Tail walking in a bottlenose dolphin community: The rise and fall of an arbitrary cultural "fad"

Bossley, M.¹, Steiner, A.², Brakes, P.^{1,3}, Shrimpton, J.¹, Foster, C.¹ and

Rendell, L.^{4,*}

1. WDC, PO Box 720, Port Adelaide BC, Port Adelaide, SA 5142, Australia

2. Les Brussattes 1, 2904 Bressaucourt, Switzerland

3. Centre for Ecology and Conservation, University of Exeter, Tremough, Penryn, Cornwall, TR10 9FE, UK

4. Centre for Social Learning and Cognitive Evolution, and Sea Mammal Research Unit, School of Biology, University of St Andrews, Fife, KY16 9TH, U.K.

*Corresponding author email: ler4@st-andrews.ac.uk

1 ABSTRACT

2 Social learning of adaptive behaviour is widespread in animal populations, but the spread of 3 arbitrary behaviours is less common. Here we describe the rise and fall of a behaviour called tail 4 walking, where a dolphin forces the majority of its body vertically out of the water and maintains the 5 position by vigourously pumping its tail, in a community of Indo-Pacific bottlenose dolphins (Tursiops 6 aduncus). The behaviour was introduced into the wild following the rehabilitation of a wild female 7 individual, Billie, who was temporarily co-housed with trained dolphins in a dolphinarium. This 8 individual was sighted performing the behaviour seven years after her 1988 release, as was one 9 other female dolphin, named Wave. Initial production of the behaviour was rare, but following 10 Billie's death two decades after her release, Wave began producing the behaviour at much higher 11 rates, and several other dolphins in the community were subsequently sighted performing the 12 behaviour. Social learning is the most likely mechanism for the introduction and spread of this 13 unusual behaviour, which has no known adaptive function. These observations demonstrate the 14 potential strength of the capacity for spontaneous imitation in bottlenose dolphins, and help explain 15 the origin and spread of foraging specialisations observed in multiple populations of this genus. 16

17

18 **KEYWORDS**

19 Social learning; Cultural transmission; Cetacean; Bottlenose dolphin

21 BACKGROUND

22 The social learning of behaviour has been studied in a range of taxa, including primates [1], birds [2], 23 fish [3] and insects [4]. When socially-learned behaviour persists long enough to become common 24 within a group or population for some period of time, it becomes a cultural tradition [5]. In cetaceans, for example, "sponging" by bottlenose dolphins [6], prey specialisation in orca [7], and 25 26 the spread of lobtail feeding in humpback whales [8] all appear to rely on social learning. However, 27 these behaviours are associated with an obvious biological function - in these examples, foraging. 28 Examples of cultural behaviours with no obvious biological function have been described in 29 primates. For example, capuchin monkeys have social behaviour traditions, such as the 'finger-in-eye 30 game' [9]. It does not follow that these traditions serve no adaptive social function simply because it 31 is not obvious and we cannot currently identify it, but they do appear to have a qualitatively 32 different role compared to behaviours that have more obvious adaptive function, such as foraging. 33 Some apparently arbitrary traditions can also be transient - for example, stone handling in a 34 community of Japanese macaques has persisted for many years, but specific variants of the 35 behaviour emerge and then disappear, and researchers refer to these as "fads" [10]. The practice of 36 carrying dead salmon adopted for a few weeks by a community of orcas in Puget Sound has also 37 been described as a fad [11]. 38 In human culture, such arbitrary traits can acquire significance as symbolic ethnic markers [12].

39 Determining the social role and potential fitness advantage of such cultural behaviours in non-

40 humans, especially when they are ephemeral and arbitrary in nature, remains a challenge.

41 Therefore, documenting examples of such phenomena is important. Here we describe the

42 emergence and spread of "tail walking", an apparently arbitrary and non-functional behaviour, in a

43 community of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*).

44

46 METHODS

The Port River estuary, on the southern coast of Australia (Figure 1), is home to a small (20-30, with transient visitors) community of *T. aduncus* [13]. Boat-based photo-identification studies of the dolphins in the Port River estuary commenced in 1988. Whenever dolphins were encountered, their location, number, and behaviour were recorded. Individuals were identified using distinguishing marks on their dorsal fins [14].

52 In addition, teams of up to five land-based, volunteer, citizen-scientists with experience observing 53 and photographing the local dolphins documented behaviour using video and still images. Initially, 54 these volunteers provided time-stamped photographs of dolphins tail walking, when observed, but 55 in 2009 they were provided with a proforma collecting information on the dates and times of tail 56 walk(s), the number of discrete tail walks observed, and the identity of the individual(s) concerned, if 57 verified with dorsal photographs. Although parts of the river observed from land were 58 approximately 200m across, individual identification was possible in 95% of cases. Unavoidably, due 59 to its voluntary nature, observer effort varied during the course of the study.

A discrete tail walk was defined as the vertical emergence from the water of the dolphin so that at least two thirds of its body was above the water, followed by backwards movement through the water of at least a metre before submerging (Figure 2). Dolphins could perform a single tail walk in a day, bouts with successive tail walks separated by a few seconds, or multiple bouts within a single day separated by an hour or more. To accommodate this variability, we report 'DTW', the number of days in which tail walking was observed at least once, irrespective of the number of discrete tail walks performed, for each individual dolphin.

67 **RESULTS**

The first dolphin to be observed tail walking in the Port River estuary was Billie. This dolphin was
photographed in the upper reaches of the Port River as a calf in the second half of 1987. On

70 December 26, 1987 Billie became trapped in a harbour and after two weeks, was captured and 71 transferred to a nearby dolphinarium for rehabilitation. This facility housed five dolphins at the time, 72 which were trained to perform various behaviours, including tail walking, in public shows. While 73 being held, Billie was never given any training, but was able to observe the captive animals 74 performing tail walks. She was subsequently freeze-branded on her dorsal fin, which allowed 75 unambiguous re-identification after several years, and released near her capture site in late January 76 1988. Billie died in August 2009, with the precise date known because she was euthanised by 77 veterinarians following recapture.

78 The first wild tail walk was observed in 1995, when Billie was estimated to have been about ten 79 years old and thus an adult. Bouts of this behaviour were subsequently observed on a total of 279 80 occasions during the study period, resulting in 261 DTW [15]. Six adult females, and five juveniles 81 (three female, two male) were observed tail walking (Table 1). The dolphin Wave accounted for a 82 large majority of observations, 65-100% of the yearly DTW counts between 2007 and 2014. The 83 frequency of Wave's tail walking increased rapidly during the period 2008 to 2010 (during which 84 period Billie died). Wave was last seen on September 18 2014 and is presumed dead; and her male 85 calf Tallula died in February 2015. Eight other dolphins were also observed tail walking during the 86 period 2009-2014, but at a lower frequency (Table 1; Figure 3). Overall, 76% of tail walks occurred in 87 the presence of other animals. Tail walking, as measured by DTW, peaked in 2010-11, and the total 88 number of dolphins observed tail walking peaked in 2011 (Figure 3). After 2011, both DTW and the 89 number of tail walkers declined.

All the identified dolphins observed tail walking were sighted regularly over several years (shaded
cells in Table 1) and most were female; no adult male was ever observed tail walking. All tail walks
occurred within the portion of the estuary shaded in Figure 1 in depths from 3m to 12m. Offshore
areas were surveyed by boat on an approximately weekly basis [13], but no tail walking was
observed there. The sighting ranges of all identified tail walkers overlapped considerably (Figure S1).

95 These ranges also overlapped with those of several animals, including three, Sparkle, TFM and Millie,
96 which were never sighted tail walking, but all had calves that were observed tail walking (Figure S2,
97 Tables S1-S2).

98 The observer effort involved in this study, totalling 30,620 hours, gradually increased from its 99 inception in 1995 until it plateaued in 2006. Thus it is possible the amount of tail walking between 100 these dates was greater than has been recorded. However, the relatively consistent observer effort 101 from 2006 to 2014 indicates that the observed changes to the relative frequency of tail walking in 102 this period are not an artefact of effort.

103 DISCUSSION

After being temporarily captive with other dolphins that had been trained to tail walk, Billie
produced the behaviour in the wild, despite never receiving any direct training. This behaviour was
subsequently produced by several other dolphins in the same community, particularly another
female, Wave, leading to high production rates some 20 years after Billie's release into the wild.
These high rates subsequently declined.

109 An obvious question is whether these changes in behaviour production were the product of social 110 learning. We have only observational data, so any arguments must rely on plausibility, with all the 111 associated caveats, such as the ease with which subtle genetic or ecological drivers can be missed [16]. Nonetheless, in this particular case, the plausibility arguments are unusually strong, for a 112 113 number of reasons. First, the motor imitation capabilities of bottlenose dolphins are well established 114 [17,18], so social learning has to be a candidate explanation for the spread of tail walking. Second is 115 the arbitrary nature of the behaviour – it is a highly energetic display, so likely costly, that produces 116 nothing energetically to offset that cost. It may produce social benefits, but these would be difficult 117 to determine without intensive study. Third is the rarity of the behaviour in wild populations - while 118 common in display performances in dolphinaria around the world, to our knowledge it does not 119 appear in any ethogram of wild bottlenose dolphins. Fourth, the rise and fall of the production rate

120 of the behaviour only in some individuals and not the whole community is strongly suggestive of 121 social effects rather than, for example, a response to changing ecological conditions that would be 122 expected to produce a more consistent response across the community. Fifth, the observations 123 reported here are inconsistent with ecological or genetic causation. Tail walkers live in sympatry 124 with animals that have never been seen doing it, and tail walking individuals have both tail walking 125 mothers and mothers that have never been seen tail walking. Finally, there is a plausible route for 126 the introduction of this unusual behaviour, during Billie's temporary captivity. Given these 127 arguments, we conclude that the introduction and spread of tail walking in the Port River bottlenose 128 dolphin community is highly likely a result of social learning.

129 This report adds to our understanding of social learning in Tursiops spp.. The lack of obvious 130 adaptive benefits for tail walking contrasts with the vertical transmission of foraging specialisations 131 from mother to calf in other similar populations [19], and supports a social function for the 132 behaviour. There was also an apparent role of horizontal/oblique transmission to calves whose 133 mothers did not tail walk, with Wave the most likely source for learning events because of her high 134 rate of production. Behavioural synchrony for social function has hitherto been most prominent 135 within male alliances [20], but this report suggests a role in female-female interactions also. 136 Such observations help explain the large diversity of foraging strategies in bottlenose dolphins 137 [19,21,22], but the apparently arbitrary nature of tail walking behaviour is especially interesting 138 since such arbitrary traditions are much less common in non-humans, and we are not aware of any

other reports in this species. It is also striking that the behaviour was not produced at high rates until
a decade after it was originally introduced, showing that anthropogenic impacts on behaviour can

141 last for decades within populations, supporting the view that cultural transmission can be an

important consideration in conservation decisions [23,24].

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- 209

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214 AUTHOR CONTRIBUTIONS

- 215 MB designed the study. MB, PB, AS, CF, JS and LR made substantial contributions to conception and
- 216 design, or acquisition of data, or analysis and interpretation of data, to drafting and revising the
- article, and gave final approval of the version to be published. All authors approve the final version
- of the manuscript and agree to be held accountable for its content.

219 DATA ACCESSIBILITY

220 Data and code are available via the Open Science Foundation (https://osf.io/xjmdt/).

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223 COMPETING INTERESTS

224 All authors declare no competing interests

225 ETHICAL STATEMENT

- 226 Methods were observational only and adhered to local guidelines. Appropriate licences were
- obtained (SA Government research permit Q26490-2).

229 TABLES

Individual	Sex	1995	1998	2007	2008	2009	2010	2011	2012	2013	2014	Total
Billy	F	1	1		5	8						15
Wave	F			3	20	33	51	40	23	25	5	200
UAF*	F				1			1	1			3
Норе	М					1	2					3
Tallula	М						3	1				4
Bianca	F						6	5	1	3	1	16
Crinkle	F							3				3
Angel	F							2	1			3
Ripple	F							9	3			12
Ali	F							1				1
Melody	F										1	1
Total		1	1	3	26	42	62	62	29	28	7	261
*UAF = unidentified adult female. Given that this dolphin had no identifying features we												

Table 1: Days tail walking occurred (DTW) by individual and year. Shaded cells indicate 230 years in which individuals were sighted. 231

23 cannot be certain that these three records are for the same animal. 233

234

236 FIGURE CAPTIONS

- Figure 1: Study area, the Port River estuary. The shaded area of the zoomed map encompasses allthe sightings of tail walking reported in the study.
- 239 Figure 2: (a) Adult female 'Wave' performing a typical tail walk Note the backwards movements
- 240 through the water as indicated by the dolphin's wake, (b) Hours of observer effort, number of
- individuals observed tail walking, and number of days tail walking observed (DTW) per 1000 hrs
- 242 observation effort, per year, across the study period. Asterisks indicate periods where DTW
- 243 occurred significantly more often than in the first five years of observation (see Supplementary
- 244 Material for modelling details).

246 FIGURE 1



247

(a)



(b)



251

SUPPLEMENTARY MATERIAL

252

FOR

- Bossley, M., Steiner, A., Brakes, P., Shrimpton, J., Foster, C. and Rendell, L.: Tail walking in a
 bottlenose dolphin community: The rise and fall of an arbitrary cultural "fad", for *Biology Letters*
- 256
- 257

258 Table S1: Demographic details of tail walking dolphins.

NAME (Abbreviation in Figure S2)	SEX	EST. DoB
Billie (BI)	Ŷ	1985 (first calf 1995)
Wave (WA)	9	<1990 (first calf 2002)
Bianca (BIA)	9	1992 (first calf 2002)
Unidentified Adult Female	9	<1997
Crinkle (CR)	9	<1980
Angel (AN)	9	Dec, 2002
Ripple (RI)	Ŷ	Jan, 2006
Melody (ME)	9	Jan, 2006 (seen as neonate)
Hope (HO)	2	Oct, 2008 (seen as neonate)
Tallula (TA)	3	Mar, 2009 (seen as neonate)
Ali (ALI)	Ŷ	Dec, 2010 (seen as neonate)

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260

261

Table S2: Mother-calf relationships involving known tail walkers. Known tail walkers in bold; all
 animals are female unless otherwise indicated.

V	Vave	Bianca	Sparkle	Millie	TFM	
\downarrow	\checkmark	\checkmark	\checkmark	\checkmark	\checkmark	
Ripple	Tallula (♂)	Hope (🖒)	Melody	Ali	Angel	
	V ↓ Ripple	Wave ↓ ↓ Ripple Tallula (්)	Wave Bianca ↓ ↓ ↓ Ripple Tallula (්) Hope (්)	Wave Bianca Sparkle ↓ ↓ ↓ ↓ Ripple Tallula (ී) Hope (ී) Melody	Wave Bianca Sparkle Millie ↓ ↓ ↓ ↓ Ripple Tallula (♂) Hope (♂) Melody Ali	

268 Table S3: Results of Poisson family GLM fitted to effort-corrected DTW time series binned into four

269 5-year epochs: (model1<-glm(TW~epoch1, family = 'poisson'))

270

Coefficient	Estimate	Std.Error	Z	Pr(> z)
Intercept (1995-1999)	0.24	0.40	0.608	0.5435
2000-2004	-17.54	1550.87	-0.011	0.9910
2005-2009	1.55	0.44	3.545	0.0004
2010-2014	2.52	0.41	6.112	9.82e-10

271 Null deviance: 231.830 on 19 degrees of freedom

272 Residual deviance: 89.506 on 16 degrees of freedom

- 274 Figure S1: Locations of boat-based survey sightings of (a) known tail walking animals and
- (b) individuals never seen tail walking, to illustrate the overlapping ranges of both.
- 276 **(a)**



278 279

280 **(b)**



Figure S2: Distribution of number of tail walk events in each observed bout, by individual,
 presented as standard boxplots (see Table S1 for full individual names).

