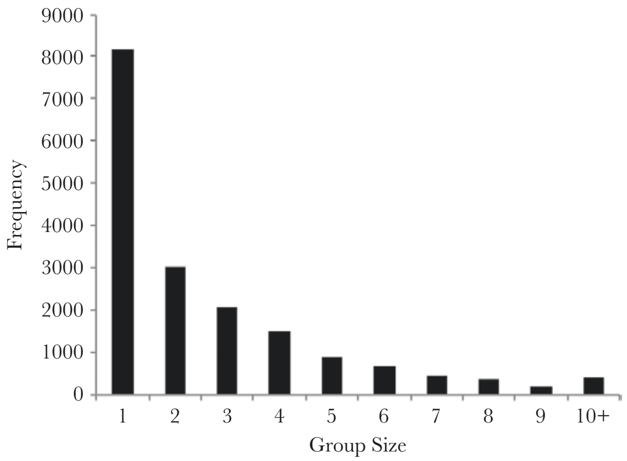

Figure 1

Histogram of group sizes of surveyed bottlenose dolphin groups. Group size only includes adults. The largest surveyed group included 45 adults. Includes 17,468 surveys collected in Shark Bay, Australia from 1985 to 2015. Mean (± SE) adult group size was 2.7 ± 0.05.

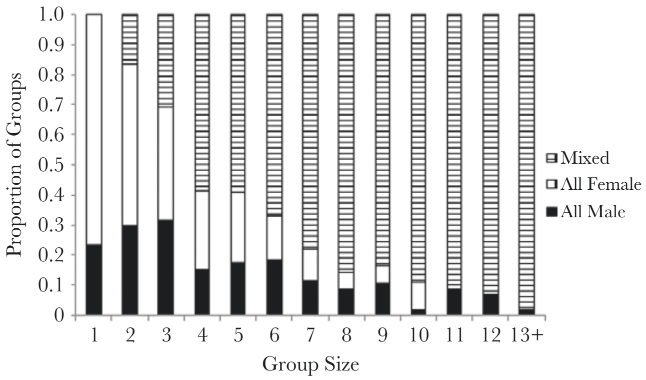

Figure 2

Group sex composition as a function of group size. $N = 17,468$ surveys.

there is a small but nonsignificant dip in sex-segregation during the breeding season (September to January, Mann et al. 2000; Wallen et al. 2017).

Overall dynamics

The mean (±SE) fission–fusion rate (or join-leave rate) for all focal individuals is 5.3 ± 0.21 joins/leaves per hour. Adult males joined adult females 3380 times and left females 2776 times. Adult females joined adult males 1572 times and left males 2987 times. The total number of joins and leaves is asymmetrical because mutual joins and leaves were excluded from analysis. Across 839 male–female dyads, 569 (68%) had positive Hinde's index values (male responsible for maintaining proximity), 165 (20%) had negative values (female responsible for maintaining proximity), and 105 (12%) had values of 0. The average Hinde's index (±SE) for all 839 dyads indicates that segregation is primarily driven by females often leaving and not joining males (Figure 6, Hinde = 0.198 ± 0.011, $P < 0.0001$).

Multi-male, multi-female groups

When multiple males and multiple females were present, males joined females 944 times and left females 1769 times. Females joined males 1202 times and left males 2091 times. Across 518 male–female dyads, 193 (37%) had positive Hinde's index values (male responsible for maintaining proximity), 270 (52%) had negative values (female responsible for maintaining proximity), and 55 (11%) had values of 0. No significant sex bias in joins and leaves was apparent (Figure 7a, Hinde = -0.029 ± 0.016, $P > 0.80$).

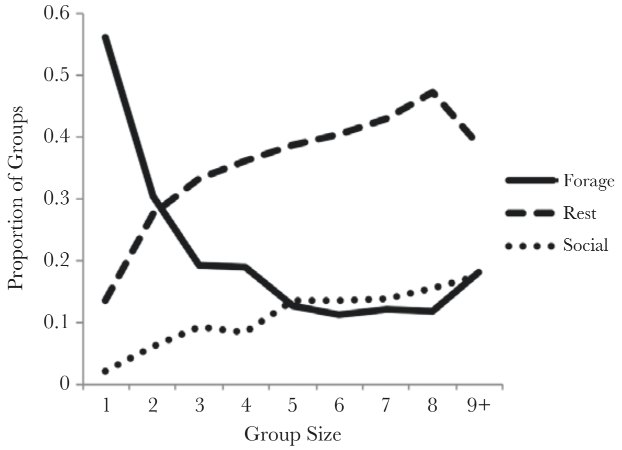

Figure 3

Proportion of groups engaged in resting, socializing, and foraging as a function of group size. Resting ($r_\tau = 0.83$, $P = 0.0009$) and socializing ($r_\tau = 0.94$, $P = 0.00005$) increased with adult group size and foraging ($r_\tau = -0.67$, $P = 0.013$) decreased with adult group size. $N = 17,468$ surveys. Activity based on predominant group activity.

Multi-male, single female groups

When multiple males and one female were present, males joined females 245 times and left females 144 times. Females joined males 10 times and left males 121 times. Across 57 male–female dyads, 43 (75%) had positive Hinde's index values (male responsible for maintaining proximity), 5 (9%) had negative values (female responsible for maintaining proximity), and 9 (16%) had values of 0. In these groups, males were responsible for maintaining proximity with females (Figure 7b, Hinde = 0.353 ± 0.046, $P < 0.0001$).

Single male, multi-female groups

When one male and multiple females were present, males joined females 783 times and left females 305 times. Females joined males 145 times and left males 258 times. Across 105 male–female dyads, 64 (61%) had positive Hinde's index values (male responsible for maintaining proximity), 20 (19%) had negative values (female responsible for maintaining proximity), and 21 (20%) had values of 0. In these groups, males were responsible for maintaining proximity with females (Figure 7c, Hinde = 0.212 ± 0.038, $P < 0.001$).

Single male, single female groups

When one male and one female were present, males joined females 69 times and left females 28 times. Females joined males 10 times and left males 19 times. Across 17 male–female dyads, 12 (71%) had positive Hinde's index values (male responsible for maintaining proximity), 2 (12%) had negative values (female responsible for maintaining proximity), and 3 (17%) had values of 0. In these groups, males were responsible for maintaining proximity to females (Figure 7d, Hinde = 0.271 ± 0.079, $P < 0.05$).

DISCUSSION

The majority of studies assessing the causes of sexual segregation focus largely on sexually dimorphic species, perhaps explaining why

Table 1

Results of multinomial logistic regression predicting group activity based on group size and group sex composition (all male or all female)

Group activity[a]		*B*-coefficient (log odds)	95% CI		SE	Wald (z)	*P*-value	Relative risk ratios
			2.5%	97.5%				
Rest	Intercept	−1.975	−2.070	−1.880	0.048	−40.8	<0.001	0.139
	All Male	−0.382	−0.494	−0.270	0.057	−6.66	<0.001	0.683
	Group Size	0.798	0.749	0.848	0.025	31.7	<0.001	2.221
Social	Intercept	−4.313	−4.501	−4.125	0.096	−45.0	<0.001	0.013
	All Male	0.553	0.350	0.757	0.104	5.33	<0.001	1.739
	Group Size	0.849	0.784	0.914	0.033	25.7	<0.001	2.338

[a] The reference categories are Forage and All Female.

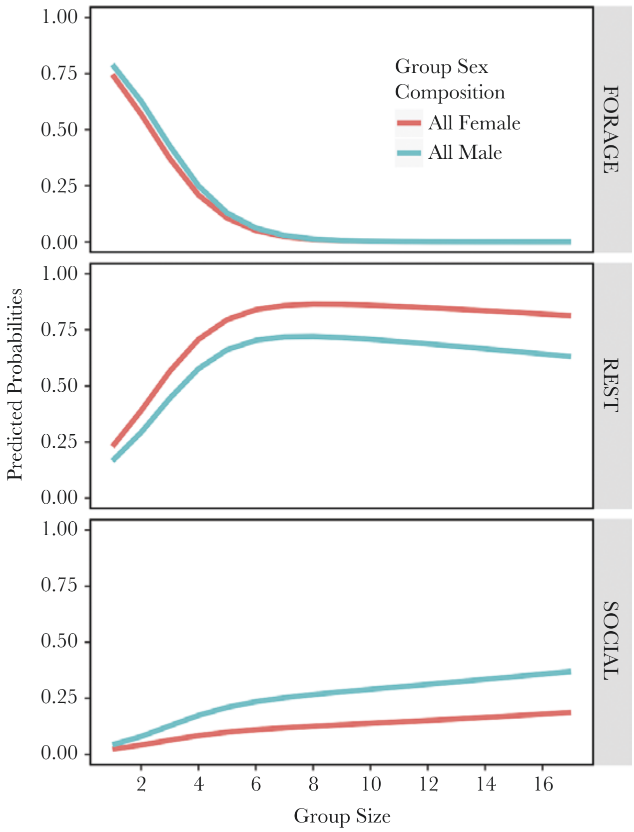

Figure 4

Predicted probabilities of group activity as a function of adult group size of either all male or all female groups, derived from a multinomial logistic regression model using "Foraging" and "All Female" as the reference categories.

more support has been found for ecological hypotheses than the social hypothesis (Main et al. 1996). Our focus on a socially complex species with minimal sexual dimorphism, paired with a dataset that allowed us to test directly for a sex-bias in fission–fusion dynamics, allowed us to assess the oft-neglected social hypothesis as well as the other hypotheses of sexual segregation. We found that our population exhibited consistent sexual segregation, including during the peak breeding season (September through January, Mann et al. 2000). This in unsurprising given that females nurse each calf for an average of 4 years (Mann et al. 2000), so only a small percentage of females are in estrous during each breeding season (Wallen et al. 2017).

Although the forage selection hypothesis is not supported given that most foraging is solitary (this study, Mann and Sargeant 2003) and there is little spatial or habitat segregation based on sex (Patterson 2012), lone females foraged more than lone males, and females spent more time alone than males (e.g., Mann et al. 2012). As group size increased, foraging behavior steadily dropped for both sexes (Figure 4). An interesting exception was large groups of 8 or more, where large foraging aggregations almost invariably of mixed sex were likely. In these instances, dolphins are feeding on large schools of fish. This is one of the few circumstances in which dolphins forage in groups in Shark Bay. In sum, although females forage more than males and have higher energetic demands due to lactation, this does not explain sex segregation in our population.

Resting became more likely as group size increased, and these were more likely to be mixed-sex groups. This suggests that dolphins of both sexes can benefit from group living (e.g., antipredation benefits; Heithaus and Dill 2002). It is notable that males were more likely to rest when alone than females, suggesting that some males may lack close associates to rest with (i.e., males that do not have alliance partners), and that females would rarely rest on their own given the risk to their dependent calves. In addition, all-female groups are more likely to rest than all-male groups. Females may target larger groups for resting more often than males because of communal calf protection from tiger sharks. All-male groups are more likely to socialize than female groups, suggesting that males generally join groups due to social competition (developing and maintaining bonds and competing for status within and between alliances) while females primarily join groups for protection.

We directly assessed the social hypothesis by analyzing the patterns of joins and leaves between individuals. One sex can drive segregation by often leaving and not joining individuals of the opposite sex. In contrast, if there is no sex-bias in join-leave dynamics, we can conclude that neither sex is disproportionately responsible for maintaining sexual segregation. Our findings indicate that females are responsible for maintaining sexual segregation in our population by often leaving and infrequently joining males. The presence of a sex-bias is consistent with the social hypothesis in that patterns of social preference and avoidance are explicitly responsible for maintaining sexual segregation, as opposed to sexual segregation being a byproduct of sex-specific ecological preferences. Previous work on our study population demonstrated same-sex preferences (Smolker et al. 1992; Gibson and Mann 2008; Mann et al. 2012), but our results also indicate opposite-sex avoidance in females (see also Strickland et al. 2017). Because females might be unable to leave male groups when they are cycling and in consortships due to male threats, these results are likely a conservative estimate of the degree of male-avoidance by females. This emphasizes

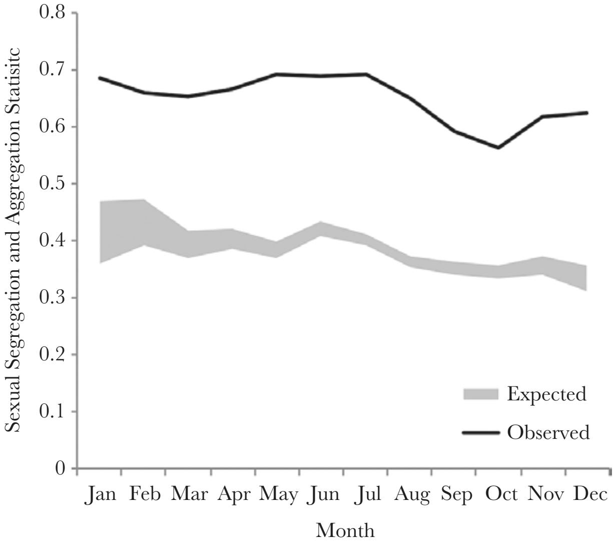

Figure 5

Sexual Segregation and Aggregation Statistic (SSAS) across seasons. The observed value consistently lies above the expected distribution, indicating sexual segregation. Monthly SSAS values were determined by aggregating all surveys of the same month from 1985 to 2015. The expected distribution assumes random association between individuals in accordance with the population sex ratio.

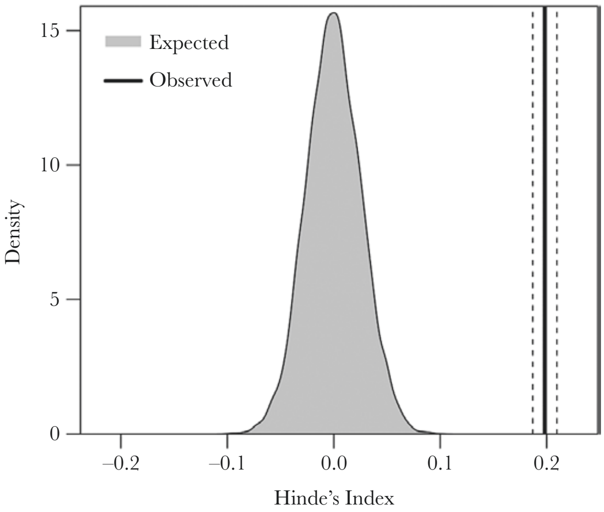

Figure 6

The mean (± SE) Hinde's index value of male–female dyads compared to the expected distribution. The mean Hinde's index value is greater than the expected distribution ($P < 0.0001$), indicating that males are responsible for maintaining proximity to females. The expected distribution was generated via 10,000 permutations, each randomizing the sexes of all individuals.

the importance of considering both same-sex preference and opposite-sex avoidance as driving factors for social segregation.

Other studies have used Hinde's index to show that males maintain proximity with females in primates (e.g., *Pan troglodytes*, Matsumoto-Oda 1999; Mysore slender lorises, *Loris lydekkerianus*, Nekaris 2006). Among ursids (grizzly bears, Wielgus 1994; polar bears Stirling et al. 1993), females appear to avoid males spatially, though group size and sex ratio were not controlled for. Our results further support this females-avoid-males model by explicitly showing that females are more likely to leave and not join males than vice versa.

While males were generally responsible for maintaining proximity to females in the population as a whole, this pattern varied by group composition. Males were responsible for maintaining proximity to females in: 1) lone-male, multi-female groups, 2) multi-male, lone-female groups, and 3) lone-male, lone-female groups. Neither sex was disproportionately responsible for maintaining proximity in groups with multiple males and multiple females. Behavioral differences in these groups can offer insight into the causes of the sex-bias in fission–fusion dynamics in the population as a whole.

Groups with multiple males and one female showed the most dramatic sex bias in fission–fusion dynamics. These are likely to be consortships, in which groups of males cooperate to aggressively sequester a female (Smolker et al. 1992). Consortships impose fitness costs on females (Scott et al. 2005; Wallen et al. 2016), giving lone females an obvious incentive to evade groups of males. Allied sexual coercion in the Shark Bay bottlenose dolphin mating system is clearly a central factor driving females to avoid male groups, especially when they are on their own. Male aggression, and particularly allied aggression, is a key factor explaining the observed sex-bias in fission–fusion dynamics and therefore sexual segregation. While lone-male, lone-female groups also exhibited a tendency for males to maintain proximity to females, the bias was much lower than when multiple males were present. Lone males might be less likely to be aggressive towards lone females given similar body size and capability. Lone males probably cannot successfully sequester or harass females on their own. Many years of observation suggest that lone males are likely to be affiliative (e.g., petting and rubbing) with females compared to when their alliance partners are present, but explicit study of this is needed. Although lone male-lone female pairs are rare, the fact that they occur provides some hint of modest social bonds between some adult males and females. Lone males may either be temporarily separated from their alliance partners, or not have alliance partners at all. At any given time, one-third of adult males are not in an alliance (defined by >0.50 coefficient of association; unpublished data). About 60% of the lone males that joined with lone females were not in alliances at the time, suggestive of an alternative strategy or other benefits for nonallied males.

Finally, we examined multi-male, multi-female groups, which did not exhibit a sex-bias in fission–fusion dynamics. As these groups were mostly larger, they were also likely to be resting groups or large foraging aggregations (this study). Since resting together provides more protection from tiger sharks (Heithaus and Dill 2002), both sexes would have an interest in resting in groups. Females might be more likely to benefit, given protection for their calves, potentially giving females an incentive to join males, especially if there are other females present. In large foraging aggregations, dolphins likely join groups to access large schools of fish, so social factors may have less of an impact on join-leave dynamics. Analyzing how male behaviors, particularly the rate of affiliative versus aggressive behaviors, changes with female cycling status and group composition, size, and activity could further reveal how much of an influence male aggression has on sexual segregation in Indo-Pacific bottlenose dolphins. To date, the data suggest that males are not particularly threatening to females as long as multiple females are present. It also suggests that female–female association mitigates sexual conflict in that multi-male, multi-female groups are the only circumstance where females do not avoid multi-male groups.

Our results likely also reflect same-sex preferences. Male–male associations are beneficial to males, as males are unlikely to achieve

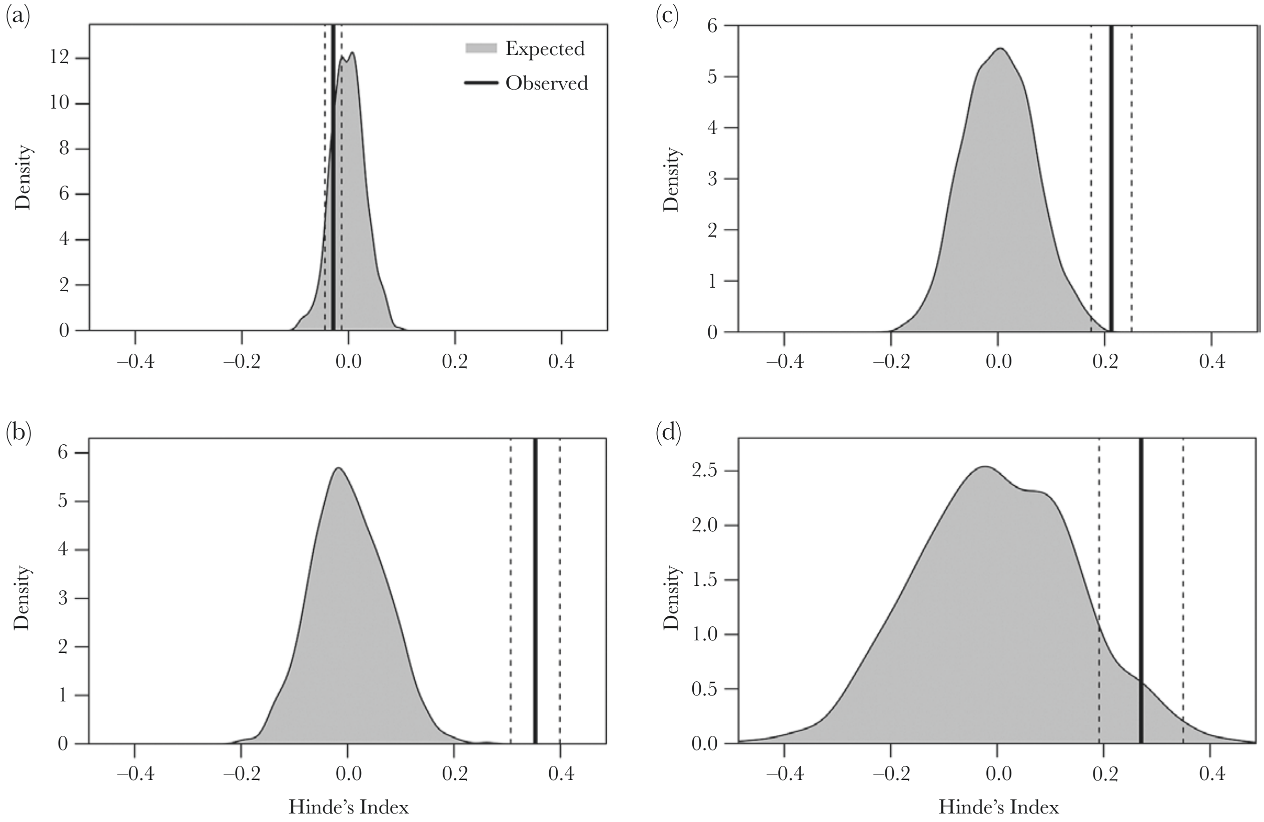

Figure 7

Mean (± SE) Hinde's index values of male–female dyads compared to expected distributions varies by group composition. (a) Groups of multiple males and females (Hinde = −0.029 ± 0.016, $P > 0.80$). (b) Groups of multiple males and one female (Hinde = 0.353 ± 0.046, $P < 0.0001$). (c) Groups of one male and multiple females (Hinde = 0.212 ± 0.038, $P < 0.001$). (d) Groups of one male and one female (Hinde = 0.271 ± 0.079, $P < 0.05$). Expected distributions were generated via 10,000 permutations, each randomizing the sexes of all individuals.

mating success if they are not in an alliance (Krützen et al. 2004). Females can benefit from same-sex associations through information sharing, calf protection, and skill development (Gibson and Mann 2008), resulting in greater calving success (Frère et al. 2010). Same-sex preferences without opposite-sex avoidance have been observed in Soay sheep (*Ovis aries*, Pérez-Barbería et al. 2005), but segregation in bottlenose dolphins in Shark Bay appears to be molded by a combination of both same-sex preferences and unidirectional avoidance of the opposite sex. Specifically, while both males and females can benefit from same-sex associations, females also benefit from actively avoiding the fitness costs of male harassment in mixed-sex groups. In contrast, males may actively seek out mixed-sex groups when attempting to sequester females. The consistent sex segregation in Shark Bay regardless of season suggests that females may regularly and successfully resist male harassment to some degree.

This study is the first to evaluate sex-biases in fission–fusion dynamics to directly assess which sex drives sexual segregation in a population. Our findings demonstrate 1) significant sexual segregation in Indo-Pacific bottlenose dolphins, using a metric that explicitly controls for group size and sex ratio, and 2) that this segregation is primarily driven by females often leaving and rarely joining males. Our results offer strong support to the oft-neglected social hypothesis of sexual segregation. Such support has been scarce compared to studies focusing on ecological hypotheses (but see Stirling et al. 1993 and Wielgus 1994), likely due to the emphasis on sexually dimorphic ungulates in the sexual segregation literature (Wearmouth and Sims 2008). Because sexual dimorphism is likely to amplify sex differences in foraging needs, predation risk, and activity budget, further studies of sexual segregation in monomorphic species may reveal the importance of social factors in the occurrence of sexual segregation. Given that social behaviors are key to explaining social structure, the lack of support for the social hypothesis of sexual segregation likely reflects a scarcity of robust behavioral data as opposed to a genuine lack of support.

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