

Counting conformity: evaluating the units of measurement in frequency-dependent social learning

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4 In a recent study (Aplin et al., 2015), we conducted a large-scale cultural diffusion experiment where
5 we used trained “demonstrator” individuals to introduce one of two alternative foraging
6 techniques into five replicate sub-populations of wild great tits (*Parus major*). Three further sub-
7 populations served as controls. By tracking the spread of these two techniques, we showed that
8 information was acquired through social learning, transmitted through social network ties, and novel
9 behaviours became established in each sub-population, forming stable arbitrary traditions (for
10 technique A or B). These traditions persisted over generations and were stable despite immigrating
11 and innovating individuals, resulting in a within-group behavioural homogeneity and between-group
12 variation. Most pertinent for this discussion, our experimental design allowed an examination of the
13 interaction between individual decision-making and population-level outcomes. We found that the
14 population-level bias for each introduced technique increased by an average of 14% per day towards
15 the common variant. This was explained both by a tendency for naïve individuals to
16 disproportionately adopt the most common behaviour (‘conformist transmission’), and for
17 individuals with experience of both techniques to change their behaviour to match the common
18 variant (‘conformity’).

19

20 While accepting our evidence for the population-level patterns, van Leeuwen, Kendal, Tennie, and
21 Haun (*in press*) have challenged the validity of our individual-level results. This is largely because of
22 the way conformist transmission was defined and measured within the context of the paper - as
23 copying the ‘majority of observed behaviours’, rather than ‘the behaviour of the majority of observed
24 individuals’. They make three main arguments: first, that there is a need for definitions to be
25 consistent with previous theoretical and empirical work. Second, that only copying the behaviour of
26 the majority of individuals represents adaptive collective cognition, while copying the majority of
27 behaviour is more likely to result in sub-optimal information. Third, that in any case, the within-group
28 convergence in traditions observed in our study was more likely to have arisen through alternative
29 mechanisms. We address each of these points in turn and present an alternative viewpoint: that
30 conformity should be considered as an umbrella term with a functional focus. We then present
31 additional analyses of our original results to demonstrate the artificiality of the argument that there is
32 only one “valid” form of positive-frequency dependent social learning.

33

34 In their commentary, van Leeuwen et al. (*in press*) argue that there is one acceptable definition of

35 conformity: copying the behaviour of the majority of individuals. First, it is important to
36 acknowledge that there have been a variety of definitions used in the literature to date (reviewed in
37 Claidiere & Whiten, 2012). In many discussions of social learning strategies, a conformist bias has
38 been defined as a “non-linear learning rule, where the probability of adopting a behavior depends
39 non-linearly on the frequency of that behavior in the population” (Whalen & Laland, 2015; also
40 Morgan & Laland, 2012) - or simply as “a propensity to preferentially adopt the cultural traits that
41 are most frequent in the population” (Heinrich & Boyd, 1998) without specifying whether the unit of
42 frequency is behaviour or individuals (Kendal, Giraldeau, & Laland, 2009; Mesoudi, 2011, 2015;
43 Mesoudi & Lycett, 2009; Mesoudi & Whiten, 2008; Nakahashi, 2007; Rendell, Boyd, et al., 2011;
44 Rendell, Fogarty, et al., 2011). This second approach reflects empirical work, where the underlying
45 unit of frequency is usually not measured or reported, and both decision-making processes are
46 together called conformist transmission (e.g. Aplin et al., 2015; Galef & Whiskin, 2008; Hopper,
47 Schapiro, Lambert, & Brosnan, 2011; van de Waal, Borgeaud, & Whiten, 2013; Whiten, Horner, &
48 de waal, 2005). The exceptions to this have been in studies of shoaling fish, where individuals are
49 necessarily making a choice between groups of demonstrators (Brown & Laland, 2002; Day,
50 Macdonald, Brown, Laland, & Reader, 2001; Pike & Laland, 2010).

51

52 Is van Leeuwen et al.’s (*in press*) insistence on a ‘behaviour of the majority of individuals’ definition
53 for conformity therefore reasonable? It is likely that in most natural and experimental situations (as
54 we discuss below), there will be a close correlation and functional equivalence between the
55 ‘behaviour of the majority of individuals’ and the ‘majority of behaviour’. If so, the two can only be
56 separable with targeted, often artificial, experiments (Haun, Rekers, & Tomasello, 2012). This raises
57 an immediate question as to whether differentiating these definitions has any functional relevance.
58 There is currently no evidence from natural human or non-human animal populations - as far as we
59 are aware - that individuals distinguish between the behaviour of the majority of individuals and the
60 majority of behaviour, or are more likely to use one or the other (Aplin et al., 2015; Claidiere,
61 Bowler, Brookes, Brown, & Whiten, 2014; van de Waal et al., 2013). Therefore it seems most
62 appropriate to take an inclusive approach - referring to all majority influences as conformity and
63 conformist transmission; then disentangling decision-making processes under this umbrella term
64 when it is of interest to do so. Note that, while van Leeuwen et al. (*in press*) state that “the majority”
65 by definition constitutes the largest portion of the population”, this is only correct if “population”
66 means a sample of countable entities. This might as well be behaviour as individuals: the use of the
67 term majority implies nothing about the type of entity that is quantified.

68

69 Second, we question the assumption that copying the behaviour of the majority of individuals is the
70 most adaptive strategy choice in all circumstances. van Leeuwen et al. (*in press*) argue that a ‘copy the
71 majority behaviour’ strategy may bias observers towards those individuals seen most frequently,
72 resulting in sub-optimal information. However in spatially heterogeneous environments such as those
73 thought to favour the evolution of conformity (Heinrich & Boyd, 1998; Kandler & Laland, 2013;
74 Nakahashi, 2007), this bias may actually result in the acquisition of the most relevant information,
75 and facilitate greater group-level cohesion (Aplin, Farine, Mann, & Sheldon, 2014). Furthermore,
76 useful additional information may be contained within the observed frequency of behaviours –
77 frequently observed individuals are likely to be more resident and may also be more successful, thus
78 possessing better local information than transient individuals observed more rarely. While the
79 interaction between population structure and selection on social learning mechanisms has been
80 relatively unexplored, social network approaches give the opportunity to examine these trade-offs by
81 quantifying each individual’s social environment (Aplin et al., 2015; Whalen & Laland, 2015).

82

83 Yet even if it were true that copying the behaviour of the majority of individuals always provides
84 better information, the most adaptive strategy does not solely depend on the quality of information.
85 A strategy based on copying the majority of individuals imposes an additional cognitive load for
86 individual recognition and book-keeping memory that might outweigh any selective advantage (i.e.
87 observers need to track both the number of behaviours and the number of individuals). In addition, if
88 individuals are not entirely consistent in the information they provide, then observers will need – in
89 effect – to do a multi-step calculation to weigh the value of observed behaviours. To illustrate this,
90 consider a focal individual that has observed 3 demonstrators (i_x) performing a behaviour 10 times
91 each, using either technique X or Y: i_A does X = 10, i_B does X = 6, and i_C does X = 3. If the focal
92 individual uses a ‘majority of behaviour’ strategy, then $(10+6+3) / 30 = 63\%$: therefore the focal
93 individual does X. By contrast, if the focal individual uses a ‘behaviour of the majority of
94 individuals’ strategy, then the calculation is $i_A: 10/10 = 100\%$ (X is most common), for $i_B: 6/10 = 60\%$
95 (X is most common), for $i_C: 3/10 = 30\%$ (Y is most common); thus $(i_A + i_B) / (i_A + i_B + i_C) =$
96 67% : therefore the focal individual does X. Note that this does not consider whether individuals also
97 weight for demonstrator uncertainty; for example, is i_A at 100% consistency treated as equal to i_B at
98 60% consistency?

99

100 Returning to Aplin et al. (2015): our results showed a sigmoidal relationship between the frequency
101 of the variant in the social group that had preceded a naïve bird’s first successful solution and the
102 probability that the naïve observer adopted that variant. This was taken as consistent with the

103 interpretation that naïve individuals were disproportionately copying the majority behaviour (Morgan
104 & Laland, 2012), as illustrated in figure 1a. To note, the mean social group size was not 100 birds, as
105 incorrectly reported in van Leeuwen et al. (*in press*) ($n=100$ is approximately the mean sub-
106 population size), but rather $\text{mean} \pm \text{s.d.} = 4.2 \pm 2.4$. Given previous knowledge of the life history of this
107 population and species, it is a reasonable inference that the focal individuals had observed the actions
108 of their social group that immediately preceded their own behaviour (Aplin et al., 2014; Aplin,
109 Farine, Morand-Ferron, & Sheldon, 2012; Aplin, Sheldon, & Morand-Ferron, 2013; Farine et al.,
110 2015; Psorakis, Roberts, Rezek, & Sheldon, 2012; Slagsvold & Wiebe, 2011). Here, we re-do this
111 analysis, but now measuring the proportion of individuals that were observed performing each
112 behavioural variant in the social group that preceded a naïve bird's first successful solution (Haun et
113 al., 2012). Within these social groups, individuals could give repeated demonstrations and were not
114 always consistent, and so were assigned to the variant they performed most often in the given time
115 period. Doing this, we again find a sigmoidal relationship, with evidence that individuals are
116 disproportionately likely to copy the behaviour of the majority of individuals (figure 1b). The
117 estimated function is very similar to that obtained from a 'copy the majority behaviour' learning rule
118 (figure 1a).

119

120 Yet on further exploration of our data, it becomes clear that it is impossible to distinguish between
121 these two potential learning strategies. In our study, there were never any instances when the
122 information provided to naïve observers from copying the majority of observed behaviours or the
123 behaviour of the majority of individuals conflicted (figure 2). This is despite variation in the number
124 of behaviours performed by each demonstrator and in the consistency of demonstrators. There is no
125 evidence that the individuals themselves were distinguishing between these two learning strategies -
126 they may have been using either or both; although given the extra complexity involved in tracking the
127 behaviour of the majority of individuals (see above), copying the majority of behaviour seems most
128 parsimonious. It also seems likely that the close correlation in the information provided by these two
129 strategies will be robust to most conditions encountered in natural populations of social
130 animals, however we acknowledge formal modeling is needed to investigate this further.

131

132 Finally, in Aplin et al. (2015) we observed a tendency for individuals to adjust their technique to
133 match the majority, even after they had acquired their own personal experience of the puzzle-box
134 ('conformity'). This occurred within sub-populations; hereof the 78 individuals that tried both
135 techniques, 74 birds moved to fixation on the majority variant. 16 of these individuals had also either
136 initially performed the alternative technique or preferred the alternative technique at some point,

137 which is inconsistent with a habit forming hypothesis (Pesendorfer et al., 2009). In addition, when
138 individuals moved between sub-populations (n=40) most that moved into new areas with the same
139 tradition retained their technique (96%), whereas those that moved into areas with a different
140 tradition changed their technique (71%). This result also echoed the behaviour described by van de
141 Waal et al. (2013) in immigrating vervet monkeys (*Chlorocebus aethiops*).

142

143 In response to these results, van Leeuwen et al. (*in press*) argue that we have insufficient evidence to
144 rule out explanations other than conformity for this within-group convergence in behaviour. They
145 propose an alternative explanation that combines two learning biases: i) that when resident
146 individuals adjust their existing behaviour to the majority, they are doing so with a ‘prefer social to
147 personal information’ learning rule, and ii) when immigrating individuals change their existing
148 behaviour to match the majority in the new sub-population they move into, they are using a ‘copy
149 when uncertain’ strategy. However a ‘prefer social to personal information’ learning rule cannot
150 explain the population-level patterns we observed (increasing bias of 14% per day towards the
151 common variant), as it would not, by itself, change the overall frequencies of behaviour in the
152 population. It is true that we cannot exclude the second part of the alternative explanation - that
153 immigrating individuals are using a ‘copy when uncertain’ learning rule when moving, as the small
154 sample size for this class (n=40) prevented in-depth analyses. However, as we have shown above,
155 such a behavioural rule could only be in addition to a conformist bias within sub-populations. This
156 replaces one explanation that is consistent with all data with two, and is not parsimonious.

157

158 To summarize, conformist transmission has long been of interest because of its potentially important
159 role in driving cultural microevolution, and as a way of linking population-level patterns with
160 individual decision-making (Mesoudi, 2015). van Leeuwen et al. (*in press*) acknowledge this role
161 when they argue that it is vital to distinguish the exact form of majority strategy used by individuals
162 because of its implications for population-level outcomes. The cultural diffusion experiment in Aplin
163 et al. (2015) resulted in stable traditions that showed both within-group homogeneity and between
164 group differences. We were then able to match these population-level outcomes with individual-level
165 behaviour consistent with conformist learning. Here, we show that this is the case whether
166 conformist transmission is treated as ‘copy the behaviour of the majority of individuals’ or ‘copy the
167 majority behaviour’, as the two are functionally equivalent in our study. More broadly, we also argue
168 that in empirical work, these two strategies will frequently be either equivalent or indistinguishable
169 (e.g. as in van de Waal et al., 2013). Selection on learning mechanisms operates through fitness
170 outcomes. Surely then the onus lies with explaining how these different definitions of conformity

171 ('copy the majority behaviour'/'copy the behaviour of the majority') could be expected to result in
172 functionally different results, and under what evolutionary conditions differences would arise and be
173 maintained. If not, aninsistence on the exclusive and artificial use of one operationalisation of conformity
174 will only impede progress in this exciting and developing field of cultural evolution.
175

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257
258

259 **FIGURES**

260

261 **Figure 1:**

262

263 Contrasting the behavioural outcomes predicted from ‘copy the majority behaviour’ and ‘copy the
264 behaviour of the majority of demonstrators’ strategies. (a) As shown in Aplin et al. (2015) – a
265 comparison of the frequency of variant A in the social group observed with the observing naïve
266 individual’s first learnt option (pooled data from subpopulations T-5). Node size represents number
267 of learning events (n=1-147). (b) A reanalysis of data from Aplin et al. (2015) – comparison of the
268 proportion of demonstrators performing variant A in the social group with the naïve individual’s first
269 learnt option (pooled data from subpopulations T1-5). Node size represents number of learning
270 events (n = 1-160). In both figures, the black line shows the expected result under unbiased copying;
271 the dashed red line shows the model fit and the dotted lines show the 95% CI.

272

273 **Figure 2:**

274

275 Relationship between information provided from ‘copy the majority behaviour’ and ‘copy the
276 behaviour of the majority of demonstrators’ strategies. The proportion of all behaviours in the social
277 group that are option A is shown on the Y-axis; the numerical difference between the number of
278 demonstrators doing option A as opposed to option B is shown on the X-axis. Node colour indicates
279 the number of learning events occurring at each point. Points where the information from each
280 strategy conflicts would fall into the top-left and bottom-right quadrants of the graph; there are no
281 instances in this dataset where they do so.

282

Highlights:

- We discuss the two possible learning processes underlying conformist transmission
- We present an extended analysis of conformity in a previous study of great tits
- This shows that both conformist processes generate similar results and outcomes
- We argue that functional equivalence is likely in most natural contexts

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Figure 1

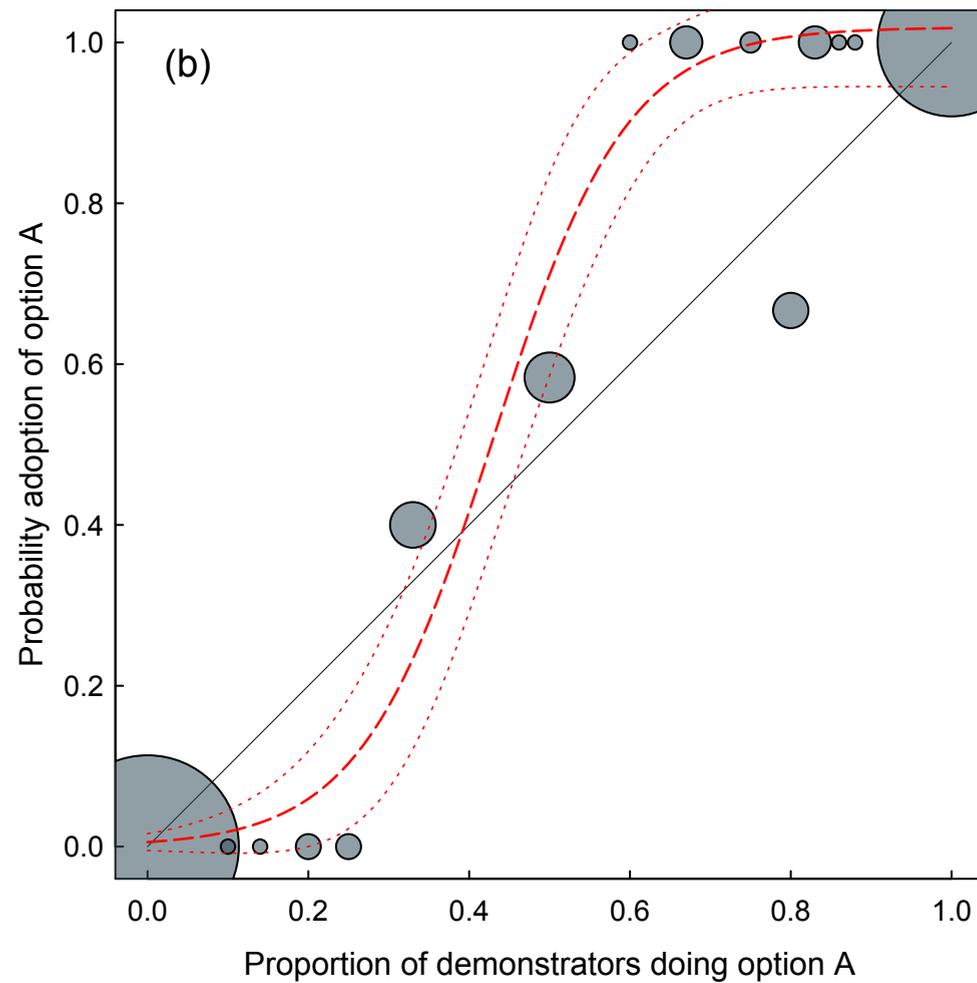
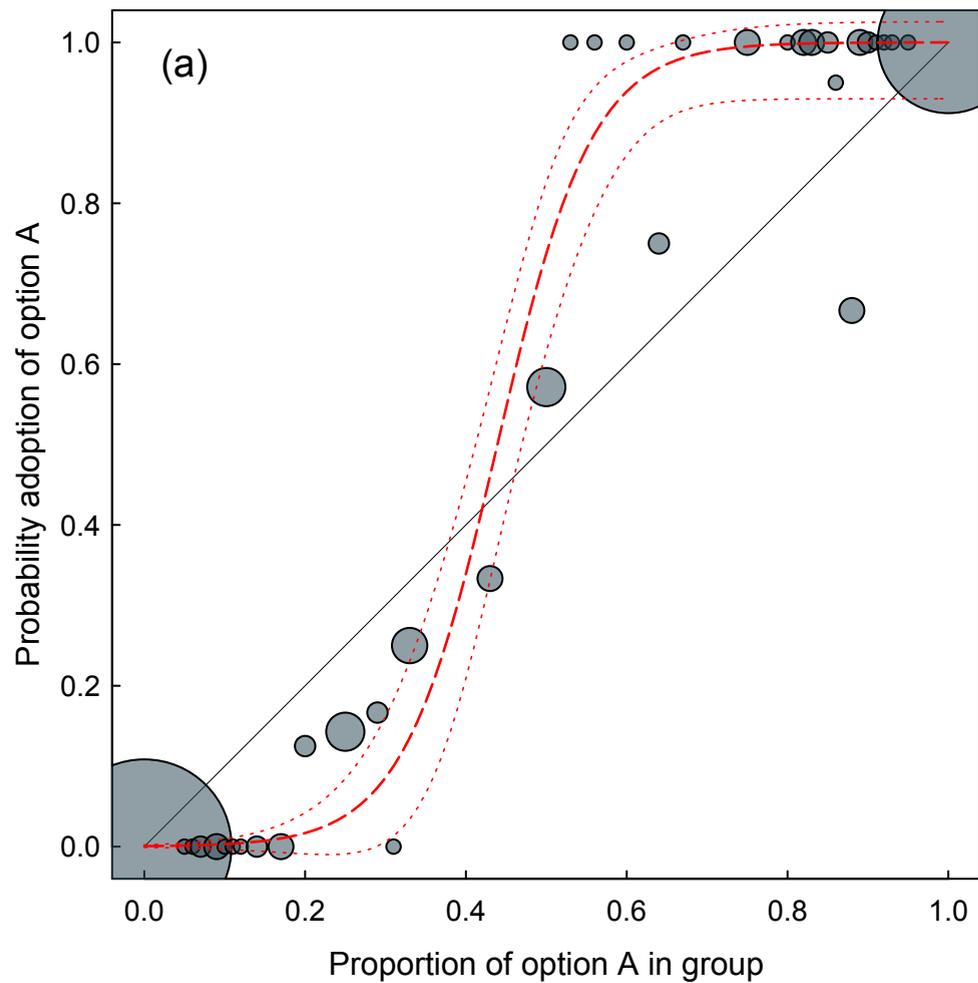


Figure 2

