



Bizzozzero, M. R., Allen, S. J., Gerber, L., Wild, S., King, S. L., Connor, R. C., ... Krützen, M. (2019). Tool use and social homophily among male bottlenose dolphins. *Proceedings of the Royal Society B: Biological Sciences*, 286(1904), [20190898]. <https://doi.org/10.1098/rspb.2019.0898>

Peer reviewed version

License (if available):  
Other

Link to published version (if available):  
[10.1098/rspb.2019.0898](https://doi.org/10.1098/rspb.2019.0898)

[Link to publication record in Explore Bristol Research](#)  
PDF-document

This is the accepted author manuscript (AAM). The final published version (version of record) is available online via The Royal Society at <https://doi.org/10.1098/rspb.2019.0898> . Please refer to any applicable terms of use of the publisher.

## University of Bristol - Explore Bristol Research

### General rights

This document is made available in accordance with publisher policies. Please cite only the published version using the reference above. Full terms of use are available:  
<http://www.bristol.ac.uk/pure/about/ebr-terms>

1 **Tool use and social homophily among male bottlenose dolphins**

2

3 **Bizzozzero MR<sup>1\*</sup>, Allen SJ<sup>1,2,3</sup>, Gerber L<sup>1</sup>, Wild S<sup>4,1</sup>, King SL<sup>2,3</sup>, Connor RC<sup>5</sup>, Friedman WR<sup>6,7</sup>, Wittwer S<sup>1</sup>, Krützen**

4 **M<sup>1</sup>.**

5

6 <sup>1</sup>Evolutionary Genetics Groups, Department of Anthropology, University of Zurich, CH-8057 Zurich, Switzerland

7 <sup>2</sup>School of Biological Sciences, University of Western Australia, Perth, WA 6009, Australia

8 <sup>3</sup>School of Biological Sciences, University of Bristol, Bristol, BS8 1TQ, United Kingdom

9 <sup>4</sup>School of Biology, University of Leeds, Leeds, LS2 9JT, United Kingdom

10 <sup>5</sup>Biology Department, University of Massachusetts Dartmouth, North Dartmouth, MA 02747, USA

11 <sup>6</sup>Department of Cognitive Science, University of California San Diego, La Jolla, CA 92093, USA

12 <sup>7</sup>National Center for Ecological Analysis and Synthesis, University of California Santa Barbara, Santa Barbara, CA

13 \*Author for correspondence: manuela.bizzozzero@uzh.com

14

15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35

**ABSTRACT –**

Homophilous behaviour plays a central role in the formation of human friendships. Individuals form social ties with others that show similar phenotypic traits, independently of relatedness. Evidence of such homophily can be found in bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia, where females that use marine sponges as foraging tools often associate with other females that use sponges. ‘Sponging’ is a socially learned, time consuming behaviour, transmitted from mother to calf. Previous research illustrated a strong female bias in adopting this technique. The lower propensity for males to engage in sponging may be due to its incompatibility with adult male-specific behaviours, particularly the formation of multi-level alliances. However, the link between sponging and male behaviour has never been formally tested. Here, we show that male spongers associated significantly more often with other male spongers irrespective of their level of relatedness. Male spongers spent significantly more time foraging, and less time resting and travelling than did male non-spongers. Interestingly, we found no difference in time spent socialising. Our study provides novel insights into the relationship between tool use and activity budgets of male dolphins, and indicates social homophily in the 2<sup>nd</sup>-order alliance composition of tool using bottlenose dolphins.

**Keywords:** bottlenose dolphins, tool use, alliance formation, activity budget, social networks, homophily

## 36 INTRODUCTION

37 Individuals acquire information and behavioural skills from conspecifics through social learning across a variety  
38 of taxa, including insects, fishes, reptiles, birds and mammals (1–4). Despite the widespread prevalence of  
39 social learning, this strategy may not always be beneficial, as knowledge gained from conspecifics can be  
40 maladaptive with one's own behavioural patterns (5). It is therefore important for individuals to learn  
41 selectively from others to maximise benefits (6). Explanations for *why*, *when* and *from whom* individuals learn  
42 include adopting behaviour performed by the majority (7), behaviour performed by kin (8) or based on  
43 increased pay-offs (9), among others (reviewed in (4,10)). However, while social learning has received  
44 considerable attention in the literature, relatively little is known about what differences exist between the  
45 sexes and what consequences such differences might hold for adult life.

46 Sexual selection theory predicts that males should primarily engage in behaviours related to increasing  
47 mating opportunities, while females should invest more in behaviours related to increasing access to resources  
48 and offspring protection (11,12). Differences in behavioural requirements or preferences are therefore  
49 expected to dictate sex biases in social learning. For example, both male and female chimpanzees (*Pan*  
50 *troglydytes*) learn socially to insert flexible tools made from vegetation into termite mounds in order to extract  
51 termites, yet females learn 'termite fishing' earlier, use it more frequently and do so more efficiently than  
52 males (13,14). The differing priorities in learning to use a tool are reflective of the different strategies of male  
53 and female chimpanzees to maximise fitness. Chimpanzees use tools in foraging contexts, thus, the benefits of  
54 engaging in such a technique should be higher for females than males. Male chimpanzees form coalitions to  
55 compete for and maintain alpha male status, a social position that confers increased reproductive opportunity  
56 (15). Consequently, males might be less inclined to invest in learning or improving complicated feeding  
57 techniques, but rather invest in social relationships with other males (16).

58 In the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) population of Shark Bay, Western Australia,  
59 sex bias is evident in a socially learned foraging technique involving the use of marine sponges as tools (17,18).  
60 Sponge-carrying ('sponging') is thought to protect the dolphin's rostrum while foraging for prey on the sea floor  
61 (17,19). Sponging allows these dolphins ('spongers') to exploit a novel ecological niche by providing access to  
62 prey not available to those dolphins unfamiliar with tool use (20). Sponging is observed in both the eastern and  
63 western gulfs of Shark Bay, but only some members of particular matriline use sponges (west: approx. 38% of  
64 all females (21); east: approx. 13% of all females (22)). This is why sponging is thought to be an exclusively

65 vertically transmitted behaviour (18,23). Around 91% of female calves adopt sponging from their sponging  
66 mothers, while only 50% of males do so. The observed female bias in sponging is most likely reflective of a sex  
67 bias in social learning propensities at a young age (24–26).

68 Sponging females are distinctive with regards to their activity budget, spending more time foraging  
69 and less time resting than their non-sponging female counterparts (21,24). When foraging, female spongers  
70 devote 95% of their time to sponging, compared to other foraging behaviours (24). They are also seen alone  
71 more often than non-spongers (22,24). However, when associating with other individuals, female spongers  
72 show a preference for other sponging females (22). While there is a considerable amount of data on female  
73 spongers, much less is known about male spongers. For instance, why proportionally fewer males learn and  
74 specialise in this foraging technique, and if and how sponging influences adult male behaviour, remain  
75 unknown. The latter is of particular relevance as male dolphins in Shark Bay exhibit one of the most complex  
76 social structures outside humans (reviewed in (27)).

77 Bottlenose dolphins in Shark Bay live in an open fission-fusion society with changing group sizes and  
78 compositions (27,28). Males form different levels of reproductive alliances with other males, driven by intense  
79 competition for access to receptive females (27). Two to three males cooperate in '1<sup>st</sup>-order' alliances to  
80 consort single oestrus females (29). These males also generally associate within larger '2<sup>nd</sup>-order' alliances  
81 comprised of 4-14 individuals, whose members cooperate to take females from rival alliances and to defend  
82 against such attacks (29). 1<sup>st</sup>- and 2<sup>nd</sup>-order allies are also frequently observed together in non-mating contexts  
83 (29). Second-order alliances are considered the stable, core unit of male social organisation in Shark Bay, while  
84 the stability of 1<sup>st</sup>-order alliances varies considerably (27). These complex social relationships among males can  
85 last for decades and are critical to each male's reproductive success (27). Alliances are considered costly, as  
86 each male must invest time in the formation and maintenance of these relationships (30).

87 Sponging is also a costly behaviour: it requires significant time investment and is associated with a  
88 decrease in overall sociability (22,24), as well as less time to rest and travel (21). The investment of time and  
89 energy into male alliance behaviours may therefore preclude engaging in time-consuming, solitary foraging  
90 techniques, such as sponging. It has been proposed that sponging might put males at a disadvantage in forming  
91 and maintaining alliances compared to males that use foraging techniques that are both less time-consuming  
92 and less solitary (17,18,21,24). However, these arguments assume that the time, social and energetic demands  
93 of sponging on males and females are similar, which has yet to be tested. Here we assess the effect of sponging

94 on male dolphin behaviour by comparing activity budgets, sociability, and association patterns of male  
95 spongers to male non-spongers.  
96

97 **METHODS**

98 **Study site and data collection**

99 Data for this study were collected in the western gulf of Shark Bay, Western Australia, in an area that includes  
100 various habitat types, such as seagrass-rich shallow waters (< 10 m) and deep water channels with sandy  
101 substrates (> 10 m) (31). We collected behavioural and genetic data during the austral winters from 2007 to  
102 2015, identifying individual dolphins by photographs of their dorsal fins (32). During boat-based surveys of  
103 dolphin groups, within the first five minutes, we recorded GPS position, environmental parameters (including  
104 sea state, water depth and temperature), group size and composition, as well as predominant group activity  
105 (rest, travel, forage, socialise, or unknown; *cf.* (33) and SI). We defined group membership according to the 10  
106 m chain rule (33). Male dolphins that had been observed carrying a sponge while foraging at least twice on  
107 different days were classified as spongers (24), while males that had never been observed sponging were  
108 classified as non-spongers. Individuals that had been observed sponging only once were classified as  
109 'unknowns'. We obtained biopsy samples from dolphins on an opportunistic basis using a purpose-designed  
110 system for sampling small cetaceans (34). The samples were used to genetically sex individuals (35) and  
111 determine pairwise genetic relatedness (18). Further details of sampling and laboratory methods are provided  
112 in the SI. Unless otherwise specified, all analyses were conducted in R V1.1.453 (36).

113

114 **Data Restriction**

115 We included only independent/weaned males and excluded dependent calves (37). Only males observed more  
116 than nine times and identified as spongers or non-spongers were included in our analyses. Sex was identified  
117 either genetically (see SI) or behaviourally by several observations of alliance-typical behaviour (being observed  
118 regularly travelling side-by-side engaging in synchronous surfacing, consorting of females, or inter-group  
119 aggression with other males; *cf.*, (27,38)). Furthermore, in order to assess males with similar association  
120 opportunities, we restricted our analyses to comparisons of male spongers with non-sponging males that also  
121 met habitat use criteria based on depth and home range overlap derived from data on sponging males. Further  
122 details on the calculation of these criteria are provided in the SI. Restricting the data in this manner resulted in  
123 a data set containing 37 male dolphins, including 13 spongers and 24 non-spongers.

124

125 **Effect of sponging on male activity budgets**

126 To investigate differences in activity budgets (proportions of resting, travelling, foraging, and socialising  
127 behaviour) between male spongers and non-spongers, we conducted a multivariate analysis of variance  
128 (MANOVA) with the sole predictor of whether an individual was classified as sponger or non-sponger  
129 (hereafter: foraging technique). As dependent variables, we calculated activity budgets by dividing the number  
130 of individual sightings per activity by the total number of individual sightings. We used Pillai's trace (V) as a test  
131 statistic due to the unequal sample sizes in our data set (39). To investigate which activity proportions, in  
132 particular, differed between male spongers and non-spongers, we performed sequential Bonferroni corrected,  
133 post-hoc, independent t-tests (Welch's t-test, (40)). While investigating the data structure of the multivariate  
134 activity budgets, we identified five outliers from the combined normal distribution. Thus, we conducted the  
135 MANOVA with outliers removed, retaining 32 males (spongers: n = 12, non-spongers: n = 20) in the data set  
136 (see SI for analysis with the full data set).

137

#### 138 **Degree of sociability of male spongers and non-spongers**

139 To investigate whether male spongers were more or less solitary than male non-spongers, we compared their  
140 levels of sociability. We constructed an index of sociability by dividing the number of solitary sightings by the  
141 total number of sightings per individual. We compared individual sociability indices of male spongers and male  
142 non-spongers in a two-sample permutation test (10,000 permutations) implemented in the 'perm' package  
143 (41).

144 To investigate the association pattern of male spongers and male non-spongers, we adhered to the  
145 following procedure. First, to maximise our ability to draw comparisons with other studies on cetaceans, we  
146 calculated Half Weight Indices (HWIs) as a measure of the proportion of time two males spent together (42).  
147 Based on the dyadic HWIs, we created a social network to analyse the association patterns between male  
148 spongers and male non-spongers. Second, we assessed whether associations in the social network followed a  
149 random pattern or whether two individuals were seen more or less often together than expected by chance  
150 (43,44). For this analysis, we specified a daily sampling period. Third, to test whether the association indices  
151 between pairs consisting of males with similar foraging techniques (sponger – sponger; non-sponger – non-  
152 sponger) were higher than between pairs with different foraging techniques (sponger – non-sponger), we  
153 carried out a Mantel test on a similarity matrix and the matrix of dyadic associations with 10,000 permutations.  
154 The similarity matrix is a 1/0 matrix providing information on whether two individuals belong to the same



155 group (either both spongers or both non-spongers = 1) or to different groups (sponger and non-sponger = 0).  
156 These analyses were conducted in SOCPROG 2.6 (45).

157 In a further step, we ran a Double Decker Semi-Partialling Multiple Regression Quadratic Assignment  
158 Procedure (MRQAP-DSP; see below and (46)) to investigate whether the documented pattern of dyadic  
159 associations (between male pairs of spongers, pairs of non-spongers, and pairs of one sponger and one non-  
160 sponger) could be predicted by similarity in foraging technique, even when controlling for pairwise relatedness  
161 (based on 27 microsatellite loci; see SI for more detailed information). Similarity in foraging technique was  
162 presented in two matrices: in the first, we coded similarity in sponging as 1; and vice versa in the second where  
163 similarity in non-sponging was coded as 1. Unequal dyads were assigned a value of 0 in both matrices. Separate  
164 similarity matrices allowed us to disentangle the contribution of similarity in sponging and non-sponging,  
165 respectively, to the association pattern.

166 An MRQAP-DSP test is similar to a partial linear multiple regression with the exception that dependent  
167 and predictor variables are presented as matrices. Thus, this method tests whether an entered predictor  
168 variable significantly contributes to the explanation of the dependent matrix, whilst controlling for the other  
169 predictors. To control for the dependencies between data points, we used the MRQAP-DSP test as  
170 implemented and described in the 'asnipe' package (47) using 10,000 permutations. We did not include  
171 mitochondrial haplotypes in the predictors due to a previously documented high correlation with foraging  
172 technique (48). Only males for which we had genetic data available were included in this test (spongers:  $n = 9$ ,  
173 non-spongers:  $n = 16$ ). We also repeated the MRQAP-DSP test including all genotyped males within our study  
174 population while additionally correcting for home range overlaps (see SI).

175 To investigate whether the association patterns found in the previous analysis were also reflected in  
176 2<sup>nd</sup>-order alliance compositions, we defined 2<sup>nd</sup>-order alliances based on dyadic HWIs. We lacked sufficient  
177 consortship data to define alliances functionally (*i.e.*, through observation of consortship behaviour) for this  
178 study, so we could use only association strength as a proxy (33). We used an average linkage agglomerative  
179 cluster analysis assuming a hierarchical social network structure (49) performed in SOCPROG (45) and defined  
180 and applied a threshold value at which a dyad can be considered to be part of the same 2<sup>nd</sup>-order alliance. To  
181 find an appropriate threshold, we conducted a change point analysis employing the Pruned Exact Linear Time  
182 (PELT) method specified in the 'change point' package (50) (*cf.* (51) and SI for more detailed information).

183

184 **RESULTS**

185 Between 2007 and 2015, we observed 124 male dolphins at least nine times. After applying the restrictions  
186 outlined above imposed, the resulting data set contained 37 male dolphins, of which 13 were spongers and 24  
187 were non-spongers (number of sightings: mean = 35; range = 17-68). We computed HWIs from a total of 549  
188 survey records over the nine-year study period. All males associated with at least five other individuals in the  
189 data set.

190

191 **Effect of sponging on male activity budgets**

192 We detected significantly different activity budgets between male spongers and non-spongers ( $V = 0.74$ ,  
193  $F(4,27) = 19.6$ ,  $p < 0.001$ ). Thus, foraging techniques significantly contributed to explaining an individual male's  
194 activity budget. Post-hoc analyses showed that male spongers foraged more, and rested and travelled less than  
195 male non-spongers. There was no significant difference in time spent socialising between male spongers and  
196 non-spongers (Tab. 1).

197

198 **Degree of sociability of male spongers and male non-spongers**

199 Male spongers were encountered significantly more often alone (sociability index: mean = 0.22, SE = 0.03) than  
200 male non-spongers (sociability index: mean = 0.04, SE = 0.01;  $p = 0.002$ ).

201 Among the 37 males, the overall mean HWI was 0.09 (1,000 bootstraps: SE = 0.03), including the zeros  
202 of no associations. Considering only non-zero associations, the more conservative measure, the mean HWI was  
203 0.17 (1,000 bootstraps: SE = 0.05). The generated network based on the dyadic association indices (Fig. 1)  
204 represented a non-random social structure (10,000 permutations, 1,000 switches;  $SD_{obs} = 0.17$ ,  $SD_{random} = 0.14$ ,  
205  $p < 0.001$ ). Thus, some males were observed more often in association than expected by chance alone,  
206 reflecting their well-documented alliance associations (27).

207 Association rates between pairs of males with similar foraging techniques (sponger – sponger; non-  
208 sponger – non-sponger; mean HWI = 0.14, SD = 0.09) were significantly higher (Mantel test,  $t = 5.75$ ;  $p < 0.01$ ;  
209 Tab. 2) than associations between pairs with different foraging techniques (sponger – non-sponger: mean HWI  
210 = 0.05, SD = 0.04).

211 The MRQAP regression model showed that sponging was a significant predictor of male association  
212 patterns, even after controlling for relatedness (Tab. 3). Related individuals did not associate above chance

213 levels. These findings were also supported by the results of the MRQAP-DSP tests including all males within our  
214 study area (see SI for more information). Our analyses demonstrate that the association pattern of male  
215 dolphins inhabiting deep water and occupying similar home ranges can at least partly be explained by foraging  
216 technique.

217 An average linkage agglomerative cluster analysis to define 2<sup>nd</sup>-order alliances resulted in a tree  
218 diagram representing the underlying data well with a cophenetic correlation coefficient of 0.98 (45,52). The  
219 PELT method resulted in a change point at HWI  $\geq$  0.27. This cut-off value is higher but well within the range of  
220 previous findings on the male dolphins of Shark Bay, in which a HWI of 0.20 has commonly been used in  
221 assigning males to 2<sup>nd</sup>-order alliances (27,33). Applying 0.27 as a threshold to define 2<sup>nd</sup>-order alliances  
222 illustrated that the tendency of male spongers to associate with other male spongers was reflected in 2<sup>nd</sup>-order  
223 alliance compositions. We identified nine 2<sup>nd</sup>-order alliances, of which two consisted exclusively of spongers,  
224 one was of mixed composition (sponger and non-sponger) and the other six were composed exclusively of non-  
225 spongers (Fig. 2). Four individuals (three spongers, one non-sponger) could not be assigned to a 2<sup>nd</sup>-order  
226 alliance. Five of the non-sponging alliances and both sponging alliances have also been observed engaging in  
227 functional alliance behaviour, *e.g.* consorting females. A similar pattern was found when we included all males  
228 in our study population (see SI for more detail).

229

230 **DISCUSSION**

231 It has been hypothesised that the investment of time and energy into the formation and maintenance of male  
232 alliances likely reduces the propensity for male dolphins to engage in time-consuming, solitary foraging  
233 techniques such as sponging, thereby resulting in the strong female bias previously documented (17,18,21,24).  
234 This hypothesis was based on the assumptions that male spongers engage in different activity and social  
235 patterns than male non-spongers. Our results support these assumptions by revealing that, at least in the  
236 austral winters when data were collected, male spongers differed in their activity budgets, foraging more, and  
237 resting and travelling less than male non-spongers. Interestingly, the time spent socialising was equal among  
238 male spongers and non-spongers despite the fact that male spongers spent more time alone than male non-  
239 spongers. When male spongers were observed with other males, they associated significantly more often with  
240 other male spongers.

241 Previous studies on female activity budgets in Shark Bay also found that spongers spent a greater  
242 proportion of their time foraging and less time resting and travelling than their non-sponging counterparts  
243 (21,24), suggesting that time investment could be a proximate cost of sponging in comparison to other foraging  
244 techniques for both sexes. A comparison between the sexes warrants further investigation. Interestingly,  
245 socialising proportions for males seem not to be affected by these time investments, suggesting that a  
246 comparatively smaller amount of time spent resting might be the proximate cost of sponging. However, these  
247 potential costs might be offset by having fewer competitors for food, as sponging may decrease competition  
248 for resources by providing access to a novel ecological niche (19,20). Indeed, the role of intraspecific  
249 competition on niche expansion has been reported across several taxa (53,54).

250 Our finding that male spongers and male non-spongers spent equal amounts of time socialising  
251 contradicts the hypothesis that sponging conflicts with cooperative male alliance behaviour. However, when  
252 comparing sociability, we found that male spongers had higher proportions of solitary sightings compared to  
253 male non-spongers. Our findings thereby corroborate previous studies indicating that sponging is a largely  
254 solitary activity (21,24). The increased solitariness of male spongers might still affect cooperative male alliance  
255 behaviour negatively to some degree, even though there is no difference in socialising time.

256 Our examination of male social structure in deep water habitat revealed that male spongers tended to  
257 associate with other male spongers rather than male non-spongers, as demonstrated by their clustering in the  
258 social network. Sponging was a significant predictor of the observed association patterns of males sharing

259 similar home ranges even after controlling for pairwise relatedness and similarity in non-sponging. Likewise,  
260 when we repeated our analysis and included all genotyped males, similarity in sponging remained a significant  
261 predictor for social structuring (see SI for more information). These results contradict a previous study on male  
262 dolphins in eastern Shark Bay (22), which did not detect a significant effect of similarity in foraging technique  
263 on social structuring. This was most likely a result of low sample size as there are far fewer spongers, and  
264 particularly male spongers, in the eastern gulf of Shark Bay compared to the western gulf (22,31). Remarkably,  
265 in our study, while similarity in foraging technique was significant in terms of impact on social structuring,  
266 pairwise relatedness was not (Tab. 3). The absence of an effect of relatedness on the social structuring of male  
267 dolphins seems plausible; previous studies on male associations and relatedness of 2<sup>nd</sup>-order alliances reported  
268 ambiguous patterns, with only a minority of alliances showing higher relatedness than the population average  
269 (55).

270           The high social affinity among male spongers could either indicate social learning of tool use from  
271 alliance partners or be explained by homophilous behaviour (*i.e.*, increased associations due to similar  
272 behaviour). The established pattern of strict vertical transition of sponging (18,23) and the reported homophily  
273 related to sponging in female dolphins of Shark Bay (22), make homophily among male spongers the more  
274 parsimonious explanation. Whether the observed homophily among male spongers is driven by the males  
275 themselves or emerges as a by-product of the high social affinity of female spongers (*i.e.*, mothers) remains  
276 unknown. Research in eastern Shark Bay has shown that juvenile males preferentially stayed in proximity to  
277 their natal associates (56), and the number of associates stays constant from infancy through the juvenile  
278 period (57). If the natal associates of spongers were also male spongers, this could explain the high social bonds  
279 between pairs or trios of sponging males. As sponging females – and hence, mothers of sponging males – are  
280 shown to cluster together (22), such a scenario seems plausible.

281           The ultimate benefit of such homophilous behaviour in male spongers could be their ability to  
282 maintain the use of such a foraging technique whilst simultaneously remaining in close proximity to males 'of a  
283 similar ilk', *i.e.*, with whom they can also engage in alliance behaviours. This argument is further strengthened  
284 when considering the composition of 2<sup>nd</sup>-order alliances. There was only one mixed 2<sup>nd</sup>-order alliance, while  
285 the other eight alliances in our data set consisted of either only male spongers or male non-spongers. The  
286 threshold resulting from our PELT analysis to identify 2<sup>nd</sup>-order alliances was higher than previously  
287 documented in Shark Bay (29), resulting in the delineation of a greater number of alliances with some having

288 fewer members than typically reported for 2<sup>nd</sup>-order alliances (27,29). The higher threshold of 0.27 may have  
289 split some 2<sup>nd</sup>-order alliances that associated at levels of >0.20 but <0.27. Thus, the smaller 2<sup>nd</sup>-order alliances  
290 identified in our study comprising only two to three males are most likely 1<sup>st</sup>-order allies. Yet, irrespective of  
291 the threshold used to define alliances, when considering the hierarchical structure of the social network (*i.e.*,  
292 dyadic associations assorted in a dendrogram, Fig. 2), social homophily is apparent. Given the need to  
293 synchronise activities when living in groups (*i.e.*, in alliances) (58), males in alliances containing sponging and  
294 non-sponging individuals might be at a disadvantage relative to non-mixed alliances. Future research needs to  
295 examine whether there are differences in the structure and complexity of 2<sup>nd</sup>- and 1<sup>st</sup>-order alliances between  
296 male spongers and non-spongers. Here we suggest that the benefits of social homophily may, to a certain  
297 extent, mitigate the costs of sponging for male alliance behaviour.

298         Apart from social homophily, behavioural plasticity might manifest itself by allied male spongers  
299 reducing the amount of time invested in sponging during the peak mating season, thus further mitigating the  
300 costs of being a male sponger to some degree. Nevertheless, the mating season in Shark Bay is only moderately  
301 seasonal, with consortships occurring during all months of the year, and a diffuse peak between September  
302 and December (59).

303         In summary, we show that while previous assumptions that sponging affects male activity budgets and  
304 social pattern hold true, this might not necessarily stand in conflict with male alliance behaviour. The apparent  
305 cost mitigating behaviours together with the observed absence of differences in socialising proportions  
306 between male spongers and non-spongers weaken the hypothesis that sponging stands in conflict with male  
307 alliance behaviour and thereby leading to a female bias in sponging. In fact, preliminary data suggest rates of  
308 female monopolisation do not differ between male spongers and male non-spongers (unpublished data).  
309 Future research might explore the costs of sponging and how it might be mitigated in more detail, leaving room  
310 for other plausible explanations regarding the female bias in social learning of sponging. For instance, time  
311 constraints on a male dolphin during its early life may play an important role. Males are weaned earlier than  
312 females (60), and therefore have less time to learn sponging from their mothers and, instead, may need to  
313 invest time in developing social bonds with other males. Indeed, juvenile male dolphins invest more time in  
314 developing social skills than juvenile females, who instead increase their foraging rates (57). In addition, a  
315 recent study showed that an extensive training period (decades) is crucial to achieve peak performance in  
316 sponging (26).

317           In conclusion, our study explored the impacts of sponging on male dolphin behaviour. We suggest that  
318 potential costs associated with sponging for male dolphins might be mitigated by social homophily. Revealing  
319 social homophily in bottlenose dolphins is interesting, as in humans, homophilous behaviour is a key factor in  
320 the emergence and maintenance of subcultures (61) and the establishment of attachment and close  
321 friendships (62). Our study thereby provides another example of convergence in social complexity, innovation  
322 and cultural behaviour between cetaceans and great apes (20,22,63,64).  
323

324 **ACKNOWLEDGEMENTS**

325 We thank Shark Bay Resources and the Useless Loop community for their generous, long-term, in-kind and  
326 logistical support. We also thank all field assistants for their help during this study.

327

328 **DATA ACCESSIBILITY AND DATA CITATION**

329 All used datasets are available as electronic supplementary material to this study.

330

331 **FUNDING**

332 This study was supported by a Swiss National Science Foundation grant (31003A\_149956) to M.K. Further  
333 financial assistance was provided by grants from the National Geographic Society, W.V. Scott Foundation,  
334 SeaWorld Research and Rescue Foundation Inc., A.H. Schultz Stiftung, and the University of Zurich. S.L.K. was  
335 supported by The Branco Weiss Fellowship—Society in Science. W.R.F. was supported by a Graduate  
336 Fellowship in Anthropogeny from the University of California, San Diego.

337



338  
339  
340  
341  
342  
343  
344  
345  
346  
347  
348  
349  
350  
351  
352  
353  
354  
355  
356  
357  
358  
359  
360  
361  
362  
363  
364  
365  
366  
367  
368  
369  
370  
371  
372  
373  
374  
375  
376  
377  
378  
379  
380  
381  
382  
383  
384  
385  
386  
387  
388  
389  
390  
391  
392  
393  
394  
395  
396  
397  
398  
399  
400  
401  
402

## REFERENCES

1. Laland K, Janik V. The animal cultures debate. *Trends Ecol Evol* [Internet]. 2006 Oct;21(10):542–7. Available from: <http://dx.doi.org/10.1016/j.tree.2006.06.005>
2. Leadbeater E, Chittka L. Social Learning in Insects - From Miniature Brains to Consensus Building [Internet]. *Current Biology*. 2007. p. R703–13. Available from: <https://doi.org/10.1016/j.cub.2007.06.012>
3. Hoppitt W, Laland KN. Chapter 3 Social Processes Influencing Learning in Animals: A Review of the Evidence [Internet]. *Advances in the Study of Behavior*. Academic Press; 2008. p. 105–65. Available from: [http://dx.doi.org/10.1016/S0065-3454\(08\)00003-X](http://dx.doi.org/10.1016/S0065-3454(08)00003-X)
4. Fogarty L, Laland KN, Morgan TJH, Webster MM, Hoppitt WJE, Rendell L. Cognitive culture: theoretical and empirical insights into social learning strategies. *Trends Cogn Sci* [Internet]. Elsevier Ltd; 2011;15(2):68–76. Available from: <http://dx.doi.org/10.1016/j.tics.2010.12.002>
5. Giraldeau L, Valone TJ, Templeton JJ. Potential disadvantages of using socially acquired information. *Philos Trans R Soc Lond B Biol Sci* [Internet]. 2002;357(1427):1559–66. Available from: <http://dx.doi.org/10.1098/rstb.2002.1065>
6. Laland KN. Social learning strategies. *Anim Learn Behav* [Internet]. 2011;32(1):4–14. Available from: <http://dx.doi.org/10.3758/bf03196002>
7. Pike TW, Laland KN. Conformist learning in nine-spined sticklebacks' foraging decisions. *Biol Lett* [Internet]. 2010;6(4):466–8. Available from: <http://dx.doi.org/10.1098/rsbl.2009.1014>
8. Henrich J, Henrich N. The evolution of cultural adaptations: Fijian food taboos protect against dangerous marine toxins. *Proc R Soc B Biol Sci* [Internet]. The Royal Society; 2010;277(1701):3715–24. Available from: <https://doi.org/10.1098/rspb.2010.1191>
9. Kendal JR, Rendell L, Pike TW, Laland KN. Nine-spined sticklebacks deploy a hill-climbing social learning strategy. *Behav Ecol* [Internet]. 2009;20(2):238–44. Available from: <http://dx.doi.org/10.1093/beheco/arp016>
10. Hoppitt W, Laland KN. Social learning: an introduction to mechanisms, methods, and models [Internet]. Princeton University Press; 2013. Available from: <https://doi.org/10.1016/j.tics.2010.12.002>
11. Trivers RL. Parental investment and sexual selection. In 'Sexual Selection and the Descent of Man 1871–1971'. (Ed. B. Campbell.) pp. 136–179. Aldine: Chicago, IL; 1972.
12. Bateman AJ. Intra-Sexual Selection in *Drosophila*. *Heredity* (Edinb). 1984;2:349–68.
13. Lonsdorf E V. Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Anim Behav* [Internet]. 2005 Sep;70(3):673–83. Available from: <http://dx.doi.org/10.1016/j.anbehav.2004.12.014>
14. Lonsdorf E V, Anderson KE, Stanton MA, Shender M, Heintz MR, Goodall J, et al. Boys will be boys: Sex differences in wild infant chimpanzee social interactions. *Anim Behav* [Internet]. Elsevier Ltd; 2014 Feb;88:79–83. Available from: <http://dx.doi.org/10.1016/j.anbehav.2013.11.015%0A>
15. Wroblewski EE, Murray CM, Keele BF, Schumacher-Stankey JC, Hahn BH, Pusey AE. Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. *Anim Behav* [Internet]. 2009 Apr;77(4):873–85. Available from: <http://dx.doi.org/10.1016/j.anbehav.2008.12.014>
16. Gilby IC, Brent L, Wroblewski EE, Rudicell RS, Hahn BH, Goodall J, et al. Fitness benefits of coalitionary aggression in male chimpanzees. *Behav Ecol Sociobiol* [Internet]. 2013 Mar 1;67(3):373–81. Available from: <http://link.springer.com/10.1007/s00265-012-1457-6>
17. Smolker R, Richards A, Connor R, Mann J, Berggren P. Sponge Carrying by Dolphins (*Delphinidae*, *Tursiops* sp.): A Foraging Specialization Involving Tool Use? *Ethology* [Internet]. 2010;103(6):454–65. Available from: <http://dx.doi.org/10.1111/j.1439-0310.1997.tb00160.x>
18. Krützen M, Mann J, Heithaus MR, Connor RC, Bejder L, Sherwin WB. Cultural transmission of tool use in bottlenose dolphins. *Proc Natl Acad Sci* [Internet]. 2005;102(25):8939–43. Available from: <https://doi.org/10.1073/pnas.0500232102>
19. Patterson EM, Mann J. The ecological conditions that favor tool use and innovation in wild bottlenose dolphins (*Tursiops* sp.). Brosnan SF, editor. *PLoS One* [Internet]. 2011 Jul 20;6(7):e22243. Available from: <https://dx.plos.org/10.1371/journal.pone.0022243>
20. Krützen M, Kreicker S, MacLeod CD, Learmonth J, Kopps AM, Walsham P, et al. Cultural transmission of tool use by Indo-Pacific bottlenose dolphins (*Tursiops* sp.) provides access to a novel foraging niche. *Proc R Soc B Biol Sci* [Internet]. 2014;281(1784):20140374. Available from: <https://doi.org/10.1098/rspb.2014.0374>
21. Kopps AM, Krützen M, Allen SJ, Bacher K, Sherwin WB. Characterizing the socially transmitted foraging tactic “sponging” by bottlenose dolphins (*Tursiops* sp.) in the western gulf of Shark Bay, Western Australia. *Mar Mammal Sci* [Internet]. 2014 Jul;30(3):847–63. Available from: <http://dx.doi.org/10.1111/mms.12089>
22. Mann J, Stanton M a, Patterson EM, Bienenstock EJ, Singh LO. Social networks reveal cultural behaviour in tool-using dolphins. *Nat Commun* [Internet]. Nature Publishing Group; 2012 Jan;3:980. Available from: <http://dx.doi.org/10.1038/ncomms1983>
23. Bacher K, Allen S, Lindholm a K, Bejder L, Krützen M. Genes or Culture: Are mitochondrial genes associated with tool use in bottlenose dolphins (*Tursiops* sp.)? *Behav Genet* [Internet]. 2010 Sep;40(5):706–14. Available from: <http://dx.doi.org/10.1007/s10519-010-9375-8>
24. Mann J, Sargeant BL, Watson-Capps JJ, Gibson QA, Heithaus MR, Connor RC, et al. Why do dolphins carry sponges? *PLoS One* [Internet]. 2008 Jan;3(12):e3868. Available from: <http://dx.doi.org/10.1371/journal.pone.0003868>
25. Mann J, Patterson EM. Tool use by aquatic animals. *Phil Trans R Soc B*. 2013;368:20120424.
26. Patterson EM, Krzyszczyk E, Mann J. Age-specific foraging performance and reproduction in tool-using wild bottlenose dolphins. *Behav Ecol* [Internet]. 2016;27(2):401–10. Available from:

- 403 <http://dx.doi.org/10.1093/beheco/arv164>
- 404 27. Connor RC, Krützen M. Male dolphin alliances in Shark Bay: Changing perspectives in a 30-year study. *Anim Behav* [Internet]. 2015;103:223–35. Available from: <http://dx.doi.org/10.1016/j.anbehav.2015.02.019>
- 405 28. Connor RC, Wells RJ, Mann J, Read A. Cetacean societies: field studies of dolphins and whales. In: Mann J, Connor R, Tyack P, Whitehead H, editors. University of Chicago Press; 2000.
- 406 29. Connor RC, Smolker RA, Richards AF. Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proc Natl Acad Sci* [Internet]. 1992;89(3):987–90. Available from: <http://dx.doi.org/10.1073/pnas.89.3.987>
- 407 30. Gerber L, Connor RC, King SL, Allen SJ, Wittwer S, Bizzozzero MR, et al. Multi-level cooperation in wild male bottlenose dolphins is predicted by long-term friendships. *Behavioural Ecol (in Rev)*. 2019;
- 408 31. Tyne JA, Loneragan NR, Kopps AM, Allen SJ, Krützen M, Bejder L. Ecological characteristics contribute to sponge distribution and tool use in bottlenose dolphins *Tursiops* sp. *Mar Ecol Prog Ser* [Internet]. 2012 Jan;444:143–53. Available from: <http://dx.doi.org/10.3354/meps09410>
- 409 32. Würsig B, Würsig M. The Photographic Determination of Group Size, Composition, and Stability of Coastal Porpoises (*Tursiops truncatus*). *Science (80- )* [Internet]. 1977 Nov 18;198(4318):755–6. Available from: <http://science.sciencemag.org/content/198/4318/755.abstract>
- 410 33. Smolker RA, Richards AF, Connor RC, Pepper JW. Sex Differences in Patterns of Association among Indian Ocean Bottlenose Dolphins. *Behaviour* [Internet]. 1992;123(1–2):38–69. Available from: <https://doi.org/10.1163/156853992X00101>
- 411 34. Krützen M, Barre L, Möller L, Heithaus M, Simms C, Sherwin W. A biopsy system for small cetaceans: darting success and wound healing in *Tursiops* spp. *Mar Mammal Sci* [Internet]. 2002;18(4):863–78. Available from: <https://doi.org/10.1111/j.1748-7692.2002.tb01078.x>
- 412 35. Gilson A, Syvanen M, Levine K, Banks J. Deer gender determination by polymerase chain reaction: Validation study and application to tissues, bloodstains, and hair forensic samples from California. *Calif Fish Game*. 1998;84(4):159–69.
- 413 36. R Core Team. A Language and Environment for Statistical Computing [Internet]. Vienna; 2013;1:12–21. Available from: <http://www.r-project.org>
- 414 37. Mann J, Connor RC, Barré LM, Heithaus MR. Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. *Behav Ecol* [Internet]. 2000;11(2):210–9. Available from: <http://dx.doi.org/10.1093/beheco/11.2.210>
- 415 38. Connor RC, Smolker R, Bejder L. Synchrony, social behaviour and alliance affiliation in Indian Ocean bottlenose dolphins, *Tursiops aduncus*. *Anim Behav* [Internet]. 2006 Dec;72(6):1371–8. Available from: <http://dx.doi.org/10.1016/j.anbehav.2006.03.014>
- 416 39. Tabachnick BG, Fidell LS, Ullman JB. Using multivariate statistics. Pearson Boston, MA; 2007.
- 417 40. Welch WJ. Construction of permutation tests. *J Am Stat Assoc* [Internet]. 1990;85(411):693–8. Available from: <https://doi.org/10.1080/01621459.1990.10474929>
- 418 41. Fay M., Shaw PA. Exact and Asymptotic Weighted Logrank Tests for Interval Censored Data: The interval R Package. *J Stat Softw* [Internet]. 2010;36(2):1–34. Available from: <http://www.jstatsoft.org/v36/i02/>
- 419 42. Cairns SJ, Schwager SJ. A comparison of association indices. *Anim Behav* [Internet]. 1987;35(5):1454–69. Available from: [https://doi.org/10.1016/S0003-3472\(87\)80018-0](https://doi.org/10.1016/S0003-3472(87)80018-0)
- 420 43. Bejder L, Fletcher D, Bräger S. A method for testing association patterns of social animals. *Anim Behav* [Internet]. 1998 Sep;56(3):719–25. Available from: <http://dx.doi.org/10.1006/anbe.1998.0802>
- 421 44. Whitehead H, Bejder L, Ottensmeyer CA. Testing association patterns: Issues arising and extensions. *Anim Behav* [Internet]. Academic Press; 2005;69(5):e1. Available from: <http://dx.doi.org/10.1016/j.anbehav.2004.11.004>
- 422 45. Whitehead H. SOCPROG: program for analyzing social structure. *Behav Ecol Sociobiol* [Internet]. 2009;63(5):765–78. Available from: <http://dx.doi.org/10.1007/s00265-008-0697-y%0A>
- 423 46. Dekker D, Krackhardt D, Snijders TAB. Sensitivity of MRQAP tests to collinearity and autocorrelation conditions. *Psychometrika* [Internet]. 2007;72(4):563–81. Available from: <https://doi.org/10.1007/s11336-007-9016-1>
- 424 47. Farine DR. Animal social network inference and permutations for ecologists in {R} using asnipe. *Methods Ecol Evol* [Internet]. 2013;4(12):1187–94. Available from: <https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/2041-210X.12121>
- 425 48. Kopps AM, Ackermann CY, Sherwin WB, Allen SJ, Bejder L, Krützen M. Cultural transmission of tool use combined with habitat specializations leads to fine-scale genetic structure in bottlenose dolphins. *Proc R Soc B Biol Sci* [Internet]. 2014;281(1782):20133245. Available from: <https://doi.org/10.1098/rspb.2013.3245>
- 426 49. Whitehead H. Analyzing animal societies: quantitative methods for vertebrate social analysis [Internet]. Chicago: University of Chicago Press; 2008. 161-168 p. Available from: <http://public.eblib.com/choice/publicfullrecord.aspx?p=408184>.
- 427 50. Killick R, Haynes K, Eckley I, Fearnhead P, Lee J. “change point”: Methods for Change point Detection [Internet]. 2016. Available from: <https://cran.r-project.org/web/packages/changepoint/changepoint.pdf>
- 428 51. King SL, Friedman WR, Allen SJ, Gerber L, Jensen FH, Wittwer S, et al. Bottlenose Dolphins Retain Individual Vocal Labels in Multi-level Alliances. *Curr Biol* [Internet]. Elsevier; 2018; Available from: <https://doi.org/10.1016/j.cub.2018.05.013>
- 429 52. Bridge PD. Classification. In: Fry J, editor. Biological data analysis. Oxford, UK: Oxford University Press; 1993. p. 219–42.
- 430 53. Smith TB, Skúlason S. Evolutionary Significance of Resource Polymorphisms in Fishes, Amphibians, and Birds. *Annu Rev Ecol Syst* [Internet]. 1996;27(1):111–33. Available from: <http://dx.doi.org/10.1146/annurev.ecolsys.27.1.111>
- 431
- 432
- 433
- 434
- 435
- 436
- 437
- 438
- 439
- 440
- 441
- 442
- 443
- 444
- 445
- 446
- 447
- 448
- 449
- 450
- 451
- 452
- 453
- 454
- 455
- 456
- 457
- 458
- 459
- 460
- 461
- 462
- 463
- 464
- 465
- 466
- 467

- 468 54. Bolnick DI. Intraspecific competition favours niche width expansion in *Drosophila melanogaster*. *Nature* [Internet].  
469 2001;410(6827):463–6. Available from: <http://dx.doi.org/10.1038/35068555>
- 470 55. Krützen M, Sherwin WB, Connor RC, Barré LM, Van De Castele T, Mann J, et al. Contrasting relatedness patterns in  
471 bottlenose dolphins (*Tursiops* sp.) with different alliance strategies. *Proceedings of the Royal Society B: Biological*  
472 *Sciences* [Internet]. 2003. p. 497–502. Available from: <http://dx.doi.org/10.1098/rspb.2002.2229>
- 473 56. Tsai YJJ, Mann J. Dispersal, philopatry, and the role of fission-fusion dynamics in bottlenose dolphins. *Mar Mammal*  
474 *Sci* [Internet]. 2012;29(2):261–79. Available from: <http://dx.doi.org/10.1111/j.1748-7692.2011.00559.x>
- 475 57. Krzyszczak E, Patterson EM, Stanton MA, Mann J. The transition to independence: sex differences in social and  
476 behavioural development of wild bottlenose dolphins. *Anim Behav* [Internet]. Elsevier; 2017;129:43–59. Available  
477 from: <https://doi.org/10.1016/j.anbehav.2017.04.011>
- 478 58. Tosi CH, Ferreira RG. Differences between solitary and group time budgets in Guiana dolphin (*Sotalia guianensis*) at  
479 northeastern Brazil. *Dolphins anatomy, Behav Threat Nov Sci Hauppauge*. 2010;197–206.
- 480 59. Smolker RA, Connor RC. “Pop” Goes the Dolphin: a Vocalization Male Bottlenose Dolphins Produce During  
481 Consortships. *Behaviour* [Internet]. 1996;133(9–10):643–62. Available from:  
482 <http://dx.doi.org/10.1163/156853996X00404>
- 483 60. Mann J, Sargeant BL. Like mother like calf: The ontogeny of foraging traditions in wild Indian Ocean bottlenose  
484 dolphins (*Tursiops* sp.). In: Fragaszy DM, Perry S, editors. *The Biology of Traditions*. Cambridge University Press;  
485 2003. p. 236–66.
- 486 61. McPherson M, Smith-Lovin L, Cook JM. Birds of a Feather: Homophily in Social Networks. *Annu Rev Sociol*  
487 [Internet]. 2001;27(1):415–44. Available from: <https://doi.org/10.1146/annurev.soc.27.1.415>
- 488 62. Rivera MT, Soderstrom SB, Uzzi B. Dynamics of Dyads in Social Networks: Assortative, Relational, and Proximity  
489 Mechanisms [Internet]. *Annual Review of Sociology*. 2010. Available from:  
490 <http://dx.doi.org/10.1146/annurev.soc.34.040507.134743>
- 491 63. Allen SJ, King SL, Krützen M, Brown AM. Multi-modal sexual displays in Australian humpback dolphins. *Sci Rep*  
492 [Internet]. 2017;7(1):1–8. Available from: <http://dx.doi.org/10.1038/s41598-017-13898-9>
- 493 64. Lonsdorf E V., Eberly LE, Pusey AE. Sex differences in learning in chimpanzees. *Nature* [Internet]. 2004  
494 Apr;428(6984):715–6. Available from: <https://doi.org/10.1038/428715a>
- 495 65. Csárdi G, Nepusz T. The igraph software package for complex network research. *J Comput Appl* [Internet].  
496 2014;Complex Sy:9. Available from:  
497 <http://pub.chinasciencejournal.com/JournalofComputerApplications/5970.jhtml>  
498

499 **FIGURE CAPTIONS**

500

501 **Fig. 1:** Social network of the male dolphins in the restricted data set ( $n = 37$ ). The nodes represent individuals  
502 and are shaded according to foraging technique. Edges (lines) below 0.27 HWI are transparent and edge  
503 thickness corresponds to edge weight (see Figure S2 for the social network showing all edges). The graph was  
504 plotted with the force directed Fruchterman-Reingold algorithm implemented in the 'igraph' package (65).

505

506

507 **Fig. 2:** Hierarchical cluster diagram based on dyadic HWI measures. A HWI value of 0.27 was used as a cut-off  
508 value (grey line) to define communities (*i.e.*, 2<sup>nd</sup>-order alliances).

509

510

## TABLES

**Tab. 1:** Post-hoc, Bonferroni corrected t-tests on activity proportions of male spongers (n = 12) and non-spongers (n = 20). Significant p- values are indicated in bold print.

proportion	spongers		non-spongers		t (df)(df)	r	p
	Mean	SD	Mean	SD			
forage	0.45	0.02	0.20	0.02	-9.42 (26.31)	0.89	<b>&lt; 0.001</b>
rest	0.18	0.01	0.28	0.01	4.83 (27.80)	0.68	<b>&lt; 0.001</b>
travel	0.16	0.02	0.31	0.02	4.83 (27.36)	0.68	<b>&lt; 0.001</b>
socialise	0.16	0.01	0.13	0.01	-1.62 (29.99)	0.28	0.23

**Tab. 2:** Mean association indices (HWI) by foraging technique of male spongers (n = 13) and non-spongers (n = 24), 666 dyadic relationships.

<b>pair composition</b>	<b>mean HWI (SD)</b>
<b>sponger – sponger</b>	0.21 (0.11)
<b>non-sponger – non-sponger</b>	0.10 (0.05)
<b>similar foraging technique</b>	0.14 (0.09)
<b>different foraging technique</b>	0.05 (0.04)
<b>overall</b>	0.09 (0.04)

**Tab. 3:** MRQAP-DSP model including only genotyped males (n = 25, 300 dyadic relationships). Significant p-values are indicated in bold print.

variable	coefficient	p
<b>sponger similarity</b>	0.19	<b>&lt;0.001</b>
<b>non-sponger similarity</b>	0.10	<b>&lt;0.01</b>
<b>relatedness</b>	0.21	0.24
F(3, 297) = 34.5, adjusted R <sup>2</sup> = 0.25, p-value < <b>0.001</b>		