ARTICLE

Marine Mammal Science

Fine-scale sociality reveals female–male affiliations and absence of male alliances in bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland

Isabel Baker[1,2] | Joanne O'Brien[1,2] | Katherine McHugh[3] | Simon Berrow[1,2]

[1]Marine and Freshwater Research Centre, Galway-Mayo Institute of Technology, Galway, Ireland

[2]Shannon Dolphin and Wildlife Foundation, Kilrush, County Clare, Ireland

[3]Sarasota Dolphin Research Program, Chicago Zoological Society, c/o Mote Marine Laboratory, Sarasota, Florida

Correspondence
Isabel Baker, Marine and Freshwater Research Centre, Galway-Mayo Institute of Technology, Dublin Road, Galway, Ireland
Email: izzybaker17@gmail.com

Abstract

Knowledge of social behavior at an individual level is central to our understanding of complex mammalian societies. In this study, we analyzed the fine-scale sociality of wild bottlenose dolphins in the Shannon Estuary, Ireland, by examining associations between members of the whole population and between specific female and male dolphins. We carried out 51 boat-based individual focal follows on 18 identifiable bottlenose dolphins over 90.8 hr (39 days) between 2014 and 2016. Additionally, we conducted 353 boat-based surveys (with 607 sightings) between 2012 and 2015, and identified 121 distinct adult/juvenile dolphins. The mean group size of focal dolphin groups was 7.2 ± 4.1 (range = 1–20) and the mean fission-fusion rate was 3.06 ± 1.35 changes/hr. The most frequent composition of within-group affiliate pairs was female–male. Focal males spent more time with female nearest-neighbors than male nearest-neighbors (p = .013). Differences between female and male activity budgets were not strongly supported (p = .13). There was no evidence for male alliance formation in the Shannon Estuary population, and all of the known-sex top-ranked associates (7) of known males (n = 10) were females. This research reveals a distinct bottlenose dolphin society with female–male affiliations and an absence of male alliances.

1 | INTRODUCTION

Knowledge of social behavior at an individual level is central to the understanding of the dynamics of social relationships (Karniski *et al.*, 2015; Mann, 1999). Coupled with network analyses of social structure at the population level (e.g., Baker, O'Brien, McHugh, Ingram, & Berrow, 2018b; Lusseau *et al.*, 2006), individual-specific data provide a deeper understanding of overall population dynamics by uncovering behavioral patterns among and between individual animals. To collect behavioral data on individuals, commonly used survey techniques can be supplemented with continuous behavioral observation sessions termed "focal follows" (Karniski *et al.*, 2015; McHugh, Allen, Barleycorn, & Wells, 2011b). During focal follows, fine-scale behavioral data are collected on individual focal animals and the groups of conspecifics in which they are found, including information on group size, activity states and positions of other individuals relative to the focal individual. While surveys are essential for gathering basic population information, focal follows allow researchers to gain much more detailed behavioral data (Altmann, 1974; Mann, 1999). For example, two individual animals might always be recorded as being in a group together, but if the group is not investigated further, it may never be known that they are always (or never) observed side by side.

Nearest-neighbor relationships provide a way of defining associations between two individuals that are distinct from that of basic group membership (Whitehead, 2008). These distinct measurements may then be used together to assess whether two individuals have a particularly strong association (a "bond"; Whitehead, 2008). Nearest-neighbor associations may have important biological significance; for example, they have been used to assess the behavioral effect on western gorillas (*Gorilla gorilla*) of the introduction of hand-reared infants into an established group (McCann & Rothman, 1999), and are likely to be of potential relevance to the analysis of mating strategies, dominance hierarchies, and social learning. In an analysis of within-group affiliations in juvenile bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida, McHugh (2010) found that individuals showed a marked preference for associating with other juveniles as nearest-neighbors, especially those of their own sex, further demonstrating the value of data collected through detailed within-group behavioral observations.

Noteworthy sex-specific behavioral differences may also be found when animals are studied at the individual level (Samuels 1996). Sex differences in behavior are likely to be most pronounced in the most dimorphic species (Magurran & Maciás Garcia, 2000; e.g., black howler monkeys [*Alouatta caraya*], Bicca-Marques & Calegaro-Marques, 1994); but even in monomorphic species, behavioral differences may result from differences in parental care (Clutton-Brock, 1991), particularly reflecting the different nutritional needs of lactating females (Clutton-Brock, 1977). Among primates, females of many species feed for longer periods than males, and in some species, females rest for longer periods too (Hemingway, 1999). Using focal follow techniques, Waples (1995) found that male bottlenose dolphins in Sarasota Bay engaged in more summertime traveling behavior than female dolphins, while females foraged, socialized, and rested more than males during the same period. In an analysis of the activity budgets of focal juvenile dolphins, McHugh (2010) found that males spent more than twice as much time socializing as females. In their study of survey vs. focal follow techniques, Karniski *et al.* (2015) determined that the sampling methods of focal follows better captured the sequence and transition of dolphin behaviors and thus produced a more complete picture of an individual's activity budget.

The examination of male–male and female–male associations can provide potential evidence for or against the formation of male alliances in a population. Previous studies have shown preferences for females to associate with

females and males with males in some bottlenose dolphin societies (e.g., McHugh, 2010; Samuels, 1996; Smolker, Richards, Connor, & Pepper, 1992). Complex sex-specific strategies exist, such as the formation of male dolphin alliances whereby males associate in long-term bonds in nested alliances and compete for access to receptive females (e.g., in Shark Bay, Western Australia, Connor, Wells, Mann, & Read, 2000; St John's River, Florida, Ermak, Brightwell, & Gibson, 2017). The formation of these alliances is therefore an important component of the mating systems in these populations (Connor and Krützen, 2015). In some other bottlenose dolphin societies, however, no evidence of male alliances has emerged (e.g., in Doubtful Sound, New Zealand, Lusseau *et al.*, 2003; the Sado Estuary, Portugal, Augusto, Rachinas-Lopes, & dos Santos, 2011; and in the northern Adriatic Sea, Genov, Centrih, Kotnjek, & Hace, 2019).

Photo-identification studies of bottlenose dolphins (*T. truncatus*) in the Shannon Estuary, Ireland, have been ongoing since 1993, resulting in the identification of many recognizable individuals (Berrow, O'Brien, Groth, Foley, & Voigt, 1996; Ingram, 2000) that show year-round presence (Berrow, 2009) and long-term site fidelity to the area (Berrow *et al.*, 2012, Levesque, Reusch, Baker, O'Brien, & Berrow, 2016). These studies have shown the population to be genetically discrete (Mirimin *et al.*, 2011). Recent research based on detailed records of cataloged individuals has estimated the extant population size to be 142 dolphins (Baker, O'Brien, McHugh, & Berrow, 2018a), with a fission-fusion social structure related to age class and area use (Baker *et al.*, 2018b). The Lower River Shannon was designated as a Special Area of Conservation (SAC) in 2000 under the EU Habitats Directive with bottlenose dolphins as a qualifying interest (National Parks and Wildlife Service [NPWS] 2012).

In this study, we report findings from the first focal follows of bottlenose dolphins in Ireland. We used an individual-follow protocol and two focal follow sampling techniques (interval and continuous sampling; Altmann, 1974; Mann, 1999) to collect behavioral data. We conducted these focal follows over three summers (May–September) from 2014 to 2016 and coupled them with a larger database of photo-id and related sightings data, based on surveys conducted between 2012 and 2015. The key aims of this study were: (1) to calculate the baseline measures of sociality for this population; (2) to examine individual-level affiliation patterns (i.e., potential nearest-neighbor preferences) within groups; (3) to test for sex-specific differences in activity budgets; and (4) to determine if any evidence existed for male alliance formation in the Shannon Estuary population. By addressing these questions, this work expands on previous research on the overall social structure and behavior of the population and illuminates interesting individual- and site-specific differences between the Shannon Estuary and other bottlenose dolphin populations.

2 | METHODS

2.1 | Study site

This study took place in the Lower River Shannon Special Area of Conservation (SAC; Site Code 002165), a 684 km^2 Natura 2000 designated site (NPWS 2012) on Ireland's west coast between County Clare, County Kerry, and County Limerick (52°36'N, 9°38'W), in which bottlenose dolphins are a qualifying interest (Figure 1).

2.2 | Data collection

Boat-based surveys occurred during daylight hours between March and November each year from 2012 to 2016 on board a dedicated research vessel, *Muc Mhara*, based in Kilrush, and two dolphin-watching tour boats, *Draíocht* and *Dolphin Discovery*, based in Carrigaholt and Kilrush (Berrow & Holmes, 1999), respectively (Figure 1). The research vessel was a 6 m rigid-hulled inflatable boat (RIB) with a 115 hp outboard motor. Trained observers on each vessel located dolphins visually by eye and with the use of binoculars (Minox 7 × 50 or 8 × 42). Research vessel surveys began by heading east or west of Kilrush, with efforts made to cover as large an area as possible, depending on dolphin group directionality and sea conditions.
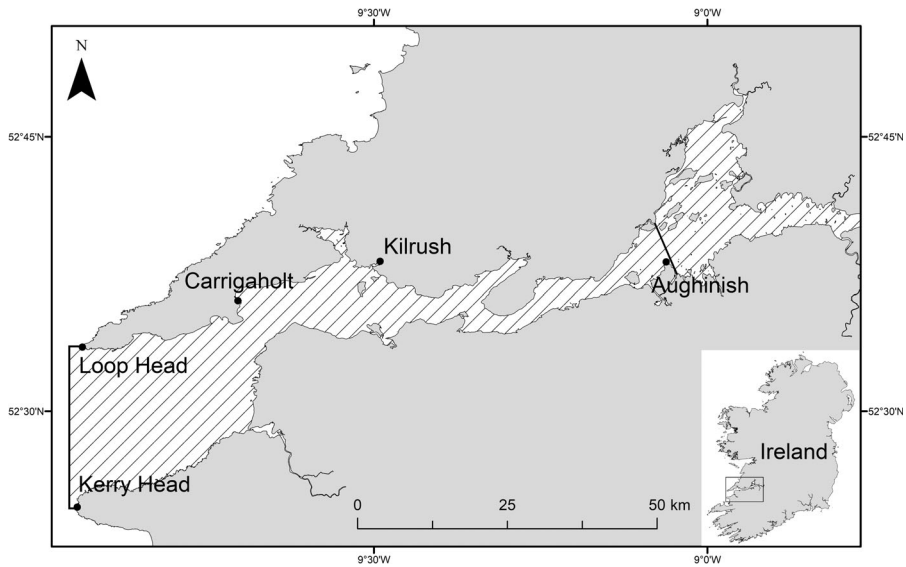
FIGURE 1 Map of the Shannon Estuary study site in Ireland. The line between Loop Head and Kerry Head represents the western boundary of the Special Area of Conservation (SAC; hatched lines) and of the study site, while the line at Aughinish represents the eastern boundary of the area surveyed during this study.

Data collection methods followed the recommendations of Mann (1999), who defines the two basic sampling decisions as "follow protocol," the length of observation and the choice of subject(s) and "sampling method," the procedure used to sample behavior. Dedicated data collection comprised two different follow protocols: survey and individual-follow.

2.2.1 | Surveys and sightings

During surveys, a dolphin encounter or "sighting" began when at least one dolphin was within 100 m of the vessel and ended after ≤30 min due to national regulations (Maritime Safety Directorate, 2005). During a sighting, all vessels maintained a position parallel to the animals and at a distance of approximately 100 m unless the dolphins approached the boat. We used Mann's (1999) survey protocol to collect data during sightings, including records of individual dolphin identifications, group size and composition, changes in group membership, environmental measures (e.g., water temperature, depth, and sea state), location (latitude and longitude; using a Garmin 72H GPS), activity states (travel, social, forage, rest, other, or unknown), and behavioral events (e.g., leap; see Baker, O'Brien, McHugh, & Berrow, 2017). We defined a group as all animals sighted together and moving in the same general direction, engaged in similar activities, or interacting with each other within a radius of approximately 100 m (McHugh, Allen, Barleycorn, & Wells, 2011a). Thus, survey sightings provided a snapshot of dolphin group activity, location, and behaviors. The sampling methods used during surveys were "predominant group activity sampling," "one–zero," and "*ad libitum*," sampling (see Baker *et al.*, 2017 for definitions).

2.2.2 | Individual focal follows

We initiated focal follows following the collection of survey data, when three necessary conditions were met: (1) all members of a dolphin group had been identified, (2) all were individually recognizable by eye to the lead researcher, and (3) sea conditions were calm (Beaufort sea state ≤2).

We conducted focal follows (carried out under NPWS permits) from the research RIB (previously described) during May–September 2014, 2015, and 2016. We developed standardized techniques for focal follows based upon Sarasota Dolphin Research Program protocols for bottlenose dolphin focal follows (SDRP, 2006), which were built upon Altmann's (1974) guidelines. The follow protocol was "individual-follow" wherein a single individual is chosen as the focal animal in a group, that is, behavioral observations ("focal follows" or "follows") conducted on specific individuals ("focal animals") (Mann, 1999; McHugh et al., 2011b). We used two sampling methods during individual-follows: continuous sampling to gather data on group dynamics and behavioral events, and point sampling at 3-min intervals to determine activity budgets, identify nearest-neighbors, and gain information on individual associations. Generally, we selected the first adult dolphin of known sex encountered during the day as a focal animal, and if two or more potential focal individuals were present in a group, we chose the individual that had been followed less often or less recently, as recommended by McHugh et al. (2011a). We determined the sex of individual dolphins through (1) genetic evidence from tissue samples collected through biopsy sampling (n = 37; collected under NPWS permits; Berrow et al. 2002, Mirimin et al. 2011); (2) photographs of the genital area (n = 1); and (3) in the case of adult females, observations of the mother swimming in close association with a dependent calf (n = 25). Overall, 48% of individuals available for analysis were of known sex; 47 of 51 follows were of focal individuals of known sex.

We conducted focal follows up to four days a month, followed focal dolphins for up to 2 hr per day, and carried out a maximum of two focal follows a day. During a follow, the research vessel maintained a position parallel to the animals and at a distance of approximately 20 m unless the dolphins approached the boat. We maintained a gradual and consistent boat speed and direction in an effort to minimize any disturbance to the dolphins (Mann, Connor, Tyack, & Whitehead, 2000). Prefollow sightings lasted at least 15 min to provide time for the habituation of dolphins to the research vessel before beginning focal follows.

We confined follows to adults (and one juvenile), as the behavior of dependent calves could not be considered independent of their mothers' behavior. We determined age class through individual size and body length (Smith, Pollock, Waples, Bradley, & Bejder, 2013), reproductive state, and/or knowledge of long-term life history (Baker et al., 2018a). Adults were fully grown animals (about 4 m in length) and well-known from long-term photo-identification studies in the Shannon Estuary (e.g., Berrow, Holmes, & Kiely, 1996; Berrow et al., 2012; Ingram, 2000; O'Brien et al., 2014). Juveniles were less than two-thirds the size of adults and were not dependent on their mothers. Calves were dolphins that were consistently in association with their adult mothers, often with visible fetal folds (dark vertical lines on the body) and swimming in a characteristic infant position alongside their mothers (Mann & Smuts, 1999).

During focal follows, we collected fine-scale behavioral data (instantaneous point samples) every 3 min on (1) GPS location of the research boat; (2) focal animal and group activity state (travel, forage, probable forage, feed, social, rest, play, or with boat; see Baker et al., 2017 for definitions); (3) group size and number of calves; (4) group composition (including the identities of all individuals in the group); (5) group spread (in meters); (6) nearest-neighbor distance (from the focal individual) and identification; and (7) focal animal position, that is, the location of the focal individual relative to the rest of the group—ahead, center, behind, side-by-side, in a lateral line, infant position, or peripheral (i.e., on the outskirts of the group). During a focal follow, if it was possible to continue to observe and monitor animals as they exceeded distances of 100 m from the main group, and to ascertain that there were no other individuals in the surrounding area, then we maintained observations of these individuals until they were greater than 300 m from the focal group. Thus, in focal follows only, a dolphin was considered to have left a group when it could no longer be observed or was beyond 300 m away from the focal group. We used the countdown timer of a phone app (*Impetus*) set to beep at 3-min intervals for 2 hr to mark each sample point for data collection. If the focal individual was below the surface of the water at the 3-min time point, we recorded the data at the first surfacing of the focal individual and the rest of their group. (Very rarely, the focal individual did not resurface within 3 min and the entry for that time point was left blank.) If the focal individual was in sight at the 3-min time point, but not the rest of the group, we considered their nearest-neighbor to be the closest member of the group when the rest of the group had surfaced. Concurrent continuous data sampling allowed us to note changes in group membership as fusion or fission events when dolphins joined or

left the group. Additionally, we recorded all behavioral events (e.g., fish toss; see Baker *et al.*, 2017) as they occurred, with information on the individuals engaged in the behavior where possible.

Upon each surfacing, the lead researcher (IB) identified each individual dolphin in real time using distinctive markings on their dorsal fins to recognize them by eye. We used the number of individuals identified to record group size and number of calves. We recorded group activity state as the predominant group activity state, that is, the activity state that over 50% of the group was engaged in at the time. To eliminate any potential interobserver variability in distance estimates, the same observer (IB) estimated group spread and nearest-neighbor distance for each point sample during every focal follow.

2.2.3 | Photo-identification

We took photographs throughout sightings and focal follows using digital SLR cameras (Nikon D300 or Canon EOS 20D with 70–300 mm lenses). Initially, we attempted to photograph each individual in each group (regardless of their degree of marking or individual differences in behavior) for individual recognition through the photo-identification of dorsal fins (Würsig & Jefferson, 1990; Würsig & Würsig, 1977). Then, once a focal follow was initiated, we took photographs throughout the follow to continuously record the identity of group members, and with particular attention to recording changes of group composition. These photos could then also be used to cross-validate the field IDs determined by the lead researcher throughout the follow. Each focal individual was well-known from the photo-id catalog and identifiable by the lead researcher in the field.

2.3 | Data management

We describe database design and management in detail in Baker *et al.* (2018a) and followed Shannon Dolphin and Wildlife Foundation (SDWF) protocols (Baker, 2015). Briefly, we maintained two databases in (1) IMatch 5.6 (https://photools.com), a photographic software environment in which we stored and processed all photos from surveys and sightings, and (2) FinBase (Microsoft Access), a relational sightings database for bottlenose dolphin research (Adams, Speakman, Zolman, & Schwacke, 2006) where we entered both written sighting records and individual dorsal fin photographs (one best photograph per individual per sighting) and where the related data could be queried for specific analytical purposes. We used a digital photo-id catalog housing the best images of each individual in the population for initial dorsal fin comparisons (see Baker *et al.*, 2018a for detailed photo-id and digital image processing protocols).

2.4 | Data analysis

2.4.1 | Analytical setup

We analyzed focal follow data in R (R Core Team, 2016) and MATLAB (version 9.2). We analyzed all data (51 follows) together for overall population results. For sex-specific analyses, we split adult female and male focal follow data for separate calculations (26 follows of 10 adults known to be female and 20 follows of five adults known to be male).

We queried survey and sighting data (2012–2015) in FinBase and entered the output into SOCPROG 2.7 (compiled version), a dedicated software package that uses data on the associations of identified individual animals for the analysis of their social structure (Whitehead, 2009), in group mode, with a supplemental file detailing individual sex and age class. We defined the sampling period as one day, based on the natural break between daylight sampling sessions and because the proportion of individuals sampled within a one-day timeframe was appropriate for data analysis. We defined associations between individuals by shared group membership, with each record/sighting constituting one group. We used the half-weight association index (HWI) as the coefficient of association. This measure represents the strength of social bonds among individuals (with a range of possible values between 0 [never seen together] and 1 [always seen together]), while also accounting for the possibility of missing individuals during

sighting encounters (which is a possibility when using opportunistic research platforms like dolphin-watching tour boats). The HWI is defined as HWI = $2N_T/(N_a + N_b)$ where N_T represents the number of times two individuals are seen in the same sighting and N_a and N_b represent the total number of times each individual is sighted, respectively (Cairns and Schwager, 1987). Thus, this association index indicates the proportion of time that each pair of individuals is seen in a group together. As recommended by Whitehead (2008), we set restrictions to include in the analysis only individuals with >5 sighting records in the database.

2.4.2 | Group composition and sociality metrics

We obtained the range, mean, median, and mode of group sizes within follows from the overall follow data set. Additionally, we calculated the range, mean, median, and mode for the number of calves in groups, group spread in meters, and nearest-neighbor distance in meters. We also determined the most common focal animal position. We described group composition by using the IDs (with individual age and sex classes) of all individuals in each group follow at any point in time.

To examine fine-scale group stability and how group composition changed over time, we calculated the fission-fusion rate for each focal individual by dividing the number of group composition changes (individual dolphins either joining or leaving the focal individual's group) during focal follows by the number of hours each focal animal was followed (McHugh et al., 2011b). We then calculated the average fission-fusion rate for females and males separately and for all focal individuals combined. We used a linear regression to test if females and males had different fission-fusion rates. The fission-fusion rate for each focal animal was entered as the outcome variable into a linear regression with sex entered as a fixed effect.

We calculated three measures of sociality for each focal individual: (1) proportion of time spent alone (including with dependent calf, if mother); (2) mean group size; and (3) number of associates (Gibson and Mann, 2008; McHugh et al., 2011b). We calculated proportion of time spent alone by summing the time that each individual was solitary, that is, without any other group members within 100 m (excluding dependent calves) during behavioral observation sessions, standardizing for observation time (McHugh et al., 2011b). We calculated the mean group size from follows for all individuals overall and for each individual separately, and then averaged it across females and males to generate means for each sex class (46 follows, of 10 known adult females [26 follows] and five known adult males [20 follows]). A Shapiro–Wilk normality test indicated that the data were normally distributed (p = .12). We used a linear mixed-effects model (LMM) to test if focal females and males had different mean group sizes during focal follows. Mean group size was entered as the outcome variable into the LMM. Sex was entered as a fixed effect and ID as a random effect.

Using the association matrix generated in SOCPROG (for all individuals with >5 sighting records; n = 106), we calculated the raw number of associates of each focal individual by summing the total number of unique individuals observed interacting with each focal individual in those years (2012–2015). We also calculated the raw number of associates for females and males separately. We then standardized each individual value by the number of sighting records of each individual to account for differences in sighting frequency among individuals. We used a generalized linear mixed-effects model (GLMM) to test if females and males had different numbers of associates. Total number of associates per focal animal was entered as the outcome variable into a GLMM with Poisson error structure. Sex was entered as a fixed effect and ID as a random intercept.

2.4.3 | Nearest-neighbor preferences/Within-group affiliation

To better understand within-group affiliation patterns, we investigated nearest-neighbor point sample data from focal follows. We defined the "nearest-neighbor" as the closest individual that overlapped in surfacing with the focal dolphin (McHugh, 2010), with the proviso that a dependent calf was recorded as a female's nearest-neighbor only at times when it was the only individual with her. We counted the number of distinct individuals observed with each focal adult individual. Then, we classed the identities of each focal individual's nearest-neighbors by sex and age to

determine if differences existed in the nearest-neighbor preferences of focal individuals, relative to the set of distinct individuals observed in all of each focal individual's groups. To account for the relative availability of different age classes of individual in the population, we then adjusted these results using the age class ratio reported by Baker et al. (2018a; 80:25:40 adult:juvenile:calf) to provide the ratio-adjusted preferential associations of focal individuals with nearest-neighbors of each age class.

To examine which individuals were the most common nearest-neighbors to each focal individual in each of 50 focal follows (one follow was eliminated because there were no nearest-neighbor data), we extracted the individual with the highest proportion of observations as nearest-neighbor to the focal individual from each follow data set, and then classified each pairing by sex of both the focal individual and the nearest-neighbor. We then calculated the frequency of sex-related pairings. We also assessed consistency in the identity of nearest-neighbors for all focal individuals with more than one follow. We used a GLMM to test if focal individual sex (female or male) had an effect on the sex of the nearest-neighbor (for all focal follow point samples for which the sexes of both the focal individual and its nearest-neighbor were known). Nearest-neighbor sex was entered as the outcome variable into a GLMM with binomial error structure. Sex of the focal individual was entered as a fixed effect and ID as a random intercept.

To illustrate the complexity of individuals' preferred nearest-neighbors, we chose the adult female and male with the largest data sets (i.e., greatest number of hours followed) as examples. We input their 3-min point samples where nearest-neighbor data were available into SOCPROG to generate results regarding age and sex preferences for within-group affiliates. We calculated the proportion of time observed with their most common nearest-neighbor during each follow to discern if a large portion of time was spent with a specific individual within follows and to get a clearer picture of patterns of affiliation.

We then investigated if a focal individual's most frequent nearest-neighbor in each of its focal follows was the same as its highest ranking associate based on HWIs from the population's sightings data. Associations in the population were generally considered to be important and strong if they were greater than twice the population's mean HWI (Whitehead, 2008), determined from previous research to be 0.07 (Baker et al., 2018b). If the nearest-neighbors (from follows) were among the focal individual's top associates (from sightings), this might be indicative of a "bond" between the animals, that is, a pair of individuals with strong relationships across two "independent" interaction/association measures (Whitehead, 2008).

2.4.4 | Sex-specific differences in activity budgets

To investigate if the proportion of time spent in different activity states differed between males and females, we used focal follow data from the five adult males (20 follows, 28.7 hr) and the 10 adult females (26 follows, 57.5 hr). Individual differences in behavior and/or follow duration can influence results so we calculated activity budgets by weighting for differences in follow durations to avoid bias towards particular activity states (Steiner, 2011). Thus, for each individual follow, we calculated the percentage of time the dolphin spent engaging in an activity, that is, one value for each activity state per follow for each focal individual. Then, we averaged the values for each activity state over all follows for each individual dolphin separately to arrive at values specific to that individual (Powell & Wells, 2011). We then averaged the individual means for each sex class to determine the overall activity means for female and male individuals. We created pie charts in R (R Core Team, 2016) to illustrate the activity budgets of female and male focal dolphins.

We statistically compared sex differences in activity means in MATLAB (version 9.2) using a custom randomization program built in MATLAB (version 7.4) by Powell and Wells (2011). To estimate the probability of differences in activity state proportions between female and male dolphins, the one-tailed test uses a test statistic (ratio between female and male dolphins) determined by randomizing a matrix 10,000 times. The values were permuted (excluding information on individual sex) to detect if there was an apparent difference between female and male individual activity state budgets with p values indicating the level of significance in any differences found.

2.4.5 | Male alliances

To investigate the potential presence of male alliances in the Shannon Estuary bottlenose dolphin population, we produced a matrix of HWIs using SOCPROG for all individual associations of known males with >5 sighting records (*n* = 10). As in previous studies, we defined male alliances as pairs of dolphins with high levels of association (very high HWIs, that is, greater than twice the population's mean) and where each member of the male pair ranks as each other's closest associate (Wells, Scott, & Irvine, 1987, Connor, Smolker, & Richards, 1992). We considered dyads to be important "friends" if their HWIs were twice the mean for all male dyads; these are pairs of individuals that are associated at least twice as much as the expected value of a dyad chosen randomly from the population (Whitehead, 2008). We then used the matrix of HWIs produced in SOCPROG for all individual associations in the population to examine each male dolphin's maximum association index (maximum HWI) with any other individual in the population, to determine the strength of their strongest association, as well as whether they were also the strongest associate of that individual (i.e., reciprocal closest associates). We also noted the sex of each male's strongest associate.

We ran a two-sided dyadic significance test (Monte Carlo test) in SOCPROG and used the results to determine the significant dyads with HWIs greater than two times the mean HWI of all males. The two-sided test for dyadic association simultaneously tests for preferred companionship (a significantly high value of the association index) or avoided companionship (a significantly low value of the association index) (Whitehead, 2008). Associations were permuted within sampling periods (20,000 permutations with 100 flips per permutation) and the coefficient of variation (*CV*) of association indices was used as the test statistic. If any pairs were identified as male alliances, the follow data would be interrogated to discover if these alliances were reflected in nearest-neighbor relationships.

3 | RESULTS

3.1 | Surveys and focal follows

Between 2012 and 2015, we carried out 353 surveys (with 607 sightings), during which 136,486 photographs were taken; 45,371 of these were used for the photographic analysis of individually identifiable bottlenose dolphins. In total, 2,948 identifications were made of 121 distinct individual adult/juvenile dolphins. We excluded dependent calves from analyses because their presence was a result of their mothers' presence in groups. When restrictions were set within SOCPROG to include only individuals with >5 sighting records, 106 distinct individual dolphins and 519 sightings were available for association analyses.

In total, we carried out 51 focal follows (over 39 days, during 39 surveys) on 18 unique individual dolphins: five adult males (20 follows), 10 adult females (26 follows), one juvenile female (1 follow), and two adults of unknown sex (4 follows). The total duration of focal follows conducted was 90.8 hr. All groups combined, we observed 60 individuals in follow groups comprising 23 females, 8 males, and 29 individuals of unknown sex; age classes consisted of 37 adults, 10 juveniles, and 13 calves. Given the current population estimate of 142 (Baker *et al.*, 2018a), these individuals represent about 42% of the Shannon Estuary bottlenose dolphin population.

3.2 | Group composition and sociality

The number of individuals recorded in a focal group ranged from one to 20 animals (mean group size = 7.2 ± 4.1; Table 1). The mean number of calves found in focal groups was 1.8 ± 1.3 (range = 0–6). Group spread varied from 1 to 400 m but was most often 10 m. The closest nearest-neighbor distance recorded was 0 m (i.e., the individuals' bodies were touching) while the farthest nearest-neighbor distance was 300 m. We recorded the focal animals in all possible positions (ahead, center, behind, side-by-side, in a lateral line, infant position or peripheral), but the most common position recorded was "center," meaning the focal animal was positioned in the center of the focal group.

TABLE 1 Group composition data summary from 51 focal follows of bottlenose dolphins in the Shannon Estuary (NN = nearest-neighbor).

	Group size	No. of calves	Group spread (m)	NN distance (m)
Minimum	1	0	1	0
Maximum	20	6	400	300
Mean ± SD	7.2 ± 4.1	1.8 ± 1.3	38.8 ± 35.5	9.0 ± 20.3
Median	6	2	30	2
Mode	2	2	10	1

FIGURE 2 Boxplots of adult female (F) and male (M) bottlenose dolphin (a) fission-fusion rate, (b) mean group size and (c) total number of associates (n = 15). A linear regression, LMM and GLMM indicated very little support for asserting an effect of sex on fission-fusion rate (p = .47), mean group size (p = .29) or total number of associates (p = .24), respectively.
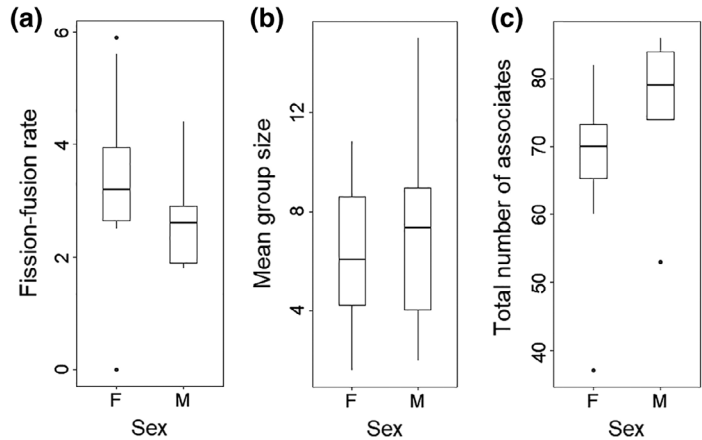
Group composition varied from follow to follow, but often contained a combination of adults, juveniles, and calves, and both females and males; of the 51 focal follows, 53% contained all three age classes, while 84% of the groups followed contained both sexes. Only 18% of followed groups contained adults exclusively. No followed groups contained solely juveniles and all of the 25 followed groups which included juveniles also contained both adults and calves. Of 44 focal follows with at least one identified known male in them, 39 (89%) had calves in them. In fact, 70% (31) of these follows had multiple calves in them. Of the 39 follow groups containing both adult males and calves, 59% (23) contained at least one young-of-year (YOY) calf, while the other 41% (16) contained older (>1 year old) calves. These results indicate the presence of groups with both male and calf members in this study population. Of the 44 focal follows containing at least one identified known adult male, all but one also contained adult females; the remaining follow consisted of a known adult male and one other individual of unknown sex. Seventeen (33%) of the follow groups contained more than one known adult male.

Group composition during follows changed frequently. The average fission-fusion rate of focal female dolphins' (n = 11) groups was 3.22 ± 1.57 changes/hr, while the average fission-fusion rate of focal male dolphins' (n = 5) groups was 2.79 ± 0.89 changes/hr (Figure 2a). Using the linear regression, we found that we could not conclude that focal individual sex had an effect on average fission-fusion rate with any great confidence (estimate = −0.62 [0.82], z = −0.75, p = .47). The overall fission-fusion rate for all focal individuals' (n = 18) groups was 3.06 ± 1.35 changes/hr (Table 2).

Bottlenose dolphins in the Shannon Estuary were rarely solitary; of 90.8 hr of focal follows, less than 5 hr included observations of focal animals on their own (or with only their dependent calf). Seven of the 18 focal individuals were observed in groups 100% of the time they were followed, and the other 11 dolphins were observed spending between 1% and 41% of their time on their own (mean = 6.6%, SD = 10.2). The two individuals with the highest proportions of time spent alone were females ID#s 011 (25%) and 118 (41%) (Table 2). In both cases, these values

TABLE 2 The sex class and ID# of focal dolphins followed during behavioral observations in the Shannon Estuary. The number of hours observed (hr obs), 3-min instantaneous behavioral observations per individual (obs 3-min), and changes in focal individual's group composition are given, as are the fission-fusion rate, mean group size (i.e., the average size of groups each focal individual spent time in), proportion of time spent alone and proportion of time spent in groups.

Sex class	ID#	Hr obs	Obs 3-min	# of changes	Fission-fusion rate	Mean group size	% time alone	% time in groups
Females (n = 11)	006	3.9	77	12	3.12	6.0	5	95
	011	1.6	32	9	5.63	5.5	25	75
	019	0.7	13	0	0.00	2.0	0	100
	044	8.3	166	23	2.77	6.6	9	91
	052	5.3	105	13	2.48	4.9	9	91
	071	7.1	141	25	3.55	9.9	5	95
	093	3.5	69	9	2.61	7.8	6	94
	118	2.7	54	16	5.93	2.8	41	59
	216	8.8	175	36	4.11	8.6	0	100
	242	15.9	317	52	3.28	6.2	2	98
	801	1.1	21	2	1.90	6.7	0	100
Males (n = 5)	008	9.2	183	17	1.86	12.1	0	100
	009	6.8	136	20	2.94	2.9	1	99
	078	0.9	18	4	4.44	7.0	0	100
	104	7.4	148	19	2.57	7.3	6	94
	313	4.5	89	8	1.80	7.8	9	91
Unknown (n = 2)	095	1.9	38	6	3.16	8.6	0	100
	211	1.7	34	5	2.94	6.4	0	100
Total (n = 18)		90.8	1,816	276				
Mean ± SD					3.06 ± 1.35	6.6 ± 2.4	6.6 ± 10.2	93.4 ± 10.2

were derived from a single follow of the focal individual wherein the females were initially sighted alone with their dependent calves, but were joined by other dolphins as the follow progressed. On average, focal dolphins in the Shannon Estuary spent 93.4% (SD = 10.2) of their time in groups with other individuals (Table 2).

When we calculated mean group size for each individual separately, the overall average group size ranged from 2.0 to 12.1 dolphins/group (mean = 6.6 ± 2.4 dolphins/group; Table 2). The average group size for all focal males was 7.4 ± 2.9 while the average group size for all focal females was 6.1 ± 2.2 (Figure 2b). However, the difference between these measures of average group size was not strongly supported (LMM, estimate = 1.57[1.41], z = 1.12, p = .29).

Results from the sightings data revealed that focal males had more unique associates than focal females (over 4 years; 2012–2015). Focal males had an average of 75 associates each (range = 53–86, SD = 11.86) compared to focal females who had an average of 67 associates each (excluding calves; range = 37–82, SD = 11.63; Figure 2c). However, we could not conclude with any certainty that focal individual sex had an effect on total number of associates (GLMM, estimate = 0.11[0.09], z = 1.18, p = .24). When standardized for number of sightings per individual (range = 21–92 sightings each), focal males had 1.46 associates per sighting compared to 1.58 for focal females. The average number of associates per individual was 71 (range = 37–86, SD = 11.85) which corresponded to an average 1.56 ± 0.85 associates per sighting.

3.3 | Nearest-neighbor preferences

The average number of distinct individuals observed interacting as nearest-neighbor with each focal adult individual of known sex was 10 ± 4.87 (range = 1–19). There was no difference in the average number of distinct nearest-neighbors (i.e., different individual dolphin IDs who took the place of nearest-neighbor during a follow) by focal individual sex (focal females = 10 ± 5.14, range = 1–19; focal males = 10 ± 4.26, range = 3–15).

For adult focal females (excluding their own dependent calves), the majority (65%) of distinct nearest-neighbors were other adults (32% females, 11% males, 22% unknown sex), followed by calves (22%) and juveniles (14%). For adult focal males, the majority (72%) of distinct nearest-neighbors were also other adults (42% females, 11% males, 19% unknown sex), followed by juveniles (19%) and calves (8%). Adjusting for the proportions of adults, juveniles and calves in the population as a whole, the focal females' nearest-neighbors were 43% adults, 29% calves, and 29% juveniles. For focal males, distinct nearest-neighbors were 48% adults, 41% juveniles, and 11% calves. So, all adult dolphins associated preferentially with other adults, and both females and males had a higher proportion of female nearest-neighbor affiliates than males or individuals of unknown sex. Adult females and males differed in their affiliation patterns in terms of age class, in that females were equally likely to associate with calves and juvenile nearest-neighbors, but males were more likely to associate with juveniles than with calf nearest-neighbors.

Excluding six follows where nearest-neighbor data were not available or the most common nearest-neighbor to the focal individual was a dependent calf, the most frequent type of nearest-neighbor pairings between two individuals of known sex was female–male, followed by female–female pairings (Table 3). During the 45 focal follows available for this analysis, there were no cases where an adult male spent the majority of his time with another known adult male (i.e., no male–male pairings).
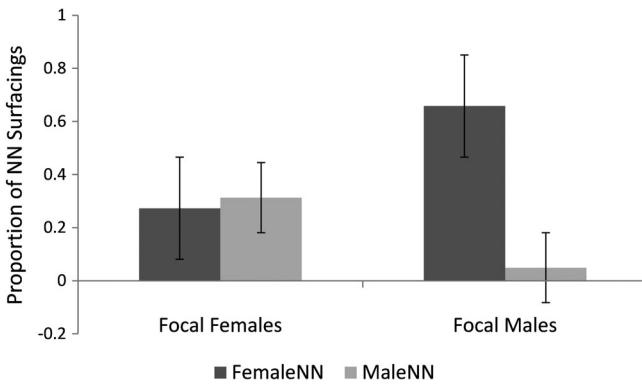
Focal individual sex had a significant effect on the sex of nearest-neighbor individuals (GLMM, estimate = −2.85 [1.15], z = −2.48, p = .013). While the proportions of time that a focal female had either a female or male nearest-neighbor were fairly similar, focal males were much more likely to have female nearest-neighbors (Figure 3).

The adult female and male with the largest data sets were ID#s 242 and 008, respectively. ID# 242 had 19 distinct nearest-neighbors during her 15.9 hr of focal follows. Of those, three were adult females, five were adult males and 11 were of unknown sex (four adults, three juveniles, and four calves). Of the four calves that ID# 242 was affiliated with, two were her own dependent calves (each recorded as her nearest-neighbor only at times when they were the only individual with her and otherwise excluded as candidates for her nearest-neighbor). Of the five focal follows conducted on ID# 242, her most frequently recorded nearest-neighbor during each follow was: (1) female ID# 093 (65% of the observation time in that follow); (2) male ID# 104 (21%); (3) male ID# 104 (64%); (4) ID# 244 (unknown sex, 20%); and (5) female ID# 118 (35%). In the two follows with male ID# 104 as her nearest-neighbor, the pair was observed in a "trio" with her calf.

The male ID# 008 was observed associating with 24 individuals during focal follows and had 15 distinct nearest-neighbors during his 9.4 hr of behavioral observations. Of those, four were adult females, one was an adult male and 10 were of unknown sex (three adults, four juveniles, and three calves). Of the five focal follows conducted on ID# 008, his most common nearest-neighbor during each follow was: (1) female ID# 118 (62% of the observation time in

TABLE 3 Nearest-neighbor pairings by sex class for the majority of time of each of 45 individual focal follows.

Sex classes of focal individual-nearest-neighbor pair	Frequency
Female–Male	17
Female–Female	7
Male–Male	0
Female-Unknown	12
Male-Unknown	8
Unknown-Unknown	1

FIGURE 3 A comparison of the proportion of time (3-min point samples) a female or male was a nearest-neighbor (NN) for all focal animal follows (for adult individuals of known sex; focal female follows on the left, focal male follows on the right). Standard error bars are shown. Focal individual sex had a significant effect on the sex of nearest-neighbor individuals (p = .013).

that follow); (2) female ID# 118 (84%); (3) ID# 236 (unknown sex, 31%); (4) female ID# 044 (68%); and (5) female ID# 044 (62%). The consecutive follows involving the same female nearest-neighbor occurred on 5 July 2016 and 18 July 2016 (with female ID# 118) and on September 6, 2016 and September 12, 2016 (with female ID# 044). In both cases, ID# 008 consistently surfaced in a trio with the female and her calf; ID# 118's calf was >1 year old (born in 2015) while ID# 044's calf was a neonate born 29 August 2016.

Bottlenose dolphins in the Shannon Estuary tended to have different nearest-neighbors each time they were followed. The proportion of time a pair spent together as nearest-neighbors within a follow was high (often >50% of the time) but the identity of focal individuals' nearest-neighbors often changed between follows. When only focal animals with >1 follow were analyzed (n = 12), their subsequent follows rarely had the same most frequent nearest-neighbor; in 72% of cases, the most frequent nearest-neighbor was a different individual.

Of each focal individual's pairings with its most frequent nearest-neighbor, 86% consisted of dyadic associations with individuals with whom they had an important and strong (>twice the population mean) HWI from sightings. However, although these dyads had generally high HWIs relative to other dyadic associations in the population, the specific individuals in each pair tended to have higher overall HWIs with a different dolphin and not their nearest-neighbor from focal follows. Thus, the nearest-neighbors (from follows) were among the strongest associates (from sightings), but almost never *the* top associate from sightings. In fact, of the 51 follows, only seven follows (four distinct pairs of individuals) presented situations where the focal animal's nearest-neighbor for the majority of the follow was also its strongest associate (greatest HWI) from sightings. These pairs were ID#s 242–104 (female–male; HWI = 0.62), 216–008 (female–male; HWI = 0.48), 095–216 (unknown sex-female; HWI = 0.5), and 313–312 (male-unknown sex; HWI = 0.44).

3.4 | Sex-specific differences in activity budgets

We constructed activity budgets for the five adult males (20 follows, 28.7 hr) and the 10 adult females (26 follows, 57.5 hr). Both female and male focal dolphins spent the majority of their time traveling (78% and 69%, respectively) with less time spent foraging, socializing, resting, milling, and with boats. Females spent more time traveling and resting than males; males spent more time foraging, socializing, and milling (Figure 4). However, the difference between female and male activity budgets was not strongly supported (randomization test, 10,000 permutations; p = .13).

3.5 | No evidence of male alliances

Wells *et al.* (1987) and Connor *et al.* (1992) proposed two criteria to define a male alliance: (1) a pair of dolphins with very high HWIs, and (2) each member of the pair ranks as each other's closest associate. In our data set, there were 263 sightings that included 10 known male dolphins (each individual had 16–101 sightings in the database). The mean male HWI, using sampling periods of days and association defined by group membership, was 0.119. Of
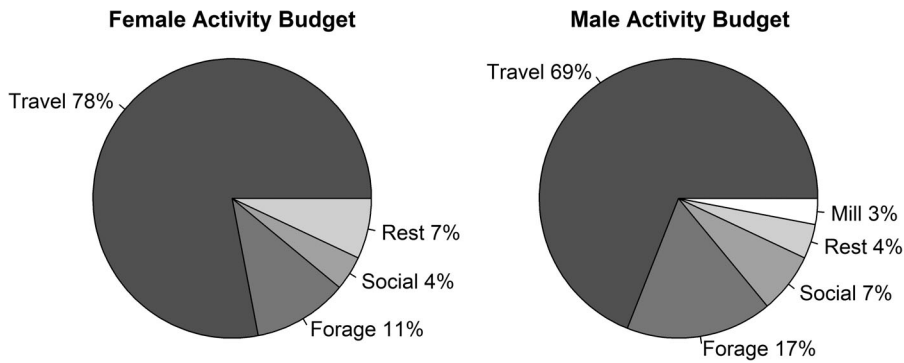
FIGURE 4 Overall mean activity budgets for adult female (n = 10) and male (n = 5) focal dolphins compiled from summer 2014–2016 individual focal follows. No milling behavior was recorded for females and with boat activity was recorded for <1% of both the female and male activity budgets.

TABLE 4 Association indices among 10 adult male bottlenose dolphins, their maximum HWI and the corresponding individual associate with whom the maximum HWI was shared. The mean male HWI, using sampling periods of days and association defined by group membership, was 0.119. Dyads with association indices at least twice the mean are shown in bold. Asterisk indicates dyadic $p > .95$ for test for preferred association using permutation of associations within sampling periods (20,000 permutations with 100 flips per permutation). The overall significance for preferred/avoided associations in this matrix, using the coefficient of variation (CV) of association indices as a test statistic, was $p = .02$ (CV = 0.84 for real data, compared with CV = 0.79 for mean of random permutations) (after Whitehead, 2008).

Male ID#	Half-weight association indices (HWIs)										Maximum HWI	Associate ID#	Associate sex
102											0.34	019	Female
104	0.06										0.62	242	Female
144	0.22	0.16									0.45	106	Unknown
016	**0.33**	0.00	0.14								0.36	027	Female
202	**0.26**	0.09	0.21	0.20							0.35	209	Female
313	0.15	**0.27**	0.12	0.07	0.10						0.44	312	Unknown
033	**0.28**	0.02	0.10	0.06	**0.27**	0.06					0.28	260/102	Female/Male
034	0.06	0.05	0.11	0.07	0.00	0.00	0.00				0.16	096	Female
008	0.06	0.18	0.14	0.04	0.00	**0.28**	0.00	0.15			0.48	216	Female
009	0.03	0.22	0.13	0.00	0.00	**0.35***	0.00	0.12	0.21		0.53	312	Unknown
	102	104	144	016	202	313	033	034	008	009			

Note: ID# 033's maximum HWI was 0.28 with two individuals, ID# 102 (male) and ID# 260 (female).

the 45 potential dyads in the matrix of association indices for male dolphins, seven pairs of dolphins had high levels of association (where the dyads' HWIs were at least twice the mean; Table 4).

The results of the two-sided dyadic association test (Monte Carlo test) revealed only one significant dyad (preferred companions) with HWI greater than two times the mean HWI for all males and with a significantly high value of the association index. These were male ID#s 009 and 313 (HWI = 0.35; dyadic $p > .95$ for test for preferred association using permutation of associations within sampling periods [20,000 permutations with 100 flips per permutation]). The overall significance for preferred/avoided associations in the matrix, using the coefficient of variation (CV) of association indices as a test statistic, was $p = .02$ with a CV of 0.84 for the real data, compared with a CV of 0.79 for the mean of the random data.

However, it was not the case for any of these pairs that each member ranked as the other's closest associate. Thus, the second criterion in the definition of male alliances was not met. In fact, each of the 10 males' maximum HWI was higher than any HWI they shared with another of the males, except for ID# 033 whose maximum HWI was 0.28 with two other dolphins (ID# 102, a male, whose highest HWI [0.34] was with female ID# 019 and ID# 260, a female). The other nine males' maximum HWI associates were either female (6) or individuals of unknown sex (3) (Table 4).

The data in this study, then, while limited to that of 10 known males, provide no evidence for the existence of male alliances in this population. On the contrary, it is noteworthy that the top associate of known sex for every male in the study was a female. The lack of sightings evidence for male alliances made it inapplicable to see if the members of these alliances were reflected within follows in nearest-neighbor relationships. However, this lack of evidence does seem consistent with the follow data presented above showing the high level of female–male nearest-neighbor pairs and the absence of any (known) male–male pairs.

4 | DISCUSSION

Using fine-scale analysis of individual female and male focal dolphin data from the Shannon Estuary, we have provided new information on the sociality, behavior and association patterns of individual bottlenose dolphins. We have reported variability in group composition, marked preferences for female–male within-group affiliations and the varied activity budgets of female and male dolphins. Furthermore, our analysis has uncovered no evidence of male alliance formation in this population.

4.1 | Group size, composition, and sociality

Bottlenose dolphin group size during focal follows averaged around seven animals, ranging from groups of 1–20 dolphins. Using sightings data from 2005 to 2011, Barker and Berrow (2016) previously estimated average dolphin group size in the Shannon Estuary to be around nine individuals (range = 1–50). The slightly smaller mean group size in the present study could be due to a difference in sampling methods, as focal follow data may be biased towards smaller groups (as follows are not initiated on large disorderly groups and may be terminated if groups become so large that not all individuals can be accounted for upon every surfacing). Nevertheless, this study supports Barker and Berrow's (2016) conclusion that the mean dolphin group size in the Shannon Estuary is larger than those found in the closest resident bottlenose dolphin populations in Cardigan Bay, Wales (4.59; Bristow and Rees, 2001) and the Moray Firth, Scotland (4.5; Wilson, 1995). Our mean group size of 7.2 dolphins is very similar to those reported for resident bottlenose dolphin populations in the Northern Adriatic Sea (7.4; Bearzi, Notarbartolo di Sciara, & Politi, 1997), Sado Estuary, Portugal (7.8; Augusto *et al.*, 2011), and Sarasota Bay, Florida (7; Scott, Wells, & Irvine, 1990).

The composition of dolphin groups during focal follows was generally mixed in terms of both sex and age of individuals. Unlike predictable group compositions from other studies, such as the female-calf nursery groups and all-male groups found in Sarasota Bay (Wells, 2014), groups of bottlenose dolphins in the Shannon Estuary often had both males and calves in them, and a mixture of other adults and juveniles. However, this high proportion of mixed groups may have been an effect of surveying almost exclusively during the breeding and calving season. Although individuals in this population often form mixed age groups, previous research has indicated that consistent long-term associations between individuals of the same age class do exist within the social structure of the population (Baker *et al.*, 2018b).

The overall fission-fusion rate for Shannon Estuary bottlenose dolphin groups was about three changes every hour, that is, once every 20 min. In Shark Bay, bottlenose dolphin group composition can change 4–10 times per hour (Mann and Karniski, 2017). The highest fission-fusion rate recorded for any focal individual in the Shannon Estuary was 5.93 changes in group composition per hour. Interestingly, the individual with the highest fission-fusion rate (female ID# 118) was also the individual with the highest proportion of time spent alone; whereas previous work suggests that individuals with high fission-fusion rates would be those who spend the most time in groups rather than alone (Stanton

and Mann, 2014). Pearson (2008) found that, during focal group follows of dusky dolphins (*Lagenorhynchus obscurus*) in New Zealand, group composition changed every five minutes. In comparison, bottlenose dolphins groups in the Shannon Estuary exhibited much less fission and fusion, perhaps indicating a higher degree of group stability.

All of the focal dolphins in this study spent more of their time in groups than alone. In fact, although measures of sociality for bottlenose dolphins in the Shannon Estuary varied, most individual dolphins were quite sociable, with seven individuals observed in groups 100% of the time they were followed. However, these results could be biased as groups might be more likely to be spotted in the field compared to solitary animals. Overall, the average size of bottlenose dolphin groups that focal individuals spent time in was 6.6 individuals. While the range of mean group sizes per focal individual recorded in this population of 2.0–12.1 dolphins/group was similar to the range of group sizes recorded in Sarasota Bay, from 1.9 to 9.8 dolphins/group, the overall mean group size for Shannon Estuary focal dolphins was almost twice the mean group size of 3.8 individuals per group recorded for focal animals in Sarasota Bay (McHugh, 2010). However, the focal individuals in the Sarasota Bay study were all juveniles, while those in the present study were primarily adults, so this may have affected the average size of the groups individuals spent time in.

Shannon Estuary focal dolphins had a larger average number of identifiable associates per individual than reported for bottlenose dolphins in the Cedar Keys, Florida, with 71 associates vs. 55 associates per individual, respectively (Quintana-Rizzo and Wells, 2001). While the number of associates recorded for individuals in the Cedar Keys ranged from 10 to 85 (Quintana-Rizzo and Wells, 2001), Shannon Estuary dolphins had a similar upper limit of 86 associates but a much higher minimum number of 37 associates. This might point to Shannon Estuary dolphins having a larger or more fluid social network overall than Cedar Keys dolphins.

Measures of the number of associates an individual has can be biased by sampling effort and the sighting frequencies of different individuals. It is important to take this into account and provide additional measures such as number of associates per sighting. Still, this may not be truly representative of the actual number of individual associates each individual has because presumably those with a low number of sightings are likely to have smaller associate counts than those with a larger number of sightings, at least to some threshold number of sightings where the number of associates could potentially plateau. Nevertheless, it is worthwhile to report these results as number of associates is a valid and interesting measure of sociality. Unfortunately the standardization of this measure remains a challenge.

When standardized by number of sightings, female dolphins in the Shannon Estuary had more associates per sighting than males, suggesting that they have larger social networks. Similarly, Quintana-Rizzo and Wells (2001) found that females had an average 10 more associates than males (64 vs. 54 associates). The generally larger social networks of female dolphins have been widely reported in other populations (e.g., Shark Bay, Smolker *et al.*, 1992; Doubtful Sound, New Zealand, Lusseau *et al.*, 2003; Sarasota Bay, Wells, 2014) and the social network metrics of Shannon Estuary dolphins also indicate that females are more socially connected than males (Baker *et al.*, 2018b).

4.2 | Nearest-neighbor affiliations

Mann (1999) states that "observing the continuous stream of individual behavior in different contexts is central to the understanding of the dynamics of social relationships" and this emphasizes the importance of using focal follow techniques to examine close associations in detail. While previous research defined associations between individuals simply as group membership (i.e., two individuals were considered associated if they were in the same group), the nearest-neighbor data in the present study has allowed for a more detailed investigation into within-group affiliations. The finding of nearest-neighbor associations and sex-specific differences at an individual level supports the findings on individual preferences and differences found at a population level in previous studies (Baker *et al.*, 2018b); for example, Baker *et al.* (2018b) found long-term associations between female and male dolphins which are now complemented by the short-term female–male affiliations found in the present study.

Bottlenose dolphins in the Shannon Estuary, whether female or male, interacted with an average of 10 distinct nearest-neighbors. This is much less than the average number of 37 distinct individuals observed interacting as

nearest-neighbor with focal juvenile individuals in Sarasota Bay (McHugh, 2010). Juveniles may socialize more and have more connections as they grow up and develop, so these values may not be directly comparable.

Among adults of known sex, both adult females and adult males associated with more distinct adult females as within-group nearest-neighbor affiliates. While the genetic relatedness of individual dolphins in the Shannon Estuary is currently unknown, Wiszniewski, Lusseau, and Möller (2010) found that both female and male Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) seemed to target kin interactions with other females. In terms of distinct individuals that dolphins spent time with as their nearest-neighbor, both adult females and adult males had the same proportion (11%) of within-group affiliations with known adult males. This low proportion could partly be due to the lower number of known males in the population. If, for example, it turned out that all the remaining adult individuals of unknown sex in the population were male, the results would indicate that adult females had 32% female and 38% male nearest-neighbors and that adult males had 42% female and 30% male nearest-neighbors. In this case, there would still be a clear preference for adult males to affiliate closely with adult females, but a closer to equal preference for adult females to affiliate closely with either female or male nearest-neighbors. As it is unlikely that *all* individuals of unknown sex will turn out to be males, the preference of both females and males to associate closely with female nearest-neighbors seems to hold true. Contrastingly, in Sarasota Bay, juvenile dolphins preferred surfacing with members of the same sex (McHugh, 2010), whereas in the Shannon Estuary, both sexes of adults preferred their nearest-neighbor to be female.

There is some evidence to suggest variable sex ratios among bottlenose dolphin populations; for example, Manlik *et al.* (2016) report sex ratios of 50:50 and 45:55 male:female for the Shark Bay and Bunbury bottlenose dolphin populations, respectively. As the sex ratio of the Shannon Estuary bottlenose dolphin population is not yet known, it is possible that the preference calculations for female vs. male nearest-neighbors might be affected by an unequal sex ratio and this could alter the results of our findings.

When we categorized the type of pairing between each focal individual and her or his nearest-neighbor by sex class, the most frequent of nearest-neighbor affiliations were between adult female and adult male dolphins. There were no cases where an adult focal male spent the majority of his time with one of the other nine known adult males during a focal follow. Additionally, the proportion of time focal adult males spent with known adult female nearest-neighbors was significantly greater than time spent with known adult male nearest-neighbors. Again, these results may be affected by the lower number of known males in the population, but it remains likely that female–male pairings were more prevalent than either female–female or male–male pairings.

Although individuals usually showed strong preferences for a specific nearest-neighbor during each follow, the identity of their most frequent nearest-neighbor was prone to change from follow to follow. A "bond" or a pair of individuals with strong relationships across two "independent" interaction/association measures (Whitehead, 2008) was potentially found between four pairs of individuals, including two female–male pairs (the other two pairs contained individuals of unknown sex). It would be interesting, in future research, to establish whether different measures of association, such as Generalized Affiliation Indices (Whitehead and James, 2015; Zanardo, Parra, Diaz-Aguirre, Pratt, & Möller, 2018) provide additional evidence for the same bonds or suggest different ones.

While previous tests for preferred/avoided associations by sex (using HWIs) in this population suggested female–male association preferences but were inconclusive (Baker *et al.*, 2018b), the results of the present study, indicating female–male affiliative (nearest-neighbor) preferences, strengthen the likelihood that important female–male preferred associations exist in this population. Similarly, the lack of male–male preferred associations, from general HWI tests conducted by Baker *et al.* (2018b), further supports the absence of male–male affiliations and associations found in the present study.

4.3 | Sex-specific activity patterns

Female and male bottlenose dolphins in the Shannon Estuary had broadly similar activity budgets. Both female and male focal individuals engaged in traveling activity for more than half of the time they were under behavioral observation. Each of the two sexes also engaged in foraging, social, and resting behavior, although only males were

observed milling. Females allocated more time to traveling and resting, while males allocated more time to socializing and foraging. In the case of both males and females, activity budgets may be biased towards surface behaviors as distinct from subsurface behaviors, since the focal individual is initially always at the surface.

The fact that these differences were not strongly supported statistically means that any discussion of the effects of sex on activity budget must proceed with caution; however, in some cases effect size should take precedence over *p* values (Whitehead, 2008). For example, the observation that female dolphins spend more time traveling and resting than male dolphins may reflect a real biological difference. It is possible that female dolphins in the Shannon Estuary spend more time resting and traveling due to the presence of their dependent calves, who often surface alongside them in infant position. Indeed, on more than one occasion, the focal female had a newborn calf; Mann and Smuts (1999) showed that mother-calf pairs tend to swim synchronously and slowly (<2 mph) during the first eight weeks of life. Additional focal follow data on a wider range of individuals would provide a better test of whether real sex differences in activity budgets exist in this population.

While it is important to consider that consecutively sampled activity state data from focal follows are inherently autocorrelated, the small size of our data set precluded any potential subsampling of the data, because if subsampling is to occur, a large initial data set is required (Karniski *et al.*, 2015). Additionally, there is some evidence to suggest that eliminating autocorrelation can reduce the biological relevance of results (de Solla, Bonduriansky, & Brooks, 1999). In their thorough study of autocorrelation in survey and focal follow data collected on bottlenose dolphins, Karniski *et al.* (2015) concluded that complete focal follow data sets retain relevant behavioral autocorrelation that is otherwise not revealed in subsampled follow data. Nevertheless, future research on the activity budgets of Shannon Estuary dolphins should be carried out in order to collect more data; this would allow for a similar analysis to investigate the appropriate sample interval for studying the behavior of Shannon Estuary bottlenose dolphins, as suggested by Steiner (2011) in her study of bottlenose dolphins in the Port River Estuary, Australia.

4.4 | Male alliances

Male alliance formation occurs in several resident bottlenose dolphin populations including in Shark Bay, Australia (Connor and Krützen, 2015; Connor *et al.*, 1992), Sarasota Bay, Florida (Owen, Wells, & Hoffman, 2002; Wells, 1991), the Moray Firth, Scotland, and Cardigan Bay, Wales (Sim, 2015), and St. Johns River, Florida (Ermak *et al.*, 2017) and is an important component of the societal structure in these populations. It might be expected that the dolphin society of the Shannon Estuary would be most similar to those of the Moray Firth or Cardigan Bay because of their geographic proximity and the fact that they involve similarly sized populations in similar temperate environments (Sim, 2015). However, previous studies reporting on the social structure of the Shannon Estuary dolphin population found no evidence of sex segregation or single sex alliances in the population (Foley, McGrath, Berrow, & Gerritsen, 2010; Ingram, 2000). The only study that investigated dyads in the Shannon Estuary (Ingram, 2000) did not find sex-specific association patterns, but mentioned that most preferred pairings (i.e., those with the highest association index between two individuals) were between probable females and probable males.

In our study, there were preferred/avoided associations among male dolphins, but there was no evidence for male alliance formation in the Shannon Estuary population. That is to say, there were no pairs of male dolphins that had high levels of association and where each member of the male pair ranked as each other's closest associate. However, our results must be taken with caution, due to the low sample size (10 males), as it is possible that alliance-forming males could exist outside the pool of known sampled individuals. Interestingly, when looking at the associate of each male with whom he shared his maximum HWI, seven of the 10 associate individuals were female (and the other three of unknown sex). In his study of Shannon Estuary bottlenose dolphins, Ingram (2000) also noted that in 13 maximum associated dyads (in which the probable sex of both individuals was assigned), 12 were female–male pairs. Contrastingly, in Shark Bay, females were never the top ranked associates of males (Smolker *et al.*, 1992). In the present study, over half of the 10 known males' strongest associates were females. The fact that we could find

no examples of male–male pairings among most frequent nearest-neighbors adds further support to the suggestion that male alliances are not a feature of this population.

Additionally, during observations of dolphin behavior, there were no groups of dolphins that appeared to behave in any ways typical of male alliances recorded in other study sites. For example, we did not observe chasing, bolting, displays, or aggression (e.g., charging or biting) that are often typical components of the behaviors exhibited by male alliances and the females they are herding during consortship behavior in Shark Bay (Baker *et al.*, 2017; Connor and Krützen, 2015; Connor *et al.*, 1992). Similarly, we never recorded any instances of dolphins in the Shannon Estuary producing popping vocalizations, nor did the dolphins exhibit "formation swimming" typical of that shown by male alliances during herding behavior (males traveling just behind and to either side of the herded female; Connor *et al.*, 1992). This lack of behavioral evidence coupled with the reported results from data analysis support the idea that the Shannon Estuary bottlenose dolphins may not form male alliances.

Various factors have been suggested to explain the presence of male alliances in other populations, such as habitat use, population density (and thus the extent of individual interactions and mating opportunities) and reproductive rates (Connor *et al.*, 2017; Ermak *et al.*, 2017; Owen, 2003). Thus, it seems likely that the ecological, social and/or environmental pressures at play in the Shannon Estuary have an opposite influence that explains the lack of male alliance formation. In her research on the mating strategies of bottlenose dolphins (*T. truncatus*) in the St. Johns River, Florida, Ermak (2014) compared the population density of her study population with that of 11 others, including the Shannon Estuary, and noted the tendency of male alliances to be reported from the study sites with the greatest population densities (between 0.60 and 6.76 dolphins/km^2). Ermak (2014) also compared interbirth intervals between nine study sites and found that only the two with the highest IBIs (Shark Bay, Australia, and Sarasota Bay, Florida) reported having male alliances. More recently, Ermak *et al.* (2017) concluded that increased male–male competition, perhaps due to long interbirth intervals and high population density, seemed to best predict alliance formation in the St. Johns River dolphin population.

In the longest-running study of alliance formation in bottlenose dolphins (*T.* cf. *aduncus*) in Shark Bay (where dolphins exhibit the most complex alliance formation known outside of humans), Connor and Krützen (2015) have proposed various demographic and ecological explanations for male alliance formation. For instance, predator and prey abundance may impact alliance formation, along with habitat use. Connor and Krützen (2015) caution against reaching conclusions based on any strict single-factor relationships between cause and effect of alliance formation, suggesting it more likely that a range of contributing factors are at play; for example, although habitat use may influence alliance formation, they have recorded variation in the size of second-order alliances in all habitats, so it cannot be a sole determining factor. In agreement with Ermak (2014), Connor and Krützen (2015) believe that the rate at which males encounter rivals (i.e., encounter rate), especially in competition over females, will influence selection for alliance formation and thus may explain differences among populations of bottlenose dolphins in alliance formation. Population density, home range, and communication range (with sound traveling further in open water relative to shallow/subdivided habitats), may work together to affect encounter rates, and thus alliance formation (Connor and Krützen, 2015).

The potential impact of different demographic and ecological factors on the formation of male alliances may be correspondingly responsible for the lack of male alliance formation in the Shannon Estuary bottlenose dolphin population. For example, this population appears to have relatively low IBIs (2.7–3.5 years; Baker *et al.*, 2018a) and a relatively low population density (0.21 dolphins/km^2; Baker *et al.*, 2018a), consistent with Ermak's (2014) observations. Examining the other factors discussed by Connor and Krützen (2015) requires further research. In the absence of male alliances, alternative mating strategies must exist, and future research should focus on distinguishing and empirically investigating the possible mating systems of this population.

4.5 | Conclusions

This study complements previous research on the overall behavior and social structure of this bottlenose dolphin population and reveals interesting individual- and site-specific differences between the Shannon Estuary population

and other dolphin populations. Employing focal follows, we were able to investigate aspects of fine-scale sociality, such as fission-fusion rates and nearest-neighbor relationships that are difficult to study in survey-based research. We found that bottlenose dolphins in the Shannon Estuary formed relatively stable fission-fusion groups of around seven individuals, larger than in Cardigan Bay or the Moray Firth, but comparable to some other populations. Group composition changed roughly three times an hour, far less often than in Shark Bay. Individuals were rarely solitary and both females and males had many more associates in the population than in the Cedar Keys. Both females and males had more adult females as distinct nearest-neighbors, but the most frequent composition of within-group affiliate pairs was female–male, and focal males spent a significantly greater proportion of their time with female nearest-neighbors than with male nearest-neighbors, a strong difference from those in Sarasota Bay. Although activity budgets showed that female dolphins spent more time traveling and resting, and less time socializing, foraging, and milling, than male dolphins, these differences were relatively small. In great contrast to Shark Bay, there was no evidence for male alliance formation in the Shannon Estuary population and over half of the 10 known males' top-ranked associates were females.

Research on the fine-scale sociality of bottlenose dolphin populations is challenging and requires detailed data collection and analysis coupled with long-term data sets. This study contributes to current knowledge of bottlenose dolphin sociality, association patterns and mating systems, and especially to an increase in the information available for populations in temperate coastal waters, as well as demonstrating the value added to survey data by employing focal follows. The presence of a potentially different societal structure to those known thus far in bottlenose dolphin societies globally emphasizes the importance of continuing to monitor and protect this population.

ORCID

Isabel Baker https://orcid.org/0000-0003-4265-2042
Joanne O'Brien https://orcid.org/0000-0003-0296-2660
Katherine McHugh https://orcid.org/0000-0002-6948-5427
Simon Berrow https://orcid.org/0000-0001-9226-6567

REFERENCES

Adams, J. D., Speakman, T., Zolman, E., & Schwacke, L. H. (2006). Automating image matching, cataloging, and analysis for photo-identification research. *Aquatic Mammals*, *32*, 374–384.
Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*, 227–267.

Augusto, J. F., Rachinas-Lopes, P., & dos Santos, M. E. (2011). Social structure of the declining resident community of common bottlenose dolphins in the Sado Estuary, Portugal. *Journal of the Marine Biological Association of the United Kingdom*, *92*, 1773–1782.

Baker, I. (2015). *Researcher's guide to protocols for fieldwork and data entry* (3rd ed.). Kilrush, County Clare, Ireland: Shannon Dolphin and Wildlife Foundation.

Baker, I., O'Brien, J., McHugh, K., & Berrow, S. (2017). An ethogram for bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland. *Aquatic Mammals*, *43*, 594–613.

Baker, I., O'Brien, J., McHugh, K., & Berrow, S. (2018a). Female reproductive parameters and population demographics of bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland. *Marine Biology*, *165*, 15.

Baker, I., O'Brien, J., McHugh, K., Ingram, S., & Berrow, S. (2018b). Bottlenose dolphin (*Tursiops truncatus*) social structure in the Shannon Estuary, Ireland, is distinguished by age- and area-related associations. *Marine Mammal Science*, *34*, 458–487.

Barker, J., & Berrow, S. (2016). Temporal and spatial variation in group size of bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy*, *116B*, 63–70.

Bearzi, G., Notarbartolo di Sciara, G., & Politi, E. (1997). Social ecology of bottlenose dolphins in the Kvarnerić (Northern Adriatic Sea). *Marine Mammal Science*, *13*, 650–668.

Berrow, S. D. (2009). Winter distribution of bottle-nosed dolphins (*Tursiops truncatus* [Montagu]) in the inner Shannon Estuary. *Irish Naturalists' Journal*, *30*, 35–39.

Berrow, S. D., & Holmes, B. (1999). Tour boats and dolphins: A note on quantifying the activities of whalewatching boats in the Shannon estuary, Ireland. *Journal of Cetacean Research and Management*, *1*, 199–204.

Berrow, S. D., Holmes, B., & Kiely, O. R. (1996). Distribution and abundance of bottle-nosed dolphins *Tursiops truncatus* (Montagu) in the Shannon Estuary. *Biology and environment: Proceedings of the Royal Irish Academy*, *96B*, 1–9.

Berrow, S. D., McHugh, B., Glynn, D., McGovern, E., Parsons, K. M., Baird, R. W., & Hooker, S. K. (2002). Organochlorine concentrations in resident bottlenose dolphins (*Tursiops truncatus*) in the Shannon estuary, Ireland. *Marine Pollution Bulletin*, *44*, 1296–1313.

Berrow, S. D., O'Brien, J., Groth, L., Foley, A., & Voigt, K. (2012). Abundance estimate of bottlenose dolphins (*Tursiops truncatus*) in the Lower River Shannon candidate Special Area of Conservation, Ireland. *Aquatic Mammals*, *38*, 136–144.

Bicca-Marques, J. C., & Calegaro-Marques, C. (1994). Activity budget and diet of *Alouatta caraya*: An age-sex analysis. *Folia Primatologica*, *63*, 216–220.

Bristow, T., & Rees, E. I. S. (2001). Site fidelity and behaviour of bottlenose dolphins (*Tursiops truncatus*) in Cardigan Bay, Wales. *Aquatic Mammals*, *27*, 1–10.

Cairns, S. J., & Schwager, S. J. (1987). A comparison of association indices. *Animal Behaviour*, *35*, 1454–1469.

Clutton-Brock, T. H. (1977). Some aspects of intraspecific variation in feeding and ranging behaviour in primates. In T. H. Clutton-Brock (Ed.), *Primate ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes* (pp. 539–556). London, UK: Academic Press Inc.

Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton, NJ: Princeton University Press.

Connor, R. C., & Krützen, M. (2015). Male dolphin alliances in Shark Bay: Changing perspectives in a 30-year study. *Animal Behaviour*, *103*, 223–235.

Connor, R. C., Cioffi, W. R., Randic, S., Allen, S. J., Watson-Capps, J., & Krutzen, M. (2017). Male alliance behaviour and mating access varies with habitat in a dolphin social network. *Scientific Reports*, *7*, 46354.

Connor, R. C., Smolker, R. A., & Richards, A. F. (1992). Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proceedings of the National Academy of Sciences of the United States of America*, *89*, 987–990.

Connor, R. C., Wells, R. S., Mann, J., & Read, A. J. (2000). The bottlenose dolphin: Social relationships in a fission-fusion society. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.). *Cetacean societies* (pp. 91–125). Chicago, IL: University of Chicago Press.

de Solla, S. R., Bonduriansky, R., & Brooks, R. J. (1999). Eliminating autocorrelation reduces biological relevance of home range estimates. *Journal of Animal Ecology*, *68*, 221–234.

Ermak, J. (2014). *The social structure and mating strategies of bottlenose dolphins (Tursiops truncatus) in the St. Johns River* (Master's thesis). University of North Florida, Jacksonville, FL.

Ermak, J., Brightwell, K., & Gibson, Q. (2017). Multi-level dolphin alliances in northeastern Florida offer comparative insight into pressures shaping alliance formation. *Journal of Mammalogy*, *98*, 1096–1104.

Foley, A., McGrath, D., Berrow, S., & Gerritsen, H. (2010). Social structure within the bottlenose dolphin (*Tursiops truncatus*) population in the Shannon Estuary, Ireland. *Aquatic Mammals*, *36*, 372–381.

Genov, T., Centrih, T., Kotnjek, P., & Hace, A. (2019). Behavioural and temporal partitioning of dolphin social groups in the northern Adriatic Sea. *Marine Biology*, *166*, 11.

Gibson, Q. A., & Mann, J. (2008). The size, composition and function of wild bottlenose dolphin (*Tursiops* sp.) mother–calf groups in Shark Bay, Australia. *Animal Behaviour*, *76*, 389–405.

Hemingway, C. A. (1999). Time budgets and foraging in a Malagasy primate: Do sex differences reflect reproductive condition and female dominance? *Behavioral Ecology and Sociobiology*, *45*, 311–322.

Ingram, S. N. (2000). *The ecology and conservation of bottlenose dolphins in the Shannon Estuary, Ireland* (Doctoral dissertation). University College Cork, Cork, Ireland.

Karniski, C., Patterson, E. M., Krzyszczyk, E., Foroughirad, V., Stanton, M. A., & Mann, J. (2015). A comparison of survey and focal follow methods for estimating individual activity budgets of cetaceans. *Marine Mammal Science*, *31*, 839–852.

Levesque, S., Reusch, K., Baker, I., O'Brien, J., & Berrow, S. (2016). Photo-identification of bottlenose dolphins (*Tursiops truncatus*) in Tralee Bay and Brandon Bay, Co. Kerry: A case for SAC boundary extension. *Biology and Environment: Proceedings of the Royal Irish Academy*, *116B*, 1–10.

Lusseau, D., Schneider, K., Boisseau, O. J., Haase, P., Slooten, E., & Dawson, S. M. (2003). The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations. *Behavioral Ecology and Sociobiology*, *54*, 396–405.

Lusseau, D., Wilson, B., Hammond, P. S., Grellier, K., Durban, J. W., Parsons, K. M., ... Thompson, P. M. (2006). Quantifying the influence of sociality on population structure in bottlenose dolphins. *Journal of Animal Ecology*, *75*, 14–24.

Magurran, A. E., & Macías Garcia, C. (2000). Sex differences in behaviour as an indirect consequence of mating system. *Journal of Fish Biology*, *57*, 839–857.

Manlik, O., McDonald, J. A., Mann, J., Raudino, H. C., Bejder, L., Krützen, M., ... Sherwin, W. B. (2016). The relative importance of reproduction and survival for the conservation of two dolphin populations. *Ecology and Evolution*, *6*, 3496–3512.

Mann, J. (1999). Behavioral sampling methods for cetaceans: A review and critique. *Marine Mammal Science*, *15*, 102–122.

Mann, J., & Karniski, C. (2017). Diving beneath the surface: Long-term studies of dolphins and whales. *Journal of Mammalogy*, *98*, 621–630.

Mann, J., & Smuts, B. B. (1999). Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour*, *136*, 529–566.

Mann, J., Connor, R. C., Tyack, P. L., & Whitehead, H. (2000). *Cetacean societies: Field studies of dolphins and whales*. Chicago, IL: University of Chicago Press.

Maritime Safety Directorate. (2005). *Marine Notice No. 15 of 2005*. Dublin, Ireland: Department of Communications Marine and Natural Resources.

McCann, C. M., & Rothman, J. M. (1999). Changes in nearest-neighbor associations in a captive group of western lowland gorillas after the introduction of five hand-reared infants. *Zoo Biology*, *18*, 261–278.

McHugh, K. A. (2010). *Behavioral development of free-ranging juvenile bottlenose dolphins (Tursiops truncatus) in Sarasota Bay, Florida (Doctoral dissertation)*. Davis, CA: University of California Davis.

McHugh, K. A., Allen, J. B., Barleycorn, A. A., & Wells, R. S. (2011a). Natal philopatry, ranging behavior, and habitat selection of juvenile bottlenose dolphins in Sarasota Bay, Florida. *Journal of Mammalogy*, *92*, 1298–1313.

McHugh, K. A., Allen, J. B., Barleycorn, A. A., & Wells, R. S. (2011b). Severe *Karenia brevis* red tides influence juvenile bottlenose dolphin (*Tursiops truncatus*) behavior in Sarasota Bay, Florida. *Marine Mammal Science*, *27*, 622–643.

Mirimin, L., Miller, R., Dillane, E., Berrow, S. D., Ingram, S., Cross, T. F., & Rogan, E. (2011). Fine-scale population genetic structuring of bottlenose dolphins in Irish coastal waters. *Animal Conservation*, *14*, 342–353.

National Parks and Wildlife Service. (2012). *Conservation objectives: Lower River Shannon SAC 002165. Version 1.0*. Ireland: Dublin.

O'Brien, J., Baker, I., Barker, J., Berrow, S., Ryan, C., O'Connell, M., & O'Donoghue, B. (2014). The first confirmed successful refloat of a stranded bottlenose dolphin (*Tursiops truncatus*) in Ireland and subsequent resighting with a neonate. *Aquatic Mammals*, *40*, 191–194.

Owen, E. (2003). *The reproductive and ecological functions of the pair-bond between allied, adult male bottlenose dolphins, Tursiops truncatus, in Sarasota Bay, Florida* (Doctoral dissertation). University Of California Santa Cruz, Santa Cruz, CA.

Owen, E. C. G., Wells, R. S., & Hofmann, S. (2002). Ranging and association patterns of paired and unpaired adult male Atlantic bottlenose dolphins, *Tursiops truncatus*, in Sarasota, Florida, provide no evidence for alternative male strategies. *Canadian Journal of Zoology*, *80*, 2072–2089.

Pearson, H. C. (2008). *Fission-fusion sociality in dusky dolphins (Lagenorhynchus obscurus) with comparisons to other dolphins and great apes (Doctoral dissertation)*. College Station, TX: Texas A&M University.

Powell, J. R., & Wells, R. S. (2011). Recreational fishing depredation and associated behaviors involving common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Marine Mammal Science*, *27*, 111–129.

Quintana-Rizzo, E., & Wells, R. S. (2001). Resighting and association patterns of bottlenose dolphins (*Tursiops truncatus*) in the Cedar Keys, Florida: Insights into social organisation. *Canadian Journal of Zoology*, *79*, 447–456.

R Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Samuels, A. (1996). *A systematic approach to measuring the social behavior of bottlenose dolphins* (Doctoral dissertation). Woods Hole Oceanographic Institution, Woods Hole, MA.

Scott, M. D., Wells, R. S., & Irvine, A. B. (1990). A long term study of bottlenose dolphins on the west coast of Florida. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 235–244). San Diego, CA: Academic Press.

SDRP. (2006). *Manual for field research and laboratory activities*. Sarasota, FL: Sarasota Dolphin Research Program.

Sim, T. (2015). *Associations or alliances? Comparisons of social relationships between male bottlenose dolphins (Tursiops truncatus) in Cardigan Bay and the Moray Firth* (Master's thesis). Bangor University, Bangor, Wales.

Smith, H. C., Pollock, K., Waples, K., Bradley, S., & Bejder, L. (2013). Use of the robust design to estimate seasonal abundance and demographic parameters of a coastal bottlenose dolphin (*Tursiops aduncus*) population. *PLoS ONE*, *8*(10), e76574.

Smolker, R. A., Richards, A. F., Connor, R. C., & Pepper, J. W. (1992). Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour*, *123*, 38–69.

Stanton, M. A., & Mann, J. (2014). Shark Bay bottlenose dolphins: A case study for defining and measuring sociality. In J. Yamagiwa & L. Karczmarski (Eds.), *Primates and cetaceans* (pp. 115–126). Tokyo, Japan: Springer.

Steiner, A. (2011). Activity budget of inshore Indo-Pacific bottlenose dolphins (*Tursiops aduncus*): A critical evaluation of methods and comparison among other populations. *Marine Mammal Science*, *27*, 20–38.

Waples, D. M. (1995). *Activity budgets of free-ranging bottlenose dolphins (Tursiops truncatus) in Sarasota Bay, Florida* (Master's thesis). University of California Santa Cruz, Santa Cruz, CA.

Wells, R. S. (1991). The role of long-term study in understanding the social structure of a bottlenose dolphin community. In K. Pryor & K. S. Norris (Eds.), *Dolphin societies: Discoveries and puzzles* (pp. 199–225). Berkeley, CA: University of California Press.

Wells, R. S. (2014). Social structure and life history of bottlenose dolphins near Sarasota Bay, Florida: Insights from four decades and five generations. In J. Yamagiwa & L. Karczmarski (Eds.), *Primates and cetaceans* (pp. 149–172). Tokyo, Japan: Springer.

Wells, R. S., Scott, M. D., & Irvine, A. B. (1987). The social structure of free-ranging bottlenose dolphins. In H. H. Genoways (Ed.), *Current Mammalogy* (pp. 247–305). New York, NY: Plenum Press.

Whitehead, H. (2008). *Analyzing animal societies: Quantitative methods for vertebrate social analysis*. Chicago, IL: University of Chicago Press.

Whitehead, H. (2009). SOCPROG programs: Analysing animal social structures. *Behavioral Ecology and Sociobiology*, *63*, 765–778.

Whitehead, H., & James, R. (2015). Generalized affiliation indices extract affiliations from social network data. *Methods in Ecology and Evolution*, *6*, 836–844.

Wilson, B. (1995). *The ecology of bottlenose dolphins in the Moray Firth, Scotland: A population at the northern extreme of the species' range* (Doctoral dissertation). University of Aberdeen, Aberdeen, Scotland.

Wiszniewski, J., Lusseau, D., & Möller, L. M. (2010). Female bisexual kinship ties maintain social cohesion in a dolphin network. *Animal Behaviour*, *80*, 895–904.

Würsig, B., & Jefferson, T. A. (1990). Methods of photo-identification for small cetaceans. *Report of the International Whaling Commission*, (Special Issue 12), 23–52.

Würsig, B., & Würsig, M. (1977). The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). *Science*, *198*, 755–756.

Zanardo, N., Parra, G. J., Diaz-Aguirre, F., Pratt, E. A. L., & Möller, L. M. (2018). Social cohesion and intra-population community structure in southern Australian bottlenose dolphins (*Tursiops* sp.). *Behavioral Ecology and Sociobiology*, *72*, 156.