

## A reappraisal of 'conformity'

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1 **Forum**

2 **A reappraisal of ‘conformity’**

3

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23 evolution, learning biases, majority influences, social learning

24

25 Whiten & van de Waal (this volume) present an answer to a critical account of their  
26 conformity interpretations (van Leeuwen et al., 2015). Their target study (van de Waal  
27 et al., 2013) evidenced immigrant male vervet monkeys adjusting their food colour  
28 preferences to the preference demonstrated by the resident vervets, which was  
29 interpreted in terms of conformity. Van Leeuwen and colleagues (2015; also see van  
30 Leeuwen & Haun, 2013 and online commentary by Tennie, Fischer, Galef & Haun,  
31 2013, at Sciencemag.org) acknowledged the insight gained from the reported  
32 observations for our understanding of social learning processes in wild primates, but  
33 criticized van de Waal et al.’s conformity interpretation (2013) as alternative learning

34 biases, other than conformity, could not be ruled out. In their reply to this critique,  
35 Whiten & van de Waal (this volume) systematically list their arguments against  
36 alternative explanations. Whiten & van de Waal (this volume) also present new data  
37 indicating that in their target study (2013) the “majority of individuals” opting to  
38 perform a specific behaviour correlated with the “majority of behaviours” performed  
39 across the population, thereby adding to a recent debate about how “the majority”  
40 should be operationalized in order to study conformist transmission (see Aplin et al.,  
41 2015a in response to van Leeuwen et al., 2015). Here, we respond to Whiten & van de  
42 Waal (this volume) by i) discussing how their arguments against our alternative  
43 explanations for their conformity interpretation (as advanced in van de Waal et al.,  
44 2013) may be misguided, ii) defending the position that their presented correlation  
45 between the “majority of individuals” and the “majority of behaviours” is tangential to  
46 the current debate, iii) presenting evidence in favour of our original suggestion to keep  
47 reliance on the “majority of individuals” and the “majority of behaviours” as two  
48 separate learning biases, and iv) realigning the debate between Aplin et al. 2015a and  
49 van Leeuwen et al. 2015 to focus again on animals’ observation records as prerequisite  
50 knowledge to interpret their behavioural decisions in terms of learning biases.

51

## 52 *Alternative explanations*

53 In line with Whiten & van de Waal (this volume), we define conformity as  
54 “abandoning personal preferences or behaviours to match alternatives exhibited by a  
55 majority of others” (Haun, van Leeuwen & Edelson, 2013). In their original study (van  
56 de Waal et al., 2013), male vervet monkeys who were trained to prefer one of two food  
57 colours in their native group immigrated to a new group where the alternative food  
58 colour was preferred and adjusted their preferences accordingly (except for one high-  
59 ranking male who maintained his native preference). These immigrants were typically

60 confronted with a large group of residents feeding from the alternative food colour,  
61 while very few or none of the residents fed from the food colour the immigrants were  
62 most familiar with (see illustrations in Whiten & van de Waal, this volume). Van de  
63 Waal et al. (2013) interpreted these behavioural adjustments by the immigrants as  
64 ‘conformity’. In response to this interpretation, van Leeuwen & Haun (2014; also see  
65 van Leeuwen et al. 2015) pointed out that although the immigrants might have been  
66 guided by inclinations to conform to the majority, alternatively, they might have been  
67 guided by other (social) learning biases that are independent of majority considerations.  
68 For instance, the immigrants might have been focused on copying particular resident  
69 individuals, like visibly dominant individuals, or indeed *any* resident individual,  
70 precipitated by their immigration-induced stress, anxiety or general state of uncertainty.  
71 Whiten & van de Waal (this volume) replied to this suggestion by arguing that any  
72 transmission bias other than ‘copy-the-majority’ is unlikely to explain the switching  
73 behaviour of the immigrants. For instance, they argue that the fact that the immigrants  
74 do not have female kin in their new group rules out a kin-based learning rule. Likewise,  
75 they propose that male vervets are relatively *poor* in recognizing the social hierarchy of  
76 females, ruling out a ‘copy high-rankers’ learning rule (Whiten & van de Waal, this  
77 volume). While these particular proposals may or may not be correct, more generally,  
78 we wish to emphasize that although field experiments with wild animals are to be  
79 applauded for their ecological validity, they do not have any superior claim on  
80 epistemological validity. When confounding effects cannot be controlled for rigorously,  
81 interpretation of observed patterns need to be made cautiously.

82         Whiten & van de Waal (this volume) argue most forcefully against the ‘random  
83 copying’ interpretation of their data, stating that: ‘...for the immigrant vervets to copy  
84 just one individual randomly would seem rather *perverse* in the face of the repeated,  
85 extensive and quite consistent scenarios of multiple monkey preferences staring

86 immigrants in the face...’ (line 95-98). We disagree. Clearly, the sheer availability of  
87 information is no guarantee it will be utilized in expected ways, or, at all. Random  
88 copying is as good a predictor of the observed patterns of transmission as conformity:  
89 When observer monkeys are consistently confronted with the majority of residents  
90 feeding from one particular food colour, while only a few, or none, of the resident  
91 monkeys feed from the alternative, copying a random individual would,  
92 probabilistically, boil down to observer monkeys tending to use the foraging option  
93 demonstrated by the majority rather than that demonstrated by the minority, irrespective  
94 of observers’ particular preference for copying the majority. We consider this a  
95 potentially more parsimonious explanation – if observer monkeys could obtain the  
96 locally practiced foraging rule by the mere inclination to copy, there is no need for them  
97 to apply a cognitively more demanding rule like ‘conform to majorities’.

98       Typically, an investigation of whether individuals copy the majority with a  
99 higher probability than the relative size of the majority (henceforth ‘the disproportionate  
100 criterion’) is applied to ascertain that individuals are indeed *majority*-biased, or at least  
101 to exclude the possibility that individuals merely copy randomly (e.g. Laland, 2004;  
102 Mesoudi, 2009). We note that the disproportionate criterion can be viewed as rather  
103 stringent and unrealistic for cases in which individuals have already obtained a working  
104 strategy, where the key behaviour of interest is the foregoing of prior information for an  
105 alternative (‘conformity’). Indeed, the disproportionate criterion is typically used in the  
106 context of naive individuals setting out to obtain a useful strategy by means of social  
107 learning; the context in which *conformist transmission* (CT) is studied (e.g. Boyd &  
108 Richerson, 1985; Morgan et al., 2014). In the CT context, when individuals are  
109 confronted with a balanced population in which only two possible strategies exist, it is  
110 assumed that copiers solely rely on social information and thus have a 50% likelihood  
111 of obtaining one or the other strategy. Similarly, when strategy A is wielded by 70% of

112 the demonstrators, and strategy B thus only by 30%, copiers have a 70% likelihood of  
113 obtaining strategy A by chance, i.e. if they were to apply a *random copying* rule. To  
114 show that individuals *preferentially* copy the majority, and not just by chance, the  
115 disproportionate criterion should be adhered to, meaning that in this case copiers should  
116 have a likelihood of obtaining strategy A that is significantly larger than 70%. However,  
117 in this same example, if individuals are *not* naive and thus have already learned to  
118 prefer one strategy over the other, e.g. strategy B, the assumption that they will obtain  
119 strategy A or B with a 50% likelihood (in the balanced 2-variant population) is  
120 unrealistic. Instead, these experienced individuals will most likely stick to their familiar  
121 strategy, in this case strategy B. In a similar vein, experienced strategy B users will not  
122 have a 70% chance of ending up with strategy A when 70% of the population they  
123 could sample from are strategy A users. If these experienced individuals turn out to start  
124 using strategy A with a 70% likelihood, in fact, one could consider this to be a strong  
125 indication ('disproportionate' in a sense) of majority influence (see Haun, Rekers &  
126 Tomasello, 2014). Thus, contrary to the CT setting, when individuals are experienced, it  
127 seems less valid to interpret a copying probability in accord with the relative majority  
128 size (here: 70%) in terms of *random copying*: past experience must be weighted in and  
129 perhaps a lower threshold than the majority display accepted as strong evidence for  
130 conformity (see van Leeuwen & Haun, 2014).

131 For the vervet monkeys (van de Waal et al., 2013), given that i) they were  
132 indeed experienced in preferring one food colour over the other when they encountered  
133 the opposing demonstrations in the new population, and ii) many of them chose to eat  
134 from the food colour in accord with these preference-opposing demonstrations (perhaps  
135 in numbers approximately matching the relative majority size, although here, crucially,  
136 this cannot be confirmed as the vervets' observation records are missing; see below for  
137 more on this topic), this might indicate that 'random copying' could be dismissed as a

138 mechanistic explanation in favour of ‘majority copying’. It is important to note,  
139 however, that this conclusion rests on the crucial assumption that no other variables  
140 were at play in the decision arena of the respective vervets, which is arguably not true.  
141 Notably, the immigrant vervets were leaving behind a familiar home range, and social  
142 setting, while moving into an unknown territory with unknown conspecifics (‘a  
143 different habitat’: van de Waal et al., 2013, p. 484). We could envisage the very  
144 predicament of the migrating vervets as sufficiently potent to induce a motivation to  
145 obtain new, locally more attuned behaviours (ecologically and/or socially). Van de  
146 Waal and colleagues (2013; also see Whiten & van de Waal, this volume) acknowledge  
147 that such drastic changes in the lives of the vervets could have facilitated the so-called  
148 ‘copy-when-uncertain’ rule (Laland, 2004), a social learning heuristic for which  
149 evidence has been found across a wide range of taxa (e.g. see Kendal et al., 2009). They  
150 explicitly echo our suggestion by writing: “The fitness of foraging decisions made by  
151 wild primates like those we studied will be governed by a host of complex factors that  
152 are inherently unknown to foragers, ranging from dietary constituents to plant toxins  
153 and competing needs such as predator vigilance: Exploiting the prior discoveries of  
154 local experts may be an optimal strategy, overriding opposing knowledge gained in a  
155 different habitat such as one’s original group.” (van de Waal et al., 2013, p. 484). Yet,  
156 crucially, neither van de Waal et al. (2013) nor Whiten & van de Waal (this volume)  
157 consider the possibility that the ‘copy-when-uncertain’ heuristic *alone* could have  
158 caused the immigrants to adjust their foraging preference upon entering their new  
159 environment. It is entirely reasonable that the uncertainty of their new environment  
160 changed the default information-gathering mode of the immigrants to “copy” anybody  
161 (instead of relying on possibly out-dated and locally inadequate personal strategies).

162         Given the discussion above, and widespread local foraging traditions, the  
163 simplest form of copying – random copying – would equip the immigrating vervets

164 with the local “majority” strategy. In other words, the transition from home to unknown  
165 territory could have reset the vervet monkeys, rendering prior information irrelevant,  
166 turning them effectively into naïve learners. We call this the “reset hypothesis”. One  
167 possible way to empirically test this hypothesis is to investigate whether immigrants  
168 would switch to the local foraging preference upon seeing a small number of residents  
169 showing a preference against an even larger background of non-behaving others, or,  
170 maybe a simpler case, upon seeing just one single resident’s demonstration of this  
171 preference (something that may have been opportunistically possible to assess had  
172 immigrant observation records been acquired, see below). If these observers would  
173 switch their preference, *majorities* would cease to be the single possible object of the  
174 immigrants’ copying efforts. Indeed, drawing on parsimony again, this finding would  
175 indicate that “conformity” is not even necessary to explain the immigrants’ behaviour.  
176 Note that even if one adheres to the conformity definition of ‘a willingness to subjugate  
177 one’s own countervailing knowledge in matching the majority’s choice’ – as in van de  
178 Waal et al. 2013 supplementary material p. 6 – one is still left with the burden of proof  
179 for the claim that ‘the majority’ is being matched, not just any individual.

180 Overall, the problem with interpreting the observations made by van de Waal et  
181 al. (2013) is the lack of nuance in the data regarding observer monkeys responding to  
182 different majority/minority ratios of (inadvertent) demonstrator monkeys. If observers  
183 are only presented with one stimulus (“the majority”), which consists of many other  
184 stimuli (“general social information”, “high-ranking individuals”, “low-ranking  
185 individuals”, “conspicuous individuals”, etc.), it is impossible to disentangle the very  
186 learning bias that the observers follow, while this is exactly what we want to know (e.g.  
187 see Heyes, 2016). For instance, if we were to investigate the evolutionary roots of  
188 conformist decision-making and we find that immigrant vervet monkeys, patas  
189 monkeys and rhesus macaques all adjust their preferences to the majority of the new



190 group, we would need to know whether they were biased to “the majority” or to any  
191 other cue provided by the majority, for without this knowledge, the apparent similarity  
192 in decision-making strategies across these species may be purely coincidental.

193

#### 194 *Majority of individuals versus majority of behaviours*

195 Due to our emphasis (van Leeuwen et al., 2015) upon the need for observation records  
196 in interpreting transmission events, we are delighted to find more detailed analysis on  
197 the observation records of the vervet monkeys (van de Waal et al., 2013) in their follow-  
198 up paper (Whiten & van de Waal (this volume)). Whiten & van de Waal (this volume)  
199 present an analysis of how the number of individuals feeding from the locally-preferred  
200 food colour correlated with the number of behaviours (handfuls of corn) regarding this  
201 same food colour. Specifically, they state: “Indeed the two variables [individuals and  
202 behaviours] show a significant correlation across the twelve sample periods ( $r = 0.67$ ,  $n$   
203  $= 12$ ,  $p = 0.018$ ). Accordingly we infer that the migrant males’ striking switch from  
204 their own to the opposite local preference was an effect of these majority displays, and  
205 hence a case of conformity” (Whiten & van de Waal, this volume, L69-73). To clarify,  
206 Whiten & van de Waal (this volume) aim to address a subject pertaining to the analysis  
207 of *conformist transmission* that was discussed in van Leeuwen et al. (2015) and Aplin et  
208 al. (2015a). In summary, where van Leeuwen et al. (2015) argued for keeping separate  
209 the biases of following the majority of individuals versus the majority of observed  
210 behaviours, and only reserving the term ‘conformist transmission’ for the former, Aplin  
211 et al. (2015a) argued for grouping the biases together under the same term, i.e.  
212 ‘conformist transmission’. Aplin et al. (2015a) based their argument on the fact that in  
213 their original great tit study (Aplin et al. 2015b), the birds did not seem to distinguish  
214 between individuals and behaviours (analysed in Aplin et al. 2015a). Following up on  
215 this debate, Whiten & van de Waal (this volume) echo Aplin et al.’s position by

216 showing that in their vervet monkey study (van de Waal et al., 2013) the frequency of  
217 *individuals* using a certain behavioural option and the frequency of demonstration of  
218 this particular behavioural option in total were not affecting the observers differently. In  
219 other words, the monkeys were indistinguishably following the majority of individuals  
220 and the majority of behaviours (Whiten & van de Waal, this volume).

221         While we acknowledge the additional analysis and appreciate its intent, we do  
222 not find it compelling for several reasons. First and foremost, in line with our previous  
223 arguments, Whiten & van de Waal (this volume) neither use the frequency of  
224 individuals nor behaviours to test their conformity hypothesis against any other (social)  
225 learning bias. Therefore, the reported correlation between the frequency of individuals  
226 and behaviours, while representing an affirmation of internal validity, has no power to  
227 falsify alternative hypotheses. For instance, Aplin et al. (2015b), though confronted with  
228 similar limitations due to working with wild animal populations, obtained detailed  
229 records of birds responding to differently-sized majorities and incorporated their  
230 majority numbers, in terms of individuals and behaviours, into statistical analyses to  
231 provide insight regarding whether the birds actually *used* the majority cue or merely  
232 obtained the most common strategy randomly. Without such analysis, our  
233 understanding of transmission biases is not furthered by the reporting of a correlation  
234 between two possible measures. Note that due to the very nature of “the majority” (i.e.  
235 comprising more than half of the sampled individuals) measures of for instance, skilful,  
236 conspicuous and high-ranking individuals will also coincide with the majority strategy.

237         Furthermore, we note that two cases of correlation between the number of  
238 individuals and behaviours indicating the use of a particular strategy (Aplin et al., 2015a  
239 and Whiten & van de Waal, this volume) do not constitute sufficient evidence in favour  
240 of the two measures being ‘functionally equivalent’. While scenarios in which the  
241 number of individuals and behaviours correlate are straightforward to envision, we

242 could imagine other scenarios in which the two respective measures would diverge,  
243 either due to individual differences in performance rates (in conjunction with relative  
244 preferences for certain strategies) or population structure (increasing the likelihood of  
245 repetitively sampling the same individuals). Moreover, for reasons of informational  
246 accuracy, it may well matter if one individual “cries wolf” ten times, or if ten  
247 individuals (independently) do so once (e.g. see Wolf et al., 2013). We conjecture that  
248 the adaptive value of relying on indiscriminate sampling of behaviours versus relying  
249 on the aggregate knowledge of similarly poised, unpredictability-reducing conspecifics  
250 will differ to the extent that under certain conditions, one particular bias is expected to  
251 evolve (at the expense of the other). Formal modelling would be a constructive way  
252 forward in fuelling our understanding and expectations regarding this pending question,  
253 which was acknowledged by Aplin et al. (2015a). In the absence of such understanding,  
254 we fail to see how grouping two potentially distinct social learning biases (see Haun et  
255 al., 2012) under one and the same denominator of “conformist transmission” could be  
256 beneficial to the (comparative) study of learning biases.

257

258 *Methodological concern for using the majority of ‘behaviours’ instead of ‘individuals’*

259 In addition to our conceptual arguments in favour of keeping separate the biases of  
260 relying on the majority of individuals versus the majority of behaviours (also see van  
261 Leeuwen et al., 2015), we now present a methodological argument in favour of this  
262 proposition. Specifically, we note that the gold standard to evidence conformist  
263 transmission has been to identify a sigmoidal relation between individuals’ probability  
264 to copy the majority and the proportional majority size (e.g., see Boyd & Richerson,  
265 1985; Chou & Richerson, 1992; Claidiere et al., 2012; Battesti et al., 2015; Aplin et al.,  
266 2015b; but see Acerbi et al., under review). A simple agent-based model may help  
267 illustrate one of the problems arising from considering the frequencies of *behaviours*,

268 instead of the frequencies of *individuals*, in detecting this sigmoidal signature of  
269 conformist transmission.

270         Imagine a population of individuals randomly initialised with one of two  
271 behaviours, A and B. At each time step, one individual X is randomly selected from the  
272 population, and performs its allocated behaviour, and another individual Y is also  
273 randomly selected from the population, and then Y always copies the behaviour  
274 performed by X. If one plots the relation between the probability of copying a behaviour  
275 and the frequency of *individuals* that possess that behaviour at time  $t$ , the relation is  
276 perfectly linear (see Figure 1, left). Each behaviour is, in other words, copied with a  
277 probability equal to the frequency of individuals that possess it in the population. This is  
278 exactly what we would expect with unbiased – i.e. random – copying (e.g. see Boyd &  
279 Richerson, 1985; Henrich & Boyd, 1998; Mesoudi, 2009).

280

281 FIGURE 1.

282

283         However, if we plot the relation between the probability of copying a behaviour  
284 and the frequency of *behaviour* observed in the population, we obtain a sigmoidal  
285 relation, that can be mistaken for a signature of conformist transmission (see Figure 1,  
286 right). The reason for this result is that, as behaviours were randomly initialised, the  
287 total frequency (over all time steps) of the majority behaviour in the population will be,  
288 in most cases, lower than the frequency of individuals that possess that behaviour at  
289 time  $t$ . Imagine that behaviour A reaches fixation in the population. The probability to  
290 copy A will be 100%, but its cumulative frequency will be somewhat lower, as, at the  
291 beginning, at least some individuals performed behaviour B. This behavioural mixture  
292 is sufficient to create the effect in the bottom-left and top-right portions of the function,  
293 typical of a sigmoidal relation.

294           This effect is an artefact of how populations are initialised in the model, i.e.  
295 starting from a random mixture of the two behaviours, but it clearly shows that different  
296 analysis may lead to different results. More specifically, in this case, the analysis based  
297 on *individuals* reveals perfect linearity, in keeping with the individual-level random  
298 copying default, whereas the analysis based on *behaviours* reveals the sigmoidal  
299 relation between copying probability and relative frequency characteristic of conformist  
300 transmission (see Aplin et al., 2015b). In other words, the analysis based on *behaviours*  
301 leads to a detection of conformist transmission where clearly there is none (because all  
302 copying here is *random*).

303           A slightly more complex model shows an analogous result, without the need to  
304 initialise the populations in the above way. In this set-up, populations start naïve, and  
305 the two possible behaviours are instead introduced through individual innovations (each  
306 behaviour – A or B – with the same probability). Note that this set-up reflects the  
307 scenario in which conformist transmission is typically studied (e.g. Boyd & Richerson,  
308 1985; Henrich & Boyd, 1998; Morgan & Laland, 2012; van Leeuwen & Haun, 2014).  
309 The guiding copying mechanism is exactly the same as in the previous model, i.e.  
310 random copying remains the only form of copying. The only twist in our new model is  
311 that innovation rate decreases over time, mimicking individuals gradually converging  
312 on a certain variant preference (we believe this to be a realistic scenario). The results are  
313 analogous to the previous model: an analysis based on *individuals* shows perfect  
314 linearity in keeping with the random copying default, but an analysis based on  
315 *behaviours* reveals a sigmoidal relation between copying probability and the variant  
316 frequency in the population (see Figure 2). The reason for this result is that an initial  
317 innovation rate creates a situation in which both behaviours become present – similar to  
318 the random mixture of behaviours with which the populations were initialised in the  
319 first model – and, after that, populations again converge on one of the two behaviours,

320 as innovation becomes less influential. Regardless, it is striking that even in the more  
321 typically studied scenario of naive individuals exploring a novel cultural landscape (the  
322 conformist transmission scenario), the illusion of conformist transmission can still  
323 emerge when analysis focuses on *behaviours* instead of *individuals*.

324

325 FIGURE 2.

326

327         In conclusion, for reasons of conceptual, empirical and methodological clarity,  
328 we propose to keep the study of conformity and conformist transmission restricted to  
329 the level of *individuals* and pursue the study of the effects of repetitive exposure to  
330 stimuli or behaviours, regardless of their executors, in its own right. Accordingly, we  
331 note that in the seminal conformity studies “the majority” did not consist of *behaviours*  
332 but *individuals*. For instance, in the Asch studies (1956), “the majority” was assembled  
333 by a group of confederates each expressing one opinion, not by one confederate  
334 expressing his/her opinion multiple times (for studies on the (mere) exposure effect, see  
335 e.g. Bornstein, 1989; Zajonc, 1968).

336

337 *The pivotal role of observation records*

338 Finally, we wish to draw attention to the most prominent matter highlighted by van  
339 Leeuwen and colleagues (2015) in reference to the study of conformity in particular and  
340 social learning biases in general: observation records. Underlying all previous  
341 considerations, e.g. whether or not the social learning rule ‘copy high-rankers’ could  
342 explain the patterns described in van de Waal et al. (2013), lies the implicit assumption  
343 that the respective decision-makers have observed all available social information. We  
344 challenge this assumption and wish to emphasize that when it comes down to  
345 pinpointing (social) learning biases, it is essential that observation records are obtained

346 and used in analysis, especially given that such data are accessible (e.g. see van  
347 Leeuwen et al., 2013; Kendal et al., 2015).

348           Whiten & van de Waal (this volume) respond to our previous criticism that in  
349 their original study (van de Waal et al., 2013) it was ‘unknown what and whom the  
350 immigrating males had observed prior to their preference switching’ (van Leeuwen et  
351 al., 2015, p.3) by stating that this is true for all studies, including experimental ones like  
352 that conducted by Haun and colleagues (2012). However, our criticism did not refer to  
353 the actual observations made by individuals – we agree that a certain level of  
354 assumption, ultimately even when using eye-tracking or more advanced technologies, is  
355 unavoidable. Instead, our criticism pertained to the assumption that the immigrants were  
356 somehow able to obtain knowledge of the available social information. The immigrant  
357 vervets’ observation records were entirely absent in the original study claiming to have  
358 identified conformity (van de Waal et al., 2013) and remain too imprecise for the  
359 investigation of conformity in the follow-up analysis (Whiten & van de Waal, this  
360 volume). In the first instance, we refer to records of what/whom the vervets could have  
361 observed because they were *present* when the social information (which would need to  
362 be quantified per observation bout) was available. In the second instance, head  
363 orientation during the inadvertent demonstrations seems a crucial measure to report.  
364 Such measures provide the necessary information to link an individual’s observational  
365 input (in this case: social information) to an individual’s behavioural output (in this  
366 case: maintaining or adjusting food colour preference), and thus the relevant  
367 information to draw conclusions on individuals’ specific learning biases.

368           Another example of individuals’ observation records receiving insufficient  
369 consideration concerns the recent great tit study by Aplin and colleagues (2015b). While  
370 this study provides detailed analyses of the birds’ tendencies to learn socially,

371 including, importantly, their propensities to copy in response to different majority sizes,  
372 the very data central to their conformist transmission analyses rest on assumptions  
373 rather than observations. The authors derived an external measure of which birds  
374 typically flocked together and calculated an average ‘group length’ of flocking (i.e. 245  
375 seconds) that was subsequently used during the experiment in order to *assume* that all  
376 birds operating the experimental task in this time-window obtained knowledge of each  
377 other’s choices. In other words, the authors did not score which birds were  
378 simultaneously present at the experimental task (or which birds observed each other),  
379 but instead relied on the assumption that the birds were in the vicinity of the  
380 experimental task at the same time as the birds that were considered to be  
381 “demonstrators”, and the further assumption that they paid attention to those  
382 demonstrations (see Aplin et al., 2015b). We feel this to be an unfortunate caveat in an  
383 otherwise excellently conceived and conducted study. Regardless of the plausibility of  
384 such assumptions, observational input is the very measure from which we aim to derive  
385 conclusions on individual’s (social) learning biases, which, in our view, makes it  
386 imperative to be as accurate as possible. We wonder, for instance, whether the birds  
387 with the most extreme copying probabilities (0 and 100%) had observed that the entire  
388 sub-group of their sub-population had not converged on one particular strategy (see  
389 Figure 1 in Aplin et al., 2015a). These data seem crucial for the sigmoidal pattern to  
390 emerge, which was used to argue for conformist transmission in the birds’ social  
391 learning patterns (Aplin et al., 2015b). Notably, new modelling insights show that this  
392 very sigmoidal pattern can emerge in the absence of individuals’ being conformist  
393 biased (Acerbi et al., under review), making it even more pertinent to know what the  
394 birds observed exactly.  
395



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397

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477 **Figure Legends**

478

479 **Figure 1.** A population of  $N=100$  individuals is randomly initialised with one of two  
480 behaviours. At each time step, a model and an observer are randomly extracted from the  
481 population, and the observer always copies the model. The simulation ends at 10,000  
482 time steps, i.e. 10,000 possible interactions. Results are based on 1,000 replications of  
483 the model. Simulated data are fitted with a linear and a sigmoid model. Copying  
484 probability is plotted against frequency of individuals (a), and frequency of behaviours  
485 (b).

486

487 **Figure 2.** Simulations start with a population of  $N=100$  naïve individuals. At each time  
488 step there is a probability that an individual, randomly extracted from the population,  
489 will innovate, i.e. will introduce, with equal probability, one of the two possible  
490 behaviours. Probability of innovation is initially equal to  $\mu=.1$  (one innovation every 10  
491 time steps on average), and decreases exponentially with time, according to  $e^{-5t/T}$ ,  
492 where  $t$  is the current time step, and  $T$  is the maximum amount of time steps. In  
493 addition, at each time step, a model and an observer are randomly extracted from the  
494 population, and the observer always copies the model. The simulation ends at 10,000  
495 time steps, i.e. 10,000 possible interactions. Results are based on 1,000 replications of  
496 the model. Simulated data are fitted with a linear and a sigmoid model. Copying  
497 probability is plotted against frequency of individuals (a), and frequency of behaviours  
498 (b).