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1 **Multi-Network-Based Diffusion Analysis reveals**
2 **vertical cultural transmission of sponge tool use**
3 **within dolphin matriline**

4
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15
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19 Abstract

20 Behavioural differences among social groups can arise from differing ecological conditions, genetic
21 predispositions and/or social learning. In the past, social learning has typically been inferred as
22 responsible for the spread of behaviour by the exclusion of ecological and genetic factors. This
23 ‘method of exclusion’ was used to infer that ‘sponging’, a foraging behaviour involving tool use in
24 the bottlenose dolphin (*Tursiops aduncus*) population in Shark Bay, Western Australia, was socially
25 transmitted. However, previous studies were limited in that they never fully accounted for
26 alternative factors, and that social learning, ecology and genetics are not mutually exclusive in
27 causing behavioural variation. Here, we quantified the importance of social learning on the diffusion
28 of sponging, for the first time explicitly accounting for ecological and genetic factors, using a multi-
29 network version of ‘network-based diffusion analysis’ (NBDA). Our results provide compelling
30 support for previous findings that sponging is vertically socially transmitted from mother to
31 (primarily female) offspring. This research illustrates the utility of social network analysis in
32 elucidating the explanatory mechanisms behind the transmission of behaviour in wild animal
33 populations.

34 Introduction

35 Various mechanisms can be responsible for causing behavioural differences among social groups or
36 populations [1]. The cultural hypothesis states that behavioural variation is the result of social
37 transmission of different behavioural innovations. The ecological hypothesis, on the other hand,
38 proposes that behavioural differences among groups can be attributed to differing ecological
39 conditions. Finally, the genetic hypothesis assumes that different groups are genetically predisposed
40 to behave in different ways [1].

41 The last few decades have seen increasing interest in animal cultural phenomena, *i.e.*, behaviours
42 that are socially transmitted among conspecifics [1]. Various methods have been used to identify
43 social learning in animal populations. For example, the method of exclusion (also termed group
44 contrast method, or ethnographic method) – commonly used among primatologists in the past e.g.
45 [2,3] - identifies patterns of variation in the behavioural repertoires of the population in question
46 and infers social transmission as at least partly responsible for differing behaviours by excluding
47 genetic and ecological differences as sufficient explanations [4] [p. 132].

48 The method of exclusion has also been used to assess patterns of transmission of ‘sponging’, a
49 foraging behaviour involving tool use in a population of Indo-Pacific bottlenose dolphins (*Tursiops*
50 *aduncus*) in Shark Bay, Western Australia [5]. This behaviour involves dolphins carrying conical
51 sponges as protective ‘gloves’ on their rostra when foraging for buried prey [6]. Sponging is female-
52 biased, and almost all sponging dolphins possess the same mitochondrial haplotype, *i.e.*, belong to
53 the same matriline [5,7]. As the deep-water channels where sponging occurs were used by both
54 ‘spongers’ and ‘non-spongers’, a purely ecological explanation seemed unlikely [5]. By considering
55 10 different pathways of potential genetic inheritance (x-linked and autosomal), Krützen *et al.* [5]
56 inferred that sponging was vertically socially transmitted from mother to female offspring.

57 The method of exclusion has been criticised, however, with considerable debate over its utility [8–
58 10]. Laland and Janik [9] argued that it is impossible to take all plausible explanations for the spread
59 of behaviour into account, and therefore, that social learning can never be inferred with absolute
60 certainty, leading to increased rates of false claims of culture [4]. Furthermore, they argued that
61 social learning, ecology and genetics are not necessarily mutually exclusive [9,10]. Instead, they can
62 simultaneously shape behaviour in a population, warranting a more nuanced approach to
63 disentangle the relative contributions of the three drivers of behavioural variation.

64 In an attempt to resolve the animal cultures debate, more quantitative methods to infer social
65 learning have been developed. For example, using repertoire-based methods on long-term

66 behavioural data from eleven orang-utan (*Pongo* spp.) populations, Krützen and colleagues [11]
67 showed that neither uniquely genetic nor ecological components explained the total observed
68 variance with regards to putative cultural elements, corroborating a cultural explanation. Further,
69 ‘network-based diffusion analysis’ (NBDA) [12,13], a network-based approach allowing the
70 quantification of the importance of social learning on the spread of behaviour, has been used
71 increasingly in recent years to detect and quantify social learning in animal populations, e.g. [14,15].
72 NBDA infers social transmission if the spread of a behaviour follows the social network, assuming
73 that more closely associated individuals have more opportunities to learn from each other [13,16].
74 Multi-network NBDA allows the inclusion of several different networks to quantify the relative
75 importance of transmission along different pathways [17].

76 Here, we use multi-network NBDA to quantify the relative importance of social learning, ecological
77 factors and genetic relatedness on the spread of sponge tool use in the dolphin population of Shark
78 Bay, Western Australia. Furthermore, we distinguished between different pathways of social
79 learning, namely vertical (between mother and offspring) and horizontal/oblique learning (among
80 peers/between older and younger generations, respectively).

81 **Methods:**

82 **Field methods**

83 We collected association and behavioural data during boat-based surveys using standardised
84 sampling methods for cetaceans between 2007 and 2018 in the western gulf of Shark Bay, Western
85 Australia. On approach to each dolphin group, we recorded GPS location, determined group
86 composition during the first five minutes of each encounter using long-established photo-
87 identification techniques [18], and recorded predominant group behaviour. All occurrences of
88 sponging were recorded and an individual was deemed a ‘sponger’ once it had been seen carrying a
89 sponge on at least two independent occasions. Biopsy samples were taken on an opportunistic basis
90 using a system designed specifically for sampling cetaceans [19].

91 **Genetic methods**

92 To test for a genetic predisposition for developing sponging behaviour, we obtained a measure of
93 genetic biparental relatedness for each dyad. Individuals for which biopsies were available (N = 295)
94 were genetically sexed [20] and genotypes determined based on 27 microsatellite markers (SI, Tab.
95 1). Using COANCESTRY 1.0.1.7 [21], we calculated dyadic biparental relatedness based on genotypes
96 for individuals with no more than three microsatellite loci missing (N = 293), using the estimator
97 TrioML [22] (SI). With a cut-off point of seven sightings (see below), genetic data were available on

98 226 out of 415 individuals, resulting in 25,425 unique dyads. For the remaining 189 individuals
99 where no genetic information was available (60,480 dyads) we used the population average
100 relatedness of 0.043.

101 We also statistically controlled for a correlation between matriline membership and sponging
102 behaviour by sequencing a 468 bp-long fragment of the mitochondrial DNA (mtDNA) control region
103 ('d-loop') to assign dolphins to mtDNA haplotypes [23].

104 **Network constructions and NBDA**

105 To assess the relative importance of social learning, ecological factors and genetics in promoting
106 the spread of sponging, we ran multi-network NBDA [17] using four different networks (NBDA
107 package v0.6.1 [24] in R 3.5.1 [25]). The first social network assessed vertical learning between
108 mother and offspring, with entries of 1 between mother and known offspring and all other
109 connections set to 0. We created the network based on behaviourally and genetically identified
110 mother-offspring pairs (N = 294; SI). The second social network allowed for horizontal/oblique
111 (henceforth 'horizontal') learning using dyadic association strengths (Simple Ratio Index [26]) among
112 all individuals but excluding mother-offspring associations, which were set to 0. Sightings of the
113 same or a subset of the original group within two hours were excluded. Association matrices were
114 created using R package 'asnipe' [27]. The third, ecological network contained dyadic home range
115 overlap as a proxy of the environmental similarity experienced by individuals. We created home
116 ranges using individual GPS locations based on 95% Epanechnikov kernel density estimates
117 ('adehabitatHR' [28]) with a customized smoothing factor (SI). Dyadic home range overlap (95%) was
118 calculated using the 'utilization distribution overlap index' ('adehabitatHR') [28,29]. Finally, the
119 fourth network contained measures of dyadic biparental genetic relatedness among individuals.
120 Since NBDA infers social learning if a behaviour follows the social network, there is a trade-off
121 between sample size and data quality. Dropping individuals with few sightings can increase certainty
122 about the strengths of connections but, at the same time, decrease power of NBDA to reliably detect
123 social learning if linking individuals are removed [30]. We ran a simulation to select a threshold that
124 maximises power of NBDA to detect social learning, revealing maximum power at seven sightings (SI)
125 [30]. In all networks, we therefore only considered individuals with a minimum of seven
126 observations.

127 We then applied the 'order-of acquisition diffusion analysis' (OADA) variant of NBDA [13] (SI).
128 For several individuals, the order of acquisition of sponging was unknown, as they were likely
129 already spongers when first encountered. In NBDA models, such individuals can be taken to be
130 'informed' at the start of the diffusion (termed 'demonstrators') [13]. We considered all individuals

131 as demonstrators who had been seen carrying a sponge within the first two encounters where
132 predominant group behaviour was foraging. We argue that an individual's information state can be
133 determined with reasonable certainty after two sightings, given spongers carry sponges 96% of the
134 time when foraging [31]. Maternity data were unavailable for nine individuals who acquired
135 sponging after 2007. These nine individuals were excluded as learners, but we allowed for other
136 individuals having learned from these spongers (SI).

137 We included several individual-level variables (ILVs) with potential influence on the learning
138 rate: sex; average water depth of each individual's sightings (a proxy for habitat use, since sponging
139 occurs in deep-water channels [32]); average group size (since sponging is a solitary activity [31]),
140 and mitochondrial haplotype as a reduced two-level factor (either haplotype E (=sponging haplotype
141 in the western gulf [7]), or other) to avoid overfitting of models. Sex was determined genetically
142 and/or by the presence of a dependent calf for females. In an NBDA, the strength of transmission
143 through a network ('s parameter') is estimated relative to a baseline rate of asocial learning. This
144 baseline was set to the mean of all continuous variables, at the mid-point between males and
145 females, and haplotype E (set as the reference level for this factor).

146 We fitted OADA with and without transmission through the networks and with all possible
147 combinations of networks and ILVs [13]. Thereby, ILVs were allowed to influence both social and
148 asocial learning rates independently ('unconstrained' models [4]; SI). Support for each model was
149 calculated based on the Akaike Information Criterion corrected for sample size (AICc) [33]. To
150 provide a more robust inference about strength of transmission for the different networks and the
151 influence of ILVs, model averaging methods were employed [33]. We calculated 95% confidence
152 intervals for model parameters using the profile likelihood method, conditional on the best
153 performing model (SI).

154 Results

155 Between 2007 and 2018, 5,300 dolphin groups were encountered in the western gulf of Shark Bay
156 and >1,000 different dolphins identified (Fig. 1a). Sponging was observed on 825 occasions and
157 restricted to the deep-water channels within the study area (Fig. 1b). A total of 76 individuals were
158 identified as spongers, of which 49 were confirmed female, 14 male and 13 of unknown sex.

159

160 After removal of individuals with fewer than seven sightings, as well as eight offspring that were
161 either dependent calves at the time of analyses or had died before weaning, 415 individuals
162 remained, of which 62 were spongers (18 learners, of which 9 were removed due to missing
163 maternity data, and 44 demonstrators). All spongers with maternity data available were born to

164 sponging mothers. All spongers with genetic data available carried haplotype E, with one exception:
165 a male sponger with haplotype H (but see SI).

166

167 [Figure 1 appr. here]

168

169 [Figure 2 appr. here]

170

171 Multi-network NBDA revealed most support for models with transmission through the vertical social
172 network ($\sum w_i=0.837$), while asocial learning, and transmission through the horizontal, ecological or
173 genetic network (or any combination of the four networks) received much less support ($\sum w_i < 0.1$;
174 Fig. 2). In the best performing model, which included vertical social transmission and sex influencing
175 social learning, s (the rate of social transmission from mothers to offspring) was estimated to be 1.23
176 $\times 10^{10}$ times greater than the rate of asocial learning (95% C.I. [33.1; infinity]; $\sum w_i = 0.425$). The
177 social learning rate was an estimated 126 times higher for females than males (95% C.I. [9.5; 2897];
178 $\sum w_i = 0.975$). This corresponds to approximately 100% of spongers learning sponging socially from
179 their mothers (95% C.I. [98.9; 100]). Average group size, average water depth and haplotype did not
180 influence social or asocial learning rate (all $\sum w_i < 0.5$; SI).

181 Discussion

182 We applied multi-network NBDA to sponging behaviour, revealing overwhelming support for social
183 transmission through the vertical mother-offspring network, with little or no support for
184 transmission through the horizontal association, ecological or genetic networks. Moreover, despite
185 the restriction of sponging to channel habitat [32,34], our analysis suggests that ecological factors
186 play only a minor role once vertical social learning has been taken into account.

187 Low support for transmission through the genetic network confirms previous findings that sponging
188 individuals in the western gulf are not more closely related than expected by chance [7]. This stands
189 in contrast to findings from the eastern gulf of Shark Bay, where spongers show higher relatedness
190 than the population average, suggesting a more recent common ancestry [5].

191 We further confirm a previously documented female sex-bias [7,31,35], which is presumably due to
192 differing sex-specific reproductive strategies between males and females [31]. After weaning, male
193 dolphins must focus on forming multi-male alliances to coerce and consort oestrous females [36–
194 38]. This requires significant investment in social relationships and is, therefore, largely incompatible
195 with a time-consuming, solitary and difficult-to-master activity like sponging [31,39]. Meanwhile,
196 female offspring are expected to invest more into developing foraging skills to maximize food intake

197 compared to male offspring [40,41]. Alternatively, Zefferman [42] proposed that the female sex-bias
198 could be the result of a maternal teaching strategy, arguing that teaching a daughter would result in
199 higher long-term fitness for a female: a potential advantage of sponging for a son would last only
200 one generation, while a daughter can pass on the behaviour to subsequent generations which all
201 gain potential benefits associated with sponging. Just 22% of spongers with known sex in the
202 western gulf were males, which corresponded to previously suggested proportions of male offspring
203 learning sponging from their mothers in Shark Bay's eastern gulf [31, but see 43].

204 Given haplotype similarity among spongers, some researchers have argued that mitochondrial genes
205 themselves might predispose dolphins to learning the sponging behaviour [9]. However, we find no
206 evidence that being a member of a particular mtDNA matriline has an effect on the rate at which
207 dolphins learn sponging, as per previous research [44]. Our findings instead support the hypothesis
208 that maternal vertical transmission of both the sponging behaviour and mtDNA results in haplotype
209 similarity among spongers, a phenomenon referred to as 'cultural hitchhiking' - a form of gene-
210 culture co-evolution in which a neutral genetic locus is inherited in parallel with a matrilineally
211 transmitted cultural behaviour [45].

212 McElreath and Strimling's [46] mathematical models predict the conditions for the evolution of
213 purely vertical transmission, concluding that "neither [vertical nor oblique] transmission should be
214 expected to dominate the other across all domains" [46]. Sponging is just one foraging strategy
215 exhibited by the dolphins, and other strategies may be transmitted obliquely and horizontally.
216 Following McElreath and Strimling's models [46], we suggest that sponging is transmitted vertically
217 either because the relevant environment (e.g. availability of sponges) may be stable. Alternatively, it
218 may only be possible for a dolphin to learn sponging from its mother, if, for example, it requires
219 repeated observations from close quarters.

220 The application of multi-network NBDA to sponging behaviour in the dolphins of western Shark Bay
221 allowed us to quantify the effects of social learning on behaviour, whilst explicitly accounting for the
222 influence of ecological and genetic factors for the first time. Documenting a strong effect of vertical
223 social learning from mother to offspring, our findings provide strong quantitative evidence to
224 support the claim that sponging is a case of vertically transmitted culture in the bottlenose dolphins
225 of Shark Bay [5].

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230 Author contributions

231 Conceptualization - SW, MK, SJA and WH. Funding – MK, SLK. Data collection - SW, SJA, MK, LG, SLK.
232 Formal analysis – SW, WH. Writing - all. All authors approved of, and agreed to be held accountable
233 for, the final manuscript.

234 Accessibility

235 Code is available in ESM, and data on dryad [47]:
236 <https://datadryad.org/review?doi=doi:10.5061/dryad.sc26m6c>.

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242 Competing interests

243 The authors declare no competing interests.

244 Ethical statement

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251

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