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# An Ethogram for Bottlenose Dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland

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## Abstract

Ethograms, or categorized lists of behavioral descriptors, are fundamental research tools in the study of animal behavior and are essential to the overall understanding of the behavioral ecology of a species. With specific definitions of activity state categories and behavioral event types, the behavior of a species can be described, quantified, and compared across populations. We present the first ethogram for bottlenose dolphins (*Tursiops truncatus*) in Ireland based on sighting records collected during 256 surveys (2014-2016) in the Shannon Estuary. The ethogram consists of 11 activity states and 45 behavioral events. The most frequently recorded activity state was *Travel* (52%), while the most frequently recorded behavioral events were *Slow travel* (40% of sightings), *Surface rush* (28% of sightings), and *Leap* (28% of sightings). The ten least frequently recorded behaviors were seen in only 10% of total sightings with < 8 records each. A video test for multiple researchers to assess inter-observer reliability in behavioral data recording demonstrated the validity of this study's behavioral data and the efficacy of the ethogram in its applicability to other studies. Validity (percentage agreement = 88.1 ± 7.0) and reliability (Fleiss' Kappa = 0.81) scores were high across 24 test participants (12 trained and 12 untrained), but results indicated that those with prior training scored significantly higher. Furthermore, we investigate the presence/absence of behaviors recorded in other studies of bottlenose dolphins. This ethogram and behavioral discussion serve to describe and compare quantitative data on the behavior of bottlenose dolphins in Ireland for the first time and provide a strong basis for further research.

**Key Words:** ethogram, repertoire, bottlenose dolphin, *Tursiops truncatus*, Shannon Estuary, Special Area of Conservation

## Introduction

Understanding the repertoire of behaviors exhibited by a species, particularly when a population is composed of individually recognizable animals, is crucial to providing baseline scientific data for many avenues of study. To allow for accurate comparison between study sites, it is important to standardize terms and categories used in behavioral research (Masatomi, 2004). Precise descriptions, definitions, and quantification of behaviors provide a valuable standard that can be used for the systematic and quantitative study of bottlenose dolphin (*Tursiops truncatus*) behavior, especially in understudied wild populations (Martin & Bateson, 1986; Lichtenberg & Hallager, 2007). Baseline data on the behavioral repertoire of a species must be collected before more complex analytical procedures can be introduced (Lehner, 1996). A systematic presentation of categorical definitions and of the specific behaviors within each category, known as an ethogram, is a fundamental research tool in the study of behavior (Mann et al., 2000). Ethograms aim to describe the full behavioral repertoire of a species (in the habitat under study) and can be the foundation(s) of research contributing to knowledge and conservation of the species as a whole (Hill et al., 2015). They are essential for collecting and analyzing sound scientific data and, thus, for understanding the behavioral repertoire of a species. In particular, when multiple observers are used to collect behavioral data, the preparation and use of an ethogram can facilitate consistency in recording (Margulis, 2010).

Ethograms have been developed for a wide range of taxa in the field of animal behavior, including chimpanzees (*Pan troglodytes*) (e.g., Nishida et al., 1999; Hobaiter & Byrne, 2011), elephants (e.g., Esposito, 2008; Riyas Ahamed, 2015), birds (e.g., Masatomi, 2004; Lichtenberg & Hallager, 2007), river otters (*Lontra canadensis*; e.g., Green et al., 2015), and fish (e.g., Bolgan et al., 2016), and have also been developed for some cetacean species (e.g., humpback whales [*Megaptera novaeangliae*], Kavanagh et al., 2016; pilot whales [*Globicephala* sp.], Scheer et al., 2004; and belugas [*Delphinapterus leucas*], Howe et al., 2015).

As one of the most extensively studied cetaceans, information on bottlenose dolphins (*Tursiops* spp.) and accounts of their surface behavior have been widely published (Shane et al., 1986; Connor et al., 2000b). There are some general surface behavior ethograms for specific populations (e.g., USA: Shane, 1990; Croatia: Bearzi et al., 1999; New Zealand: Lusseau, 2006b; Australia: Steiner, 2011), but many published studies place specific emphasis on particular associations such as mother–infant relationships (e.g., Gubbins et al., 1999; Mann & Smuts, 1999), behaviors such as foraging (e.g., Nowacek, 2002; Sargeant et al., 2006; Sargeant & Mann, 2009), or human interactions (e.g., Jaiteh et al., 2013). In many cases, ethograms come from research on captive dolphins (e.g., von Streit, 2011) or are limited to describing only the broad activity state categories (e.g., Mann & Watson-Capps, 2005; Genov et al., 2008; Baş et al., 2015; Karniski et al., 2015).

In the study of animal behavior, it is important to distinguish between *states* (long-duration behaviors) and *events* (short-duration behaviors) (Altmann, 1974; Connor et al., 2000b). For example, *eyes open* is a behavioral state of some duration, whereas *blinking* is an essentially instantaneous behavioral event (Nowacek, 2002). Herein, we use the terms *activity state* and *behavioral event* to distinguish between these two types of behavior.

A table of behavioral definitions was published by Bearzi et al. (1999) for bottlenose dolphins in the Adriatic Sea, largely based on work carried out in the United States (Weaver, 1987; Shane, 1990). Bottlenose dolphin surface behavior has also been studied to varying degrees in other European study sites (e.g., Italy: Díaz López & Shirai, 2008; Slovenia: Genov et al., 2008; Portugal: Augusto et al., 2011). No ethograms currently exist for any of the three discrete populations of bottlenose dolphins in Ireland (including the resident population in the Shannon Estuary) or for the two geographically closest resident populations in the Moray Firth, Scotland, and Cardigan Bay, Wales.

There have been few detailed behavioral studies of dolphins in the temperate waters of the northeast Atlantic. A number of studies in Ireland have included behavioral components, mainly as part of impact assessments focusing on cause and effect (e.g., behavioral responses to acoustic pingers; Leeney et al., 2007). Some studies of behavior in common dolphins (*Delphinus delphis*; Berrow et al., 2008) and killer whales (*Orcinus orca*; Ryan & Wilson, 2003) have also been conducted. In the Moray Firth and Cardigan Bay, researchers have used broad categories to record bottlenose dolphin behavior (e.g., Pierpoint et al., 2009; Pirotta et al., 2015), but information on specific behavioral events within activity state categories for these populations is lacking.

Few published papers present basic activity budget data on the frequency of activity states in cetacean populations (Mann & Würsig, 2014), even though these are important data for understanding the life history of a species and informing conservation management (Karniski et al., 2015). Even fewer studies present behavioral event data in which the distinct surface behaviors of wild bottlenose dolphins are described and their occurrence quantified, with only a handful of studies attempting to then explain the context and purpose of these surface behaviors (e.g., Lusseau, 2006a; Furuichi et al., 2014). However, the collection of behavioral data is integral to the overall understanding of animal populations (Lehner, 1996).

When sighting data on activity states and behavioral events are collected by multiple independent observers, tests are required to assess the reliability and validity of these data (Martin & Bateson, 1986; Kaufman & Rosenthal, 2009). The literature on the collection and analysis of data on cetacean surface behavior contains few examples of such tests (Mann, 1999). Kavanagh et al. (2016) carried out inter-observer reliability tests using video data during a study of humpback whales to examine the effects of observers' experience and native language on data reliability and validity. Using video data incorporating 16 behavioral event types, they found that neither factor had a significant effect on behavioral data recording by observers. However, their test results did highlight specific behavioral event types that were more accurately and consistently recorded than others, and they suggested that future studies could use similar tests to assess the suitability of specific behavioral event types for analysis.

The bottlenose dolphin population in the Shannon Estuary, Ireland, is composed of about 120 individuals (Berrow et al., 2012) and is genetically discrete (Mirimin et al., 2011). Dolphins are present in the estuary year-round (Berrow et al., 1996; Ingram, 2000; Berrow, 2009) and have been observed exclusively in the Shannon Estuary and adjacent Tralee and Brandon Bays (Ryan &

Berrow, 2013; Levesque et al., 2016). This species also occurs around the entire Irish coast (O'Brien et al., 2009) and in offshore waters (Louis et al., 2014), but these are thought to constitute distinct populations (Oudejans et al., 2015). The Shannon Estuary is a Special Area of Conservation (SAC) for bottlenose dolphins (National Parks and Wildlife Service [NPWS], 2012), which are listed in Annex II of the European Union Habitats Directive. Given the level of protection assigned to this population, information on the behavior of dolphins in the estuary is vital for their long-term conservation and the development of specifically tailored management plans.

This article aims to describe a detailed ethogram for wild bottlenose dolphins in the Shannon Estuary, to provide some quantitative data on the frequency of different activity states and behavioral events, and to report the presence or absence of behaviors recorded in other studies. Its more general aim is to provide a tool for future bottlenose dolphin behavioral research that will give insight into the behavioral repertoire and activity budget of bottlenose dolphins in the estuary and highlight common and rare behaviors. A greater understanding of bottlenose dolphin behavior will contribute towards the management and conservation of bottlenose dolphin stocks in Ireland (especially those in SACs) (NPWS, 2012) and of the species throughout its geographical range.

## Methods

*Study Site and Vessels*

The study site was within the Lower River Shannon SAC (Site Code: 002165) for bottlenose dolphins, a 684 km$^2$ Natura 2000 designated site (NPWS, 2012) on Ireland's west coast between Co. Clare, Co. Kerry, and Co. Limerick (52° 36' N, 9° 38' W). Surveys occurred west of Shannon Airport and east of Loop Head and Kerry Head (Figure 1).

Long-term photo-identification studies of bottlenose dolphins in the Shannon Estuary have been ongoing since the early 1990s (Berrow et al., 2010, 2012; O'Brien et al., 2014). Additionally, over this time period, a dolphin-watching tourism industry has been established in which two main companies operate dolphin-watching tour boats and provide opportunistic platforms for research (Berrow & Holmes, 1999). The dolphin-watching tour boats, *Draíocht* and *Dolphin Discovery*, operated from the ports of Carrigaholt and Kilrush, respectively

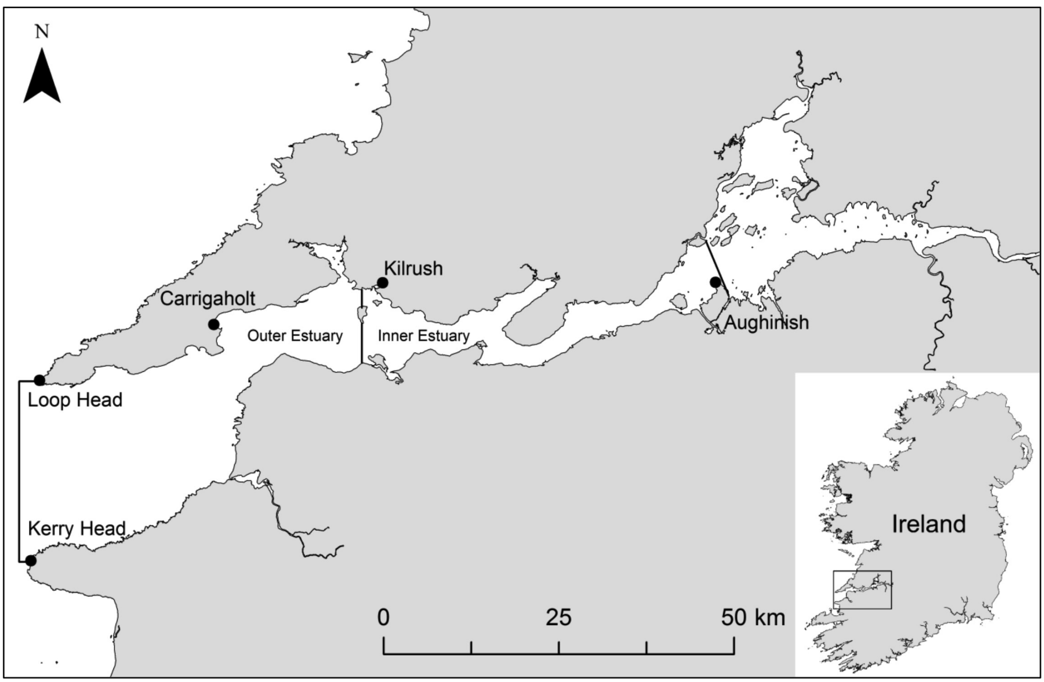


**Figure 1.** Map of the Shannon Estuary study site in Ireland. The line between Loop Head and Kerry Head represents the western boundary of the Special Area of Conservation (SAC), while the line at Aughinish represents the boundary of the area within the SAC surveyed during this study. The study site is divided between the outer and inner estuary areas by a north-south line drawn through Scattery Island near Kilrush.

(Figure 1). *Draíocht* and *Dolphin Discovery* primarily concentrated effort in the outer and inner estuary areas, respectively, with a mean dolphin-watching trip length of 2.3 h (Berrow & Ryan, 2009; Barker & Berrow, 2016). The research vessel based in Kilrush was a 6-m XS RIB (rigid-hulled inflatable boat) with which surveys were conducted throughout all areas of the estuary. Observers on the Carrigaholt tour boat were positioned on the top deck at a height of ~4 m, while observations from the Kilrush tour boat and the research vessel were made from the bow of the boats at < 1 m above sea level. In general, behavioral observations were made visually, but observers were also equipped with digital SLR cameras (Nikon D300 or Canon EOS 20D with 70 to 300 mm lenses), binoculars (Minox 7 × 50 or 8 × 42), GPS (Garmin 72H), and datasheets.

*Data Collection*

In addition to reviewing published ethograms (e.g., Weaver, 1987; Shane, 1990), eight researchers who manage different bottlenose dolphin research projects worldwide were contacted for expert advice and information on ethograms from the populations with which they work to gain insight for constructing our initial ethogram. These research projects and study sites were chosen based on geographical region, personal contacts, and length of study.

A pilot study was carried out in the Shannon Estuary in 2013 from commercial dolphin-watching tour boats and a dedicated research vessel to collect behavioral data, refine bottlenose dolphin behavioral event descriptors, and determine if it was necessary to supplement the proposed ethogram with additional behaviors observed in the field.

Activity states and behavioral events were subsequently recorded during three field seasons: (1) March-September 2014, (2) June-September 2015, and (3) May-September 2016. Observers made visual observations from the three different platforms previously described. Sighting datasheets were completed during every survey in which encounters with dolphin groups (sightings) occurred. A 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). A *group* was defined as all animals sighted together moving in the same general direction, engaged in similar activities, or interacting with each other within a radius of approximately 100 m (McHugh et al., 2011a).

Behavioral data collection methods were based on the recommendations of Mann (1999) who defines the two basic sampling decisions as (1) *follow protocol*—the length of observation and the choice of subject(s)—and (2) *sampling method*—the procedure used to sample behavior. The follow protocol used was *survey*, with sightings providing a snapshot of dolphin activity, including group estimates, GPS location, and behaviors. The sampling methods used were predominant group activity sampling, one-zero sampling, and *ad libitum* sampling. *Predominant group activity sampling* involved selecting the activity state that > 50% of individuals in a group were engaged in within the first 5 min of a sighting; *one-zero sampling* involved scoring whether or not specific behavioral events occurred within the first 5 min of a sighting; and ad libitum *sampling* was used to make additional anecdotal comments throughout the duration of a sighting.

For each sighting, the observer selected one of six options—(1) Rest, (2) Travel, (3) Social, (4) Forage, (5) Other, and (6) Unknown—as the predominant (> 50% of individuals) group activity state during the first 5 min of a sighting. Five minutes was used as the initial period within which to record behavior in an effort to record how the dolphins were most likely to have been behaving before the boat arrived in the vicinity. In addition, the observer circled all behaviors seen within the first 5 min from the behavioral events listed on the datasheet and recorded additional activity states and behavioral events (after 5 min) in the Comments section of the datasheet with the time of occurrence.

*Inter-Observer Validity and Reliability Testing*

During dedicated behavioral surveys from the research RIB, video footage of bottlenose dolphins was recorded. Seventeen segments, each < 35 s in duration, were extracted from these videos for three of the ethogram's major activity states and 14 behavioral event types and used to assess inter-observer reliability in selecting visually observed behaviors. (The video segments are available on the "Supplementary Material" page of the *Aquatic Mammals* website: www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147.) To verify the video test behaviors, an experienced dolphin behavior researcher (KM) completed the test prior to commencement of trials. The expert's answers matched those of the test designer and compiler of the overall ethogram (IB) prior to the test going live.

The 17 videos were shown to 24 people—12 trained research assistants who collected the data and 12 other marine biologists with no previous marine mammal behavior research experience and who had not participated in the fieldwork of this study. Each trained research assistant had at least 2 wks of training in fieldwork methods, equipment usage, and data collection protocols with the Shannon Dolphin and Wildlife Foundation before independently collecting data. At the end of the final field season, each participant was provided with a copy of the ethogram and was requested to identify the activity state or behavioral event exhibited by the dolphin(s) in each video segment—that is, to code each clip.

Using similar methodologies to Kavanagh et al. (2016), percentage agreement and Kappa score statistical analyses were employed to measure the validity and reliability of the behaviors recorded by the test participants (Kaufman & Rosenthal, 2009). Percentage agreement was calculated to measure how often observers agreed on the correct classification of a behavior (Martin & Bateson, 1986). Percentage agreement scores were calculated for each of the behaviors and each of the test participants. As validity data were non-normally distributed (Levene's test), Mann-Whitney U tests were used to compare validity scores between trained and other test participants (Venables & Ripley, 2002).

Kappa scores (which include a correction for chance) were used to examine the reliability of the recording of individual behaviors by each observer (Fleiss, 1971; Conger, 1980), using the designer's (IB) scores as baseline data within the *R* (R Core Team, 2016) package *irr* (Gamer et al., 2012). Category-wise Kappa scores were generated for all behaviors used in the test. These scores compute the probability of a randomly chosen observer assigning a specific behavior to a video given that another randomly chosen observer has also assigned that behavior to that video. Where behaviors were misclassified (i.e., a participant selected a different behavior to the baseline), the behavior most frequently selected in each case was recorded and presented.

The test had two aims: (1) to establish whether trained observers agreed sufficiently well to validate the behavioral data collected and used in the present study, and (2) to validate the broader use of the ethogram by marine biologists to accurately record dolphin behavior (which could reduce significant variability in long-term monitoring projects).

*Behavioral Analysis*

Activity state and behavioral event data were entered into a specially adapted version of *FinBase* (*MS Access*), a relational sightings database for bottlenose dolphin research (Adams et al., 2006). Using one form per sighting, activity states were entered as Initially Observed (first 5 min) and sometimes as Observed (after 5 min) if an additional activity state was recorded in the Comments section. A specifically designed ethogram subform within the sighting form in *FinBase* was used to enter all of the behavioral events recorded during each sighting.

Behavioral data from sightings were queried in *FinBase*, and summary statistics were calculated using *MS Excel* and *R* (R Core Team, 2016). Analyses used predominant group activity data recorded exclusively within the first 5 min of each sighting, while both one-zero and *ad libitum* behavioral event data were used for behavioral events analysis. Percentage occurrence and activity budgets were calculated by summing the records of each behavior from the sightings and dividing by the total number of data points.

In addition to the written data recorded during sightings, photographs were taken simultaneously, primarily for photo-identification of individuals but with the benefit of obtaining photographic data on behaviors. Photos from all surveys and sightings were maintained in a database using the photographic software environment *IMatch*, Version 5.6 (https://photools.com; Westphal, 2016). The Categories Assignment tool was used to categorize every photo in which a behavioral event from the ethogram was exhibited by one or more dolphins. These photographs were used during the training of multiple observers for collecting behavioral data in the field.

*Comparison with Other Studies*

Data from other studies of bottlenose dolphin behavior were gathered to generate tables comparing the activity states of the Shannon Estuary dolphins with those of other populations. The classification of behaviors, terminology, and definitions employed by these studies were compared with those used in the present study. Behavioral events that have been described in other studies but which have not (yet) been observed or recorded in the present study were noted.

## Results

*Summary of Data Collection*

Of the 489 sightings (256 surveys), 209 sightings (91 surveys) were made from the tour boat *Draíocht*, 154 sightings (116 surveys) were made from the tour boat *Dolphin Discovery*, and 126 sightings (49 surveys) were made from the research RIB. Overall, 18 observers contributed sighting records to the database, but the top ten observers with the most records collectively contributed the data from 81% (395) of the sightings.

In 2014, 2015, and 2016, both activity states and behavioral events were recorded for 193 sightings (100 surveys), 145 sightings (76 surveys), and 151 sightings (80 surveys), respectively. However, no behavioral events were observed in 62 of these sightings (14, 24, and 24 sightings in 2014, 2015, and 2016, respectively). Thus, a total of 489 sighting records with activity states and 427 sighting records with behavioral events were available for analysis. The average length of a sighting was 24 min, representing approximately 200 h of total dolphin observation time. Overall survey effort was approximately 765 h.

*Bottlenose Dolphin Ethogram*
Overall, our ethogram contains codes and descriptions for 11 activity states and 45 behavioral event types (Tables 1 to 4) for bottlenose dolphins in the Shannon Estuary. In the sightings data collected for the present study, information on six activity states and 35 behavioral event types was recorded and quantified (Tables 7 & 8). The ethogram is divided into four categorized sections, beginning with 11 activity state definitions adapted from those published by McHugh et al. (2011b), which are based on Waples (1995) (Table 1). This section is followed by three separate behavioral event sections detailing surface behaviors, foraging/feeding, and social behaviors (Tables 2-4). Many of these behavioral definitions are adapted from Richard Connor's ethogram (pers. comm., 25 January 2017) for Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia. The activity states recorded were *Travel*, *Forage*, *Social*, *Rest*, *Other*, and *Unknown*. However, *Probable forage*, *Feed*, *Mill*, *Play*, and *With boat* have also been observed as part of the Shannon Estuary bottlenose dolphins' behavioral repertoire and are included in the ethogram. Each of these activity states is mutually exclusive.

A total of 27 behavioral event types for observed surface behaviors were defined (Table 2), many of which were observed during more than one type of activity state. Twenty of these behavioral events were recorded at least once during sightings. A total of ten behavioral event definitions for observed feeding/foraging behaviors (Table 3) were included in the ethogram. Nine of these behavioral events were recorded at least once during sightings. Eight behavioral event definitions were included for social behaviors (Table 4) observed during social activity by bottlenose dolphins in the Shannon Estuary. Six of these behavioral events were recorded at least once during sightings.

*Inter-Observer Validity and Reliability Testing*
The mean percentage agreement score and standard deviation (data validity) across 24 test participants was 88.1 ± 7.0. The scores of trained research assistant (mean = 92.5 ± 3.4) and other marine biologist (mean = 83.8 ± 7.1) test participants differed significantly (Mann-Whitney U test: W = 19.5, $p < 0.05$). Fleiss's Kappa score (data reliability) across all participants was 0.81. The Kappa score of the trained participants was 0.88 and of the other participants was 0.74.

Every test participant correctly assigned the first two activity states (*Forage* and *Travel*) to their respective videos with only one incorrectly assigning the third (*Rest* instead of *Social*). All 24 test participants correctly assigned four of

**Table 1.** Activity states for bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland, including a description for each activity state. Behaviors in italics were not recorded or quantified separately in this study: *Feed*, *Mill*, and *Probable forage* were recorded as *Forage*, while *Play* and *With boat* were recorded as *Other* during sightings.

| Unit | Code | Name | Description |
|---|---|---|---|
| Activity states | FE | *Feed* | Dolphin observed catching a fish or with a fish in its mouth |
| | FO | Forage | Indications of searching for prey, prey capture, or feeding behaviors |
| | MI | *Mill* | Nondirectional movement with no overall spatial progress |
| | OT | Other | Observed activity is clear but does not fit any other definition |
| | PL | *Play* | Interactions with objects other than dolphins which serve no obvious purpose |
| | PFO | *Probable forage* | Indications of foraging but not confirmed |
| | RE | Rest | Slow, steady activity in absence of other identifiable activities, often with long dive bouts (1 to 5 min) |
| | SO | Social | All active interactions with conspecifics, including body contact, chasing/following, and sexual behaviors |
| | TR | Travel | Regular directional movement, including zig-zag and meandering movement |
| | UN | Unknown | Activity cannot be defined |
| | WB | *With boat* | All cases during which dolphins interact with a boat, including bow- and wake-riding |

**Table 2.** Surface behaviors for bottlenose dolphins in the Shannon Estuary, including a description for each behavioral event. *Halfway = to the dolphin's belly button but genital slit is not visible above water. Behaviors in italics were not quantified in this study but have been recorded during focal follows and/or as anecdotal data during sightings.

| Unit | Code | Name | Description |
|---|---|---|---|
| Surface behaviors | BKS | Backslap | Body exits halfway* out of water and falls against dorsal surface |
| | BST | Backstroke | Body is horizontal, and ventral part of body is visible above surface with both pectoral fins extended |
| | BEL | Belly roll | Body rotates c. 180° in water so that light ventral underside of the animal becomes visible |
| | BOW | *Bow-riding* | Dolphins surfacing at the bow of a moving vessel |
| | BR | Breach | Body exits water over halfway* and vertically and then falls horizontally creating white water |
| | BB | *Bubble-blow* | Bubble(s) emitted underwater from blowhole |
| | CNS | Chinslap | Body exits halfway* out of water and falls against ventral surface |
| | CHF | Chuff | Strong, audible exhale from blowhole |
| | DEF | Defecation | Faeces are emitted from body |
| | FTR | Fast travel | Directed movement at a speed of over 10 km/h |
| | HO | Head out | Head and rostrum emerge above water surface and reenter water smoothly |
| | HD | *Headstand* | Dolphin is vertical with tail-end of body exposed above water surface |
| | LP | Leap | Body exits water entirely in an arcuate path and reenters water smoothly |
| | MO | *Motorboating* | Tailslapping repeatedly in forward motion at the water surface |
| | ONS | On side | Body rotates c. 90° in water |
| | PEC | Pec out | Pectoral fin is extended above water surface |
| | PP | Porpoise | Repeated leaps in a straight direction |
| | SCO | *Scouting* | An individual dolphin leaves its group to approach the boat before returning again to its group |
| | SHK | *Sharking* | Dolphin moves forward with only the tip of its dorsal fin breaking the surface of the water |
| | SDS | Sideslap | Body exits halfway* out of water and falls against flank |
| | STR | Slow travel | Directed movement at a speed of under 10 km/h |
| | SNG | Snag | Body is stationary, horizontal; dorsal part of body is visible at surface |
| | SQ | *Squeeze breath* | A sound emitted from the blowhole that sounds like air escaping a balloon |
| | SR | Surface rush | Fast movement breaking the surface causing a flurry of white water at either side of the animal |
| | TO | Tail out | Tail is exposed above water surface |
| | TS | Tailslap | Flukes raised above water surface and then lowered making a strong, audible impact |
| | WS | With seaweed | Dolphin interacting with seaweed—in its mouth or draped over its dorsal fin, body, or fluke |

the 14 videos of single behavioral events with the behaviors *Tail dive*, *Tailslap*, *Fish toss*, and *With seaweed*. Of the remaining ten videos, test participants correctly assigned behaviors to varying degrees. The behaviors *Tail out* (0.95, 95.8%) and *Slow travel* (0.84, 95.8%) had relatively high reliability and validity scores, with only one misclassified behavior each—*Pec out* and *Fast travel*, respectively—out of all 24 test responses (Table 5). *Snag* (0.91, 91.7%) and *Surface rush* (0.91, 91.7%) were misclassified twice, each with the same two incorrect behavior assignations—*Slow travel* and *Fast swim*, respectively. *Peduncle dive* (0.86, 87.5%) and *With fish in mouth* (0.86, 87.5%) were both misclassified three times each, but with a different behavior each time—*Slow*

**Table 3.** Feeding/foraging behaviors for bottlenose dolphins in the Shannon Estuary, including a description for each behavioral event. Behavior in italics was not quantified in this study but has been recorded during focal follows and/or as anecdotal data during sightings.

| Unit | Code | Name | Description |
|---|---|---|---|
| Feeding/Foraging | CF | Catch fish | Dolphin catches a fish |
| | FSW | Fast swim | Dolphin moves quickly through water, apparently chasing fish |
| | FJ | Fin jerk | Abrupt movement of dorsal fin, indicating possible prey capture |
| | FS | Fish seen | A fish is seen next to a dolphin, in the water or air, with no evidence of a fish toss |
| | FT | Fish toss | Dolphin throws fish into the air from its mouth |
| | HS | *Humping surface* | Dolphin arches its body at surface and moves up and down |
| | LF | Leap feeding | Many dolphins are leaping, apparently chasing fish |
| | PD | Peduncle dive | Dolphin dives, and peduncle is visible but its tail is not |
| | TD | Tail dive | Dolphin dives, and tail is visible |
| | WF | With fish in mouth | Dolphin has fish in its mouth |

**Table 4.** Social behaviors for bottlenose dolphins in the Shannon Estuary, including a description for each behavioral event. Behaviors in italics were not quantified in this study but have been recorded during focal follows and/or as anecdotal data during sightings.

| Unit | Code | Name | Description |
|---|---|---|---|
| Social | CHA | *Chase* | One dolphin in pursuit of another dolphin |
| | GEN | Genital slit/Genitals | Pink genital area or erect penis observed |
| | GS | *Goose* | One dolphin contacts another's genital slit with its rostrum |
| | PR | Pec rub | One dolphin rubs along another's pectoral fin |
| | PET | Pet | Gentle contact between pectoral fin of one dolphin and body of another |
| | RUB | Rub | Gentle to vigorous body-body contact |
| | SPL | Splash | Water splash caused by movement of dolphin(s), but action cannot be defined |
| | SPY | Spyhop | Head and rostrum emerge vertically from water, and dolphin appears to view its surroundings |

*travel*, *Head out*, and *Leap* for *Peduncle dive*; and *Catch fish*, *Fish toss,* and *Chuff* for *With fish in mouth*. The scores for *Chinslap* (0.59, 62.5%), *Spyhop* (0.46, 50.0%), and *Breach* (0.12, 20.8%) were the lowest. *Breach* was the behavior most frequently misclassified, with five of the 24 participants correctly assigning the behavior and 16 misclassifying it as *Sideslap* and three as *Backslap*.

When differences between trained research assistant and other marine biologist test participant assignations were investigated, six of the behaviors had both higher validity scores (> 10% difference in percentage agreement) and reliability scores (> 0.10 difference in Kappa) for the trained participants than the other participants, compared to zero behaviors for the other participants vs the trained participants (Table 6). These behaviors were *Surface rush*, *With fish in mouth*, *Leap*, *Spyhop*, *Peduncle dive*, and *Snag*. *Leap* was the only behavior misclassified consistently by both trained and other test participants as a single alternative behavior, *Breach*. Of the 17 behaviors tested, trained participants had three validity scores under 80%, and the other participants had six validity scores under 80%.

*Activity State Budgets*

Using our ethogram, six of the activity states and 35 of the behavioral events observed in this bottlenose dolphin population were recorded and quantified. Activity states were recorded for 489 sightings during 256 surveys (on 171 d) from 2014 to 2016, and activity state budgets were calculated (Table 7). A single predominant group activity state (in the first 5 min) was recorded for

**Table 5.** Percentage agreement (validity) and category-wise Kappa (reliability) scores for behaviors used in the inter-observer video test, with the most common misclassification for each behavior

| Behavior | Percentage agreement | Category-wise Kappa | Most common misclassification |
|---|---|---|---|
| Forage | 100.0 | 1.00 | -- |
| Travel | 100.0 | 1.00 | -- |
| Social | 95.8 | 0.95 | Rest |
| Breach | 20.8 | 0.12 | Sideslap |
| Fish toss | 100.0 | 0.96 | -- |
| Chinslap | 62.5 | 0.59 | Head out |
| Surface rush | 91.7 | 0.91 | Fast swim |
| Slow travel | 95.8 | 0.84 | Fast travel |
| Tail dive | 100.0 | 1.00 | -- |
| Tailslap | 100.0 | 1.00 | -- |
| With fish in mouth | 87.5 | 0.86 | Catch fish/Fish toss/Chuff |
| Leap | 83.3 | 0.71 | Breach |
| Spyhop | 50.0 | 0.46 | Backslap/Backstroke/Head out |
| With seaweed | 100.0 | 1.00 | -- |
| Peduncle dive | 87.5 | 0.86 | Slow travel/Head out/Leap |
| Snag | 91.7 | 0.91 | Slow travel |
| Tail out | 95.8 | 0.95 | Pec out |

**Table 6.** Percentage agreement (validity) and category-wise Kappa (reliability) scores for behaviors assigned by trained research assistant and other marine biologist test participants in the inter-observer video test, with the most common misclassification for each behavior for each test group

| | Trained research assistants | | | Other marine biologists | | |
|---|---|---|---|---|---|---|
| Behavior | Percentage agreement | Category-wise Kappa | Most common misclassification | Percentage agreement | Category-wise Kappa | Most common misclassification |
| Forage | 100.0 | 1.00 | -- | 100.0 | 1.00 | -- |
| Travel | 100.0 | 1.00 | -- | 100.0 | 1.00 | -- |
| Social | 100.0 | 1.00 | -- | 91.7 | 0.90 | Rest |
| Breach | 25.0 | 0.09 | Sideslap | 16.7 | 0.12 | Sideslap |
| Fish toss | 100.0 | 1.00 | -- | 100.0 | 0.92 | -- |
| Chinslap | 66.7 | 0.62 | Head out | 58.3 | 0.53 | Head out/Fast travel |
| Surface rush | 100.0 | 1.00 | -- | 83.3 | 0.81 | Fast swim |
| Slow travel | 91.7 | 0.90 | Fast travel | 100.0 | 0.80 | -- |
| Tail dive | 100.0 | 1.00 | -- | 100.0 | 1.00 | -- |
| Tailslap | 100.0 | 1.00 | -- | 100.0 | 1.00 | -- |
| With fish in mouth | 100.0 | 1.00 | -- | 75.0 | 0.72 | Catch fish/Fish toss/Chuff |
| Leap | 91.7 | 0.82 | Breach | 75.0 | 0.57 | Breach |
| Spyhop | 75.0 | 0.72 | Backstroke | 25.0 | 0.17 | Head out |
| With seaweed | 100.0 | 1.00 | -- | 100.0 | 1.00 | -- |
| Peduncle dive | 100.0 | 1.00 | -- | 75.0 | 0.72 | Leap/Head out/Slow travel |
| Snag | 100.0 | 1.00 | -- | 83.3 | 0.81 | Slow travel |
| Tail out | 100.0 | 1.00 | -- | 91.7 | 0.90 | Pec out |

**Table 7.** The six recorded activity states during 489 sightings of bottlenose dolphins in the Shannon Estuary, including the number (*n*) and percentage (%) of records for each year and all years pooled together. **Note:** Percentages are rounded but exact figures add up to 100.

| | | | 2014 | | 2015 | | 2016 | | All years | |
|---|---|---|---|---|---|---|---|---|---|---|
| Unit | Code | Name | *n* | % | *n* | % | *n* | % | *n* | % |
| Activity states | TR | Travel | 132 | 68 | 52 | 36 | 70 | 46 | 254 | 52 |
| | FO | Forage | 28 | 15 | 64 | 44 | 47 | 31 | 139 | 28 |
| | SO | Social | 19 | 10 | 14 | 10 | 7 | 5 | 40 | 8 |
| | RE | Rest | 5 | 3 | 9 | 6 | 18 | 12 | 32 | 7 |
| | OT | Other | 1 | 1 | 2 | 1 | 2 | 1 | 5 | 1 |
| | UN | Unknown | 8 | 4 | 4 | 3 | 7 | 5 | 19 | 4 |
| | | Total | 193 | 100 | 145 | 100 | 151 | 100 | 489 | 100 |

every sighting. For the sightings in this study, the five additional states listed in the ethogram were not separately recorded and were pooled under either *Forage* (*Probable forage*, *Feed*, and *Mill*) or *Other* (*Play* and *With boat*).

*Travelling* was the predominant group activity state in over half (52%) of all sightings, while *Foraging* was recorded in over one quarter (28%) of sightings. *Socializing* was the predominant group activity state for 8% of sightings, while *Resting* was recorded during 7% of sightings. Together, *Other* and *Unknown* activity states were recorded during 5% of sightings. A significant difference was found between annual activity budgets ($\chi^2 = 60.499$, df $= 10$, $p < 0.0001$). Of all 3 y, the highest proportion for *Travelling* (68%) was recorded in 2014, the highest for *Foraging* (44%) was recorded in 2015, and the highest for *Resting* (12%) was recorded in 2016. The lowest proportion for *Socializing* (5%) was recorded in 2016 (Table 7).

### *Behavioral Events*

Behavioral events were recorded for 427 sightings during 250 surveys (on 169 d) between 2014 and 2016. Of the 35 behavioral events used for analysis, each was observed at least once. In total, 1,452 behavioral events were recorded; of these, 198 were recorded in *ad libitum* data and excluded in further analysis. Thus, 1,254 behavioral event records were used for analysis. The average number of behavioral events recorded during the first 5 min of a sighting was three (0.59 behaviors/min; range: 0 to 14) behavioral events (Table 8).

The most frequently observed behaviors in the surface behaviors, feeding/foraging, and social ethogram categories were *Slow travel* (14% of records), *Tail dive* (8% of records), and *Splash* (2% of records), respectively (Table 8). Of all behavioral events, the five most frequently observed behaviors were *Slow travel* (seen in 40% of all sightings), *Leap* (28% of sightings), *Surface rush* (28% of sightings), *Tail dive* (23% of sightings), and *Tailslap* (22% of sightings). These five behaviors accounted for 48% of the overall records. The ten least frequently recorded behaviors were *Pet*, *Spyhop*, *Porpoise*, *Catch fish*, *Genital slits/Genitals*, *Fin jerk*, *Snag*, *Pec rub*, *Defecation*, and *Backstroke*. These ten behavioral events were seen in only 10% of total sightings, with < 8 records each.

There are ten additional behavioral events defined in our ethogram that have been observed but not yet quantified for Shannon Estuary bottlenose dolphins. *Motorboating* (MO) (a series of rapid and repetitive tailslaps during forward progress by a dolphin; Weaver, 1987) has been observed twice during focal follows. Video footage and photographs of *Headstand* (HD) behavior exist wherein the dolphin is completely vertical with its tailstock in the air above the surface of the water for a few seconds in a stationary position. It is possible that some headstands were recorded in the present study as *Tail outs*. Dolphins in the Shannon Estuary are regularly observed *Bow-riding* (BOW) the research vessel, tour boats, recreational vessels, and large ships, but this behavioral event has not yet been quantified. On two occasions during focal follows, a snagging dolphin emitted a squeaky sound from its blowhole defined as a *Squeeze breath* (SQ). *Bubble-blows* (BB) (Lusseau, 2006a), equivalent to Weaver's (1987) subsurface exhalation, have also been observed periodically wherein a dolphin under water emits air from its blowhole creating bubbles at the surface. *Sharking* (SHK) has been seen at least ten times during focal follows wherein the tip of a dolphin's dorsal fin is visible cutting through the water surface at one level, while the rest of the dolphin's body remains under water. During one encounter, an individual dolphin exhibited *Scouting* (SCO) behavior (Bearzi et al.,

**Table 8.** The 35 recorded behavioral events in the ethogram, recorded during the first 5 min of sightings of bottlenose dolphins in the Shannon Estuary, including the number of records made from each platform, the total number of records (*n*), and the percentage (%) of records and sightings for each behavioral event. RBI = Rigid-hulled inflatable boat.

| Behavior | RIB | *Draíocht* | *Dolphin Discovery* | *n* | % of records | % of sightings |
|---|---|---|---|---|---|---|
| Slow travel | 43 | 57 | 72 | 172 | 14 | 40 |
| Leap | 31 | 44 | 46 | 121 | 10 | 28 |
| Surface rush | 37 | 45 | 38 | 120 | 10 | 28 |
| Tail dive | 31 | 43 | 26 | 100 | 8 | 23 |
| Tailslap | 25 | 32 | 36 | 93 | 7 | 22 |
| Peduncle dive | 23 | 45 | 21 | 89 | 7 | 21 |
| Head out | 10 | 33 | 26 | 69 | 6 | 16 |
| Fast travel | 11 | 24 | 24 | 59 | 5 | 14 |
| Breach | 8 | 21 | 24 | 53 | 4 | 12 |
| Belly roll | 14 | 18 | 19 | 51 | 4 | 12 |
| Tail out | 13 | 19 | 18 | 50 | 4 | 12 |
| Fish seen | 8 | 11 | 7 | 26 | 2 | 6 |
| Fast swim | 4 | 11 | 10 | 25 | 2 | 6 |
| Splash | 1 | 12 | 11 | 24 | 2 | 6 |
| Sideslap | 7 | 7 | 9 | 23 | 2 | 5 |
| Fish toss | 5 | 8 | 5 | 18 | 1 | 4 |
| Pec out | 7 | 4 | 6 | 17 | 1 | 4 |
| On side | 8 | 2 | 6 | 16 | 1 | 4 |
| Rub | 2 | 9 | 5 | 16 | 1 | 4 |
| Chinslap | 6 | 6 | 3 | 15 | 1 | 4 |
| Leap feeding | 2 | 6 | 6 | 14 | 1 | 3 |
| Backslap | 1 | 8 | 3 | 12 | 1 | 3 |
| With fish | 4 | 2 | 4 | 10 | 1 | 2 |
| Chuff | 0 | 7 | 3 | 10 | 1 | 2 |
| With seaweed | 1 | 3 | 5 | 9 | 1 | 2 |
| Pet | 1 | 3 | 3 | 7 | 1 | 2 |
| Spyhop | 1 | 2 | 4 | 7 | 1 | 2 |
| Porpoise | 2 | 3 | 1 | 6 | 0.5 | 1 |
| Catch fish | 2 | 1 | 3 | 6 | 0.5 | 1 |
| Genital slits/Genitals | 4 | 0 | 0 | 4 | 0.3 | 1 |
| Fin jerk | 1 | 2 | 0 | 3 | 0.2 | 1 |
| Snag | 0 | 3 | 0 | 3 | 0.2 | 1 |
| Pec rub | 0 | 0 | 3 | 3 | 0.2 | 1 |
| Defecation | 1 | 1 | 0 | 2 | 0.2 | 0.5 |
| Backstroke | 0 | 0 | 1 | 1 | 0.1 | 0.2 |
| Total behaviors | 314 | 492 | 448 | 1,254 | | |
| Total surveys | 49 | 85 | 116 | 250 | | |
| Total sightings | 114 | 169 | 144 | 427 | | |
| Total min | 570 | 845 | 720 | 2,135 | | |
| Behaviors/min | 0.55 | 0.58 | 0.62 | 0.59 | | |

1999) in leaving the rest of its group and approaching the research vessel before returning to its group. *Humping surface* (HS) behavior has been noted *ad libitum* on a few separate occasions in which a dolphin has remained at the water surface moving up and down with its back arched. *Goosing* (GS), contact between the rostrum of an individual dolphin and the genital slit of another, was recorded twice during focal follows; on both occasions, these events involved only juvenile dolphins. During one focal follow, repeated *Chase* (CHA) behavior (two dolphins actively surfacing, with one dolphin following another; Lusseau, 2006a; Steiner, 2011) was observed by an adult following a juvenile, interspersed with intense socializing.

*Comparison with Other Studies*

Although studies of bottlenose dolphin behavior elsewhere have reported activity budgets of strikingly different proportions, the daytime activity budgets observed in the Shannon Estuary fall within the ranges observed for this species in other areas (Table 9). All of the studies used for comparison included *Travel*, *Forage*, *Social*, and *Rest* activity states except for Sanibel Island (Shane 1990), which did not include *Rest* in its analyses and included two additional activity state definitions for *Travel/Feed* and *Social travel*. Other studies also included *Mill*, *Travel/Feed*, and *Play* in their activity budget breakdowns.

While 52% of the Shannon Estuary bottlenose dolphins' activity budget during this study was allocated to travelling, dolphins in the Port River Estuary, South Australia (Steiner, 2011), and the Patos Lagoon Estuary, Brazil (Mattos et al., 2007), had much lower travelling proportions (23 and 29%, respectively). The highest travelling proportion in the investigated studies was

**Table 9.** Daytime activity budgets (in percentages) of bottlenose dolphins in the Shannon Estuary and from the published literature: Port River Estuary, South Australia (Steiner, 2011; foraging and feeding combined); Patos Lagoon Estuary, Brazil (Mattos et al., 2007); San Diego County, California (Hanson & Defran, 1993); Sanibel Island, Florida (Shane, 1990); Sarasota Bay, Florida (Waples, 1995; McHugh et al., 2011b [juveniles only], combined and averaged); Shark Bay, Western Australia (Gero et al., 2005; Karniski et al., 2015 [estimated from Figure 1; females only], combined and averaged); Moreton Bay, Queensland (Chilvers et al., 2003 [nontrawler dolphin community only]); and Cardigan Bay, Wales (Veneruso & Evans, 2012)

| Study area: | Shannon Estuary | Port River | Patos Lagoon | San Diego | Sanibel Island | Sarasota Bay | Shark Bay | Moreton Bay | Cardigan Bay |
|---|---|---|---|---|---|---|---|---|---|
| Study method: | Survey | Individual follow | Group follow | Group follow | Group follow | Individual follow | Survey | Survey | Survey |
| Travel | 52 | 23 | 29 | 63 | 46 | 61 | 23 | 55 | 43 |
| Forage | 28 | 48 | 38 | 19 | 17 | 16 | 30 | 34 | 50 |
| Social | 8 | 14 | 6 | 12 | 7 | 5 | 10 | 8 | 6 |
| Rest | 7 | 11 | 1 | 3 | | 1 | 37 | 3 | 0 |
| Other | 1 | 4 | | | | 1 | | | |
| Unknown | 4 | | | | | | | | |
| Mill | | | 4 | | | 16 | | | |
| Travel/Feed | | | 22 | | 21 | | | | |
| Social travel | | | | | 10 | | | | |
| Play | | | | 3 | | | | | |

**Table 10.** Behaviors described in this study's ethogram and some comparable descriptors for similar behaviors in other studies

| Behavior name | Behavioral descriptor | Reference(s) |
|---|---|---|
| Slow travel | Directed movement at a speed of under 10 km/h | This study |
| Fast travel | Directed movement at a speed of over 10 km/h | This study |
| Straight travel | Travelling in a general direction with all surfacings in that direction | Waples, 1995 |
| Zig-zag travel | Travelling in a general direction by straight segments of different directions | Waples, 1995 |
| Meandering travel | Travelling in a general direction but orientation changes frequently | Waples, 1995 |
| Surface rush | Fast movement breaking the surface causing a flurry of white water at either side of the animal | This study |

| | | |
|---|---|---|
| Active surfacing | Rapid surfacing with spray; a major part of the back is visible during the surfacing | Lusseau, 2006a |
| Racing | Regular dive performed at high speed with more of dolphin's back exposed and white water forming as animal surfaces | Bearzi et al., 1999 |
| Feeding rush | A sudden acceleration and splash | Shane, 1990 |
| Rapid surface | A rapid surface in which the dolphin maintains a normal horizontal posture, and the dolphin's ventrum does not clear the water surface | R. Connor, pers. comm. |
| Leap | Body exits water entirely in an arcuate path and reenters water smoothly | This study |
| Forward leap | Exit and enter head first with venter facing down | Shane, 1990 |
| Backward leap | Exit and enter with dorsum facing down | Shane, 1990 |
| Side leap | Exit and enter with either side facing down | Shane, 1990 |
| Snag | Body is stationary, horizontal; dorsal part of body is visible at surface | This study |
| Floating | Stationary position at interface exposing foresection of animal in pronounced concave arc | Bearzi et al., 1999 |
| Lie at surface | Dolphin lies stationary with part of body exposed at surface for 5 s or more | Shane, 1990 |
| Snaggle | Dolphin floats stationary at the water surface, with its body horizontally flexed | Lusseau, 2006a |
| Chuff | Strong, audible exhale from blowhole | This study |
| Forced blow | Dolphin forcefully exhales above water producing a loud "chuff" sound | Lusseau, 2006a |
| Noisy blow | Dolphin made a loud noise with the blowhole at the surface | Steiner, 2011 |
| Cough | A loud, forceful exhalation | Shane, 1990 |
| Tailslap | Flukes raised above water surface and then lowered making a strong, audible impact | This study |
| Upside-down tailslap | Flukes raised above the surface, and dorsal side slapped downward | Shane, 1990 |
| Inverted tailslap | The dorsal side of the flukes is brought down flatly on the water surface by an animal in the inverted position | Weaver, 1987 |
| Tail slapping dorsal | Dolphin slapped the surface with the dorsal side of the tail | Steiner, 2011 |
| Head out | Head and rostrum emerge above water surface and reenter water smoothly | This study |
| Head out | Entire head exposed at surface; rostrum pointed at an angle; dolphin stationary | Shane, 1990 |
| Peek | Head raised out of the water far enough to expose the eyes; rostrum pointed forward; occurs during forward motion | Shane, 1990 |
| Tail out | Tail is exposed above water surface | This study |
| Tail out | Exposure of the caudal section at the surface in a head-down position; the straight tailstock is elevated by a modulated upward movement, and the flukes may be flipped up or moved up and down briefly during exposure | Weaver, 1987 |
| Fluke up | Exposure of one fluke at the surface by a moving or stationary animal; the fluke is usually angled and may flex briefly, often with splashing | Weaver, 1987 |
| With seaweed | Dolphin interacting with seaweed, in its mouth or draped over its dorsal fin, body, or fluke | This study |
| Weed rub | A dolphin rubs into a patch of weed while rolling side or belly up; pectorals and flukes are often lifted out of the water, draped with weed | R. Connor, pers. comm. |
| Kelp dragging | Strands of kelp are hooked around the front of the dorsal fin and trail off either side of the body as the animal makes forward progress at the interface | Weaver, 1987 |
| Carry weed | Dolphin carries algae on its beak, fin, flippers, or tail fluke | Lusseau, 2006a |
| Squeeze breath | A sound emitted from the blowhole that sounds like air escaping a balloon | This study |
| Squeeze breath | Audible and brief expulsion of air from the blowhole that sounds like air escaping the tightened neck of a balloon | Weaver, 1987 |
| Fart blow | Dolphin exhales above water with its blowhole contracted producing a fart-like sound | Lusseau, 2006a |
| Sharking | Dolphin moves forward with only the tip of its dorsal fin breaking the surface of the water | This study |
| Sharking | Dolphin swims horizontally at the water surface with its dorsal fin visible above water | Lusseau, 2006a |
| Surface finning | The dorsal fin is continuously visible and the only exposed part as the animal makes forward progress at the interface at any speed | Weaver, 1987 |
| Humping surface | Dolphin arches its body at surface and moves up and down | This study |
| Humping surface | A normal speed surface in which the dolphin "humps up" its posterior half to break its forward motion as it descends (when dolphins are pursuing fish) | R. Connor, pers. comm. |
| Buck | Body bent forward and back hunched and exposed at surface while dolphin bounces vigorously (social) | Shane, 1990 |

recorded for bottlenose dolphins in San Diego County, California (Hanson & Defran, 1993), at 63%. Foraging proportions ranged from 16% in Sarasota Bay (Waples, 1995; McHugh et al., 2011b) to 50% in Cardigan Bay (Veneruso & Evans, 2012), with similar proportions of 28, 30, and 34% in the Shannon Estuary, Shark Bay (Gero et al., 2005; Karniski et al., 2015), and Moreton Bay (Chilvers et al., 2003), respectively. *Social* behavior proportions ranged from 5% in Sarasota Bay to 14% in the Port River Estuary, while *Rest* behavior proportions ranged from 1% in Sarasota Bay and the Patos Lagoon Estuary to a high of 37% in Shark Bay. A systematic review of published studies shows some variation in the classification of behavioral event descriptors (Table 10).

## Discussion

*Bottlenose Dolphin Ethogram*

The search for ethograms of surface behavior in the published literature and in research project protocols resulted in a varied set of behavioral terms and descriptions for bottlenose dolphins globally. Some behavioral studies have not used detailed ethograms with behavioral events to date (T. Genov, pers. comm., 14 March 2016; K. Robinson, pers. comm., 14 March 2016; G. Veneruso, pers. comm., 14 March 2016; K. McHugh, pers. comm., 14 April 2017), and others have unpublished ethograms, which they use as a basis for behavioral research (E. Krzyszczyk, pers. comm., 8 February 2016; S. Gazda, pers. comm., 9 March 2016; K. Sprogis, pers. comm., 19 March 2016; R. Connor, pers. comm., 25 January 2017). Some very detailed ethograms have been created as elements of students' Master's theses (e.g., Weaver, 1987; Waples, 1995). Of the ethograms found in the peer-reviewed literature, the terms and definitions are different for every study site, although many of the descriptions describe the same or similar behaviors. Because many of these published ethograms were used for specific studies, only a small number are appropriate to the general description of adult bottlenose dolphin behaviors within a population.

All of the behaviors that were observed in our study were added to the present ethogram with detailed descriptions and should lend themselves to straightforward comparison with behaviors documented elsewhere. These behaviors have all been described in the literature on bottlenose dolphins, but some are rarely mentioned (e.g., *Defecation*); and in one case, we have used our own term *Backstroke*, which is possibly equivalent to inverted motorboating as described in Weaver's (1987) ethogram.

In some comparable studies, behavioral events have been described which have not (yet) been observed or recorded in the present study of Shannon Estuary bottlenose dolphins. Surface behaviors, such as *Stretching* (Weaver, 1987; Steiner, 2011) wherein a dolphin stretches its back with its head, and sometimes tail flukes, lifting above the surface, and *Swell-riding* wherein a stationary animal faces land until a swell passes and then moves forward with it, exposing the dorsal fin and tailstock (Weaver, 1987), have not been observed in the Shannon Estuary.

Many foraging behaviors in the literature have not been observed in the Shannon Estuary population. These include *Sponging* (carrying a sponge on the rostrum; Smolker et al., 1997), *Strand-feeding* (surging out of the water in unison onto mud banks to feed on small fish; Duffy-Echevarria et al., 2008; Jiménez & Alava, 2015), and *Kerplunking* (fluke-slapping that produces a high splash of water and an audible sound (Connor et al., 2000a). *Pinwheels* (flip-turns performed by a dolphin in side-swim orientation; Nowacek, 2002), *Benthic-feeding methods* (e.g., Rossbach & Herzing, 1997), *Fish whacking* (propelling a fish into the air with a forceful thrust of the flukes; Nowacek, 2002), and *Belly up behavior* (a dolphin upside-down chasing a fish at the surface; R Connor, pers. comm., 25 January 2017) have also not yet been observed.

Social behaviors described in the literature that have not been recorded in the Shannon Estuary include *Jaw clap* (dolphin clapping its mouth at the surface, without anything in it; Waples, 1995; Steiner, 2011), *Bite* (one dolphin bites another; Lusseau, 2006a), and *Headbutt* (two dolphins jump simultaneously and hit their heads together; Lusseau, 2006a; K. Robinson, pers. comm., 14 March 2016). Neither *Bonding* (two dolphins swimming next to one another with prolonged pectoral fin contact) nor *Head-to-head* (two or more dolphins facing one another rostrum-to-rostrum for a prolonged period) behaviors described by Richard Connor (pers. comm., 25 January 2017) have been observed in the Shannon Estuary. No clear displays, such as the elaborate synchronous ones by male bottlenose dolphins, described by Connor et al. (2006), have been observed in the Shannon Estuary to date.

There are various reasons why some of the behaviors recorded in other studies may not yet have been recorded in ours. One very obvious constraint is that water visibility in the Shannon Estuary is poor (< 1 m) compared to other study sites (e.g., Shark Bay, where visibility into the water from the boat is 2 to 8 m; Mann & Smuts, 1999). In this study, we focused exclusively on surface behaviors. Occasional days of good water visibility may present opportunities for documenting underwater dolphin behavior in the Shannon Estuary in the future, but these opportunities are limited. Many clear-water sites have *T. aduncus* rather than *T. truncatus*, and it may be that subtle differences exist between the overall behavioral repertoires of these two different species. In addition, observations were restricted seasonally, and further behaviors might be documented if behavioral observations were made in winter months. As with any catalog of behaviors, the ethogram we developed should be interpreted as an evolving document and not a full list of Shannon Estuary bottlenose dolphin behavior.

There is no evidence to suggest that the presence of either our research vessel or the tour boats had an effect on the behavior of the dolphins. However, land-based research using our ethogram could help to reinforce that the sighting records from boats illustrate the true behavioral repertoire and budgets of the dolphins (although the different perspectives of observing from land vs water might also affect this).

*Inter-Observer Validity and Reliability Testing*

The high validity and reliability scores obtained in the inter-observer video test by trained research assistants suggest that errors in behavioral data collected for this study did not have a significant impact on our results. The higher results for trained research assistants compared to the other participants indicate that training in the field will remain an important component of good behavioral research. The fact that some behaviors, such as breaches, were misclassified more often than others points to the need for specific attention to such behaviors in the training process. Nevertheless, the relatively high validity and reliability of the test even for other marine biologist participants suggest that our ethogram is well-suited for being used as a research tool by other research groups and for facilitating a behavioral comparison between different populations.

*Activity State Budgets*

Our results suggest that bottlenose dolphins in the Shannon Estuary spend over half (52%) of their time travelling, a quarter (28%) of their time foraging, and the rest of their time (20%) engaged in all other activities. These results are somewhat similar to Ingram's (2000) for Shannon Estuary bottlenose dolphins: 64% travel, 26% forage, 8% social, and 2% rest, calculated from land-based observational data. A comparison of our results with activity budgets in the literature leads to interesting parallels and some differences: time spent travelling for this population is relatively high (52%), maybe because the habitat is a geographically narrow but long estuary. However, in contrast, another estuarial population (the Port River Estuary, South Australia; Steiner, 2011) had a much lower proportion of travelling (23%), although the estuary shape was quite different. Comparison with the Patos Lagoon Estuary in Brazil (Mattos et al., 2007) is more difficult because of that study's distinction between travel (29%) and travel/feed (22%).

Foraging proportions vary substantially across populations ranging from 16% in Sarasota Bay (Waples, 1995; McHugh et al., 2011b) to 50% in Cardigan Bay (Veneruso & Evans, 2012). The Shannon dolphins' foraging budget (28%) is similar to Shark Bay (30%) (Gero et al., 2005; Karniski et al., 2015) and Moreton Bay (34%) (Chilvers et al., 2003). What accounts for such a wide variation in foraging proportions? Presumably it is partly explained by differences in the availability of prey, habitat geography, different nutritional requirements, and foraging strategies hand-in-hand with changing environmental effects. In addition, it is also possible that differences in the vessels used as research platforms might have an effect on dolphin behavior. Christiansen et al. (2010) reported that dolphins (*T. aduncus*) around tour boats were more likely to be travelling or foraging than resting or socializing. A further explanation for behavioral differences is habitat use; depending on where surveys were conducted in a study site, dolphins could be found to be engaging in behaviors related to that part of the survey area.

Social behavior proportions range from 5% in Sarasota Bay to 14% in the Port River Estuary (Waples, 1995; McHugh et al., 2011b; Steiner, 2011). The Shannon dolphins spent 8% of their time engaged in social activity, a similar proportion to Shark Bay dolphins (Gero et al., 2005; Karniski et al., 2015). Interestingly, Shark Bay dolphins have much higher resting rates (37%) than those of other populations used for comparison. Dolphins in the Shannon Estuary spent 7% of their time resting, while bottlenose dolphins in the Patos Lagoon Estuary and Sarasota Bay allocated only 1% of their daytime activity budgets to resting (Waples, 1995; Mattos et al., 2007; McHugh et al., 2011b). Further research should investigate if differences in activity state budgets could help to explain differences found in behavioral event occurrence. For example, dolphins snag much more in Shark Bay than in the Shannon Estuary, and snagging behavior is associated with resting (R. Connor, pers. comm., 25 January 2017). Thus, the fact that the social activity budget is similar in both of these populations may be very important in the further study of the social behavior of Shannon Estuary bottlenose dolphins, especially in comparing the societal complexity of these two populations.

The study population's activity budget was considerably different in different survey years, particularly for foraging and travelling activity.

Dolphins spent less time foraging and more time travelling in 2014, and vice versa in 2015 (with values for 2016 between the values of these two years), and this inter-annual variation in foraging activity is likely to be related to changing environmental conditions in the Shannon Estuary. This, in turn, affects prey distribution and abundance. The differences in activity budget proportions allocated to socializing and resting may be explained by reproduction, with inter-annual calving rates also playing a role in changing activity budgets. There is no clear explanation for the differences between years, but this certainly warrants further attention; and the addition of further years of data may help to explain fluctuations in the activity budget proportions over different years for this population.

*Limitations and Further Study*

The data used in this article do not distinguish among classes of animals or individuals. It, therefore, was not possible to examine whether there were significant behavioral differences between, for example, males and females or adults and juveniles. Anecdotal observations suggest that head out behavior is displayed more frequently by dependent calves in their first 2 y of life, but this hypothesis needs to be investigated further. In other studies (e.g., Nowacek, 2002), individual dolphins within the same community displayed different, though overlapping, repertoires of foraging behavior. In this study, our observations suggest that one individual, a dolphin with scoliosis, often displayed a head out and tail out in quick succession during a surfacing bout, which was probably related to its deformity. Some individuals seem to leap or tailslap more than others. These and other individual differences need further investigation.

The data used in this article are based on observations of less than 30 min that were made primarily from the opportunistic platform of tour boats adhering to marine regulations (Maritime Safety Directorate, 2005). The data, therefore, provide little information about potentially rare behaviors. In addition, the tour boats often target the same areas, which leads to a sampling bias in survey effort. In other studies, longer observations from dedicated research vessels have identified behaviors that seem unique to particular populations such as sponging (Smolker et al., 1997) and beach hunting (Sargeant et al., 2005). Lusseau (2006a) identified some behaviors in the Doubtful Sound bottlenose dolphin population which relate to cues for the start and end of certain activity states. Longer observations using focal follows and dedicated survey transects may provide greater insights into the role of specific, and rare, behaviors and perhaps of behaviors unique to this population.

The data used in this article were collected over a limited period, primarily during the summers of 3 y. Therefore, a comparison of behaviors between seasons was not applicable, nor was year-to-year variation discoverable over the long-term. Future research over more consecutive years, as well as throughout each year, is necessary to answer questions about how this population's behavior varies over time.

Our ethogram is an extremely useful tool because it likely covers all age classes, sexes, group sizes, and survey areas within the Shannon Estuary. The sampling of different areas provides good coverage of different individuals in the population. On some occasions, both tour boats and the research vessel sampled at the same time on the same day simultaneously (in different areas of the estuary), providing a widespread snapshot of bottlenose dolphin sightings across the study site.

*Conclusions*

The purpose of this article was to provide the first ethogram for bottlenose dolphins in the Shannon Estuary, to describe and quantify these behaviors, and to compare behaviors documented in this study with those of other studies of bottlenose dolphins in different geographical locations. The ethogram presented contains 11 activity state and 45 behavioral event definitions. The results presented are based on observational records from 3 y of study, and the ethogram behaviors quantified were each recorded at least once for dolphins in the Shannon Estuary, with ten additional behaviors included from anecdotal records. We expect our ethogram to develop over time, adding some of the behaviors reported for bottlenose dolphins elsewhere as, and if, they are observed in the Shannon Estuary. The behaviors reported herein are some of the most frequently observed and documented for bottlenose dolphins in other wild environments; however, this ethogram is the first for temperate European waters and will provide a fundamental tool for future behavioral research.

Activity states and behavioral events recorded in the Shannon Estuary were quantified, and an activity state budget for this bottlenose dolphin population was presented. Bottlenose dolphins in the Shannon Estuary allocated relatively more time to travelling and less to resting compared to other populations. These results make an important contribution to global dolphin research by adding to a remarkably varied set of activity budgets reported for other populations, for which some similarities and some differences are apparent. Overall, this study establishes a foundation for investigating the behavior of the Shannon Estuary bottlenose dolphin population and for engaging in the systematic comparison with other populations necessary for understanding the complex lives of these social mammals.

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