

## A reappraisal of 'conformity'

van Leeuwen, E. J. C., Acerbi, A., Kendal, R. L., Tennie, C., Haun, D. B. M.

Date of deposit	25/10/2016
Document version	Author's accepted manuscript
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Citation for published version	van Leeuwen, E. J. C., Acerbi, A., Kendal, R. L., Tennie, C., & Haun, D. B. M. (2016). A reappraisal of 'conformity'. <i>Animal Behaviour</i> .
Link to published version	<a href="https://doi.org/10.1016/j.anbehav.2016.09.010">https://doi.org/10.1016/j.anbehav.2016.09.010</a>

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## 1 **A re-appreciation of “conformity”**

2

3 Whiten & van de Waal (this volume) present an answer to a critical account of their  
4 conformity interpretations (van Leeuwen et al., 2015). Their target study (van de Waal  
5 et al., 2013) evidenced immigrant male vervet monkeys adjusting their food colour  
6 preferences to the preference demonstrated by the resident vervets, which was  
7 interpreted in terms of conformity. Van Leeuwen and colleagues (2015; also see van  
8 Leeuwen & Haun, 2013 and online commentary by Tennie, Fischer, Galef & Haun,  
9 2013, at Sciencemag.org) acknowledged the insight gained from the reported  
10 observations for our understanding of social learning processes in wild primates, but  
11 criticized van de Waal et al.’s conformity interpretation (2013) as alternative learning  
12 biases, other than conformity, could not be ruled out. In their reply to this critique,  
13 Whiten & van de Waal (this volume) systematically list their arguments against  
14 alternative explanations. Whiten & van de Waal (this volume) also present new data  
15 indicating that in their target study (2013) the “majority of individuals” opting to  
16 perform a specific behaviour correlated with the “majority of behaviours” performed  
17 across the population, thereby adding to a recent debate about how “the majority”  
18 should be operationalized in order to study conformist transmission (see Aplin et al.,  
19 2015a in response to van Leeuwen et al., 2015). Here, we respond to Whiten & van de  
20 Waal (this volume) by i) discussing how their arguments against our alternative  
21 explanations for their conformity interpretation (as advanced in van de Waal et al.,  
22 2013) may be misguided, ii) defending the position that their presented correlation  
23 between the “majority of individuals” and the “majority of behaviours” is tangential to  
24 the current debate, iii) presenting evidence in favour of our original suggestion to keep  
25 reliance on the “majority of individuals” and the “majority of behaviours” as two  
26 separate learning biases, and iv) realigning the debate between Aplin et al. 2015a and

27 van Leeuwen et al. 2015 to focus again on animals' observation records as prerequisite  
28 knowledge to interpret their behavioural decisions in terms of learning biases.

29

30 *Alternative explanations*

31 In line with Whiten & van de Waal (this volume), we define conformity as  
32 “abandoning personal preferences or behaviours to match alternatives exhibited by a  
33 majority of others” (Haun, van Leeuwen & Edelson, 2013). In their original study (van  
34 de Waal et al., 2013), male vervet monkeys who were trained to prefer one of two food  
35 colours in their native group immigrated to a new group where the alternative food  
36 colour was preferred and adjusted their preferences accordingly (except for one high-  
37 ranking male who maintained his native preference). These immigrants were typically  
38 confronted with a large group of residents feeding from the alternative food colour,  
39 while very few or none of the residents fed from the food colour the immigrants were  
40 most familiar with (see illustrations in Whiten & van de Waal, this volume). Van de  
41 Waal et al. (2013) interpreted these behavioural adjustments by the immigrants as  
42 ‘conformity’. In response to this interpretation, van Leeuwen & Haun (2014; also see  
43 van Leeuwen et al. 2015) pointed out that although the immigrants might have been  
44 guided by inclinations to conform to the majority, alternatively, they might have been  
45 guided by other (social) learning biases that are independent of majority considerations.  
46 For instance, the immigrants might have been focused on copying particular resident  
47 individuals, like visibly dominant individuals, or indeed *any* resident individual,  
48 precipitated by their immigration-induced stress, anxiety or general state of uncertainty.  
49 Whiten & van de Waal (this volume) replied to this suggestion by arguing that any  
50 transmission bias other than ‘copy-the-majority’ is unlikely to explain the switching  
51 behaviour of the immigrants. For instance, they argue that the fact that the immigrants  
52 do not have female kin in their new group rules out a kin-based learning rule. Likewise,

53 they propose that male vervets are relatively *poor* in recognizing the social hierarchy of  
54 females, ruling out a ‘copy high-rankers’ learning rule (Whiten & van de Waal, this  
55 volume). While these particular proposals may or may not be correct, more generally,  
56 we wish to emphasize that although field experiments with wild animals are to be  
57 applauded for their ecological validity, they do not have any superior claim on  
58 epistemological validity. When confounding effects cannot be controlled for rigorously,  
59 interpretation of observed patterns need to be made cautiously.

60         Whiten & van de Waal (this volume) argue most forcefully against the ‘random  
61 copying’ interpretation of their data, stating that: ‘...for the immigrant vervets to copy  
62 just one individual randomly would seem rather *perverse* in the face of the repeated,  
63 extensive and quite consistent scenarios of multiple monkey preferences staring  
64 immigrants in the face...’ (line 95-98). We disagree. Clearly, the sheer availability of  
65 information is no guarantee it will be utilized in expected ways, or, at all. Random  
66 copying is as good a predictor of the observed patterns of transmission as conformity:  
67 When observer monkeys are consistently confronted with the majority of residents  
68 feeding from one particular food colour, while only a few, or none, of the resident  
69 monkeys feed from the alternative, copying a random individual would,  
70 probabilistically, boil down to observer monkeys tending to use the foraging option  
71 demonstrated by the majority rather than that demonstrated by the minority, irrespective  
72 of observers’ particular preference for copying the majority. We consider this a  
73 potentially more parsimonious explanation – if observer monkeys could obtain the  
74 locally practiced foraging rule by the mere inclination to copy, there is no need for them  
75 to apply a cognitively more demanding rule like ‘conform to majorities’.

76         Typically, an investigation of whether individuals copy the majority with a  
77 higher probability than the relative size of the majority (henceforth ‘the disproportionate  
78 criterion’) is applied to ascertain that individuals are indeed *majority*-biased, or at least

79 to exclude the possibility that individuals merely copy randomly (e.g. Laland, 2004;  
80 Mesoudi, 2009). We note that the disproportionate criterion can be viewed as rather  
81 stringent and unrealistic for cases in which individuals have already obtained a working  
82 strategy, where the key behaviour of interest is the foregoing of prior information for an  
83 alternative ('conformity'). Indeed, the disproportionate criterion is typically used in the  
84 context of naive individuals setting out to obtain a useful strategy by means of social  
85 learning; the context in which *conformist transmission* (CT) is studied (e.g. Boyd &  
86 Richerson, 1985; Morgan et al., 2014). In the CT context, when individuals are  
87 confronted with a balanced population in which only two possible strategies exist, it is  
88 assumed that copiers solely rely on social information and thus have a 50% likelihood  
89 of obtaining one or the other strategy. Similarly, when strategy A is wielded by 70% of  
90 the demonstrators, and strategy B thus only by 30%, copiers have a 70% likelihood of  
91 obtaining strategy A by chance, i.e. if they were to apply a *random copying* rule. To  
92 show that individuals *preferentially* copy the majority, and not just by chance, the  
93 disproportionate criterion should be adhered to, meaning that in this case copiers should  
94 have a likelihood of obtaining strategy A that is significantly larger than 70%. However,  
95 in this same example, if individuals are *not* naive and thus have already learned to  
96 prefer one strategy over the other, e.g. strategy B, the assumption that they will obtain  
97 strategy A or B with a 50% likelihood (in the balanced 2-variant population) is  
98 unrealistic. Instead, these experienced individuals will most likely stick to their familiar  
99 strategy, in this case strategy B. In a similar vein, experienced strategy B users will not  
100 have a 70% chance of ending up with strategy A when 70% of the population they  
101 could sample from are strategy A users. If these experienced individuals turn out to start  
102 using strategy A with a 70% likelihood, in fact, one could consider this to be a strong  
103 indication ('disproportionate' in a sense) of majority influence (see Haun, Rekers &  
104 Tomasello, 2014). Thus, contrary to the CT setting, when individuals are experienced, it

105 seems less valid to interpret a copying probability in accord with the relative majority  
106 size (here: 70%) in terms of *random copying*: past experience must be weighted in and  
107 perhaps a lower threshold than the majority display accepted as strong evidence for  
108 conformity (see van Leeuwen & Haun, 2014).

109         For the vervet monkeys (van de Waal et al., 2013), given that i) they were  
110 indeed experienced in preferring one food colour over the other when they encountered  
111 the opposing demonstrations in the new population, and ii) many of them chose to eat  
112 from the food colour in accord with these preference-opposing demonstrations (perhaps  
113 in numbers approximately matching the relative majority size, although here, crucially,  
114 this cannot be confirmed as the vervets' observation records are missing; see below for  
115 more on this topic), this might indicate that 'random copying' could be dismissed as a  
116 mechanistic explanation in favour of 'majority copying'. It is important to note,  
117 however, that this conclusion rests on the crucial assumption that no other variables  
118 were at play in the decision arena of the respective vervets, which is arguably not true.  
119 Notably, the immigrant vervets were leaving behind a familiar home range, and social  
120 setting, while moving into an unknown territory with unknown conspecifics ('a  
121 different habitat': van de Waal et al., 2013, p. 484). We could envisage the very  
122 predicament of the migrating vervets as sufficiently potent to induce a motivation to  
123 obtain new, locally more attuned behaviours (ecologically and/or socially). Van de  
124 Waal and colleagues (2013; also see Whiten & van de Waal, this volume) acknowledge  
125 that such drastic changes in the lives of the vervets could have facilitated the so-called  
126 'copy-when-uncertain' rule (Laland, 2004), a social learning heuristic for which  
127 evidence has been found across a wide range of taxa (e.g. see Kendal et al., 2009). They  
128 explicitly echo our suggestion by writing: "The fitness of foraging decisions made by  
129 wild primates like those we studied will be governed by a host of complex factors that  
130 are inherently unknown to foragers, ranging from dietary constituents to plant toxins

131 and competing needs such as predator vigilance: Exploiting the prior discoveries of  
132 local experts may be an optimal strategy, overriding opposing knowledge gained in a  
133 different habitat such as one's original group." (van de Waal et al., 2013, p. 484). Yet,  
134 crucially, neither van de Waal et al. (2013) nor Whiten & van de Waal (this volume)  
135 consider the possibility that the 'copy-when-uncertain' heuristic *alone* could have  
136 caused the immigrants to adjust their foraging preference upon entering their new  
137 environment. It is entirely reasonable that the uncertainty of their new environment  
138 changed the default information-gathering mode of the immigrants to "copy" anybody  
139 (instead of relying on possibly out-dated and locally inadequate personal strategies).

140         Given the discussion above, and widespread local foraging traditions, the  
141 simplest form of copying – random copying – would equip the immigrating vervets  
142 with the local "majority" strategy. In other words, the transition from home to unknown  
143 territory could have reset the vervet monkeys, rendering prior information irrelevant,  
144 turning them effectively into naïve learners. We call this the "reset hypothesis". One  
145 possible way to empirically test this hypothesis is to investigate whether immigrants  
146 would switch to the local foraging preference upon seeing a small number of residents  
147 showing a preference against an even larger background of non-behaving others, or,  
148 maybe a simpler case, upon seeing just one single resident's demonstration of this  
149 preference (something that may have been opportunistically possible to assess had  
150 immigrant observation records been acquired, see below). If these observers would  
151 switch their preference, *majorities* would cease to be the single possible object of the  
152 immigrants' copying efforts. Indeed, drawing on parsimony again, this finding would  
153 indicate that "conformity" is not even necessary to explain the immigrants' behaviour.  
154 Note that even if one adheres to the conformity definition of 'a willingness to subjugate  
155 one's own countervailing knowledge in matching the majority's choice' – as in van de

156 Waal et al. 2013 supplementary material p. 6 – one is still left with the burden of proof  
157 for the claim that ‘the majority’ is being matched, not just any individual.

158 Overall, the problem with interpreting the observations made by van de Waal et  
159 al. (2013) is the lack of nuance in the data regarding observer monkeys responding to  
160 different majority/minority ratios of (inadvertent) demonstrator monkeys. If observers  
161 are only presented with one stimulus (“the majority”), which consists of many other  
162 stimuli (“general social information”, “high-ranking individuals”, “low-ranking  
163 individuals”, “conspicuous individuals”, etc.), it is impossible to disentangle the very  
164 learning bias that the observers follow, while this is exactly what we want to know (e.g.  
165 see Heyes, 2016). For instance, if we were to investigate the evolutionary roots of  
166 conformist decision-making and we find that immigrant vervet monkeys, patas  
167 monkeys and rhesus macaques all adjust their preferences to the majority of the new  
168 group, we would need to know whether they were biased to “the majority” or to any  
169 other cue provided by the majority, for without this knowledge, the apparent similarity  
170 in decision-making strategies across these species may be purely coincidental.

171

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

173 Due to our emphasis (van Leeuwen et al., 2015) upon the need for observation records  
174 in interpreting transmission events, we are delighted to find more detailed analysis on  
175 the observation records of the vervet monkeys (van de Waal et al., 2013) in their follow-  
176 up paper (Whiten & van de Waal (this volume)). Whiten & van de Waal (this volume)  
177 present an analysis of how the number of individuals feeding from the locally-preferred  
178 food colour correlated with the number of behaviours (handfuls of corn) regarding this  
179 same food colour. Specifically, they state: “Indeed the two variables [individuals and  
180 behaviours] show a significant correlation across the twelve sample periods ( $r = 0.67$ ,  $n$   
181  $= 12$ ,  $p = 0.018$ ). Accordingly we infer that the migrant males’ striking switch from



182 their own to the opposite local preference was an effect of these majority displays, and  
183 hence a case of conformity” (Whiten & van de Waal, this volume, L69-73). To clarify,  
184 Whiten & van de Waal (this volume) aim to address a subject pertaining to the analysis  
185 of *conformist transmission* that was discussed in van Leeuwen et al. (2015) and Aplin et  
186 al. (2015a). In summary, where van Leeuwen et al. (2015) argued for keeping separate  
187 the biases of following the majority of individuals versus the majority of observed  
188 behaviours, and only reserving the term ‘conformist transmission’ for the former, Aplin  
189 et al. (2015a) argued for grouping the biases together under the same term, i.e.  
190 ‘conformist transmission’. Aplin et al. (2015a) based their argument on the fact that in  
191 their original great tit study (Aplin et al. 2015b), the birds did not seem to distinguish  
192 between individuals and behaviours (analysed in Aplin et al. 2015a). Following up on  
193 this debate, Whiten & van de Waal (this volume) echo Aplin et al.’s position by  
194 showing that in their vervet monkey study (van de Waal et al., 2013) the frequency of  
195 *individuals* using a certain behavioural option and the frequency of demonstration of  
196 this particular behavioural option in total were not affecting the observers differently. In  
197 other words, the monkeys were indistinguishably following the majority of individuals  
198 and the majority of behaviours (Whiten & van de Waal, this volume).

199         While we acknowledge the additional analysis and appreciate its intent, we do  
200 not find it compelling for several reasons. First and foremost, in line with our previous  
201 arguments, Whiten & van de Waal (this volume) neither use the frequency of  
202 individuals nor behaviours to test their conformity hypothesis against any other (social)  
203 learning bias. Therefore, the reported correlation between the frequency of individuals  
204 and behaviours, while representing an affirmation of internal validity, has no power to  
205 falsify alternative hypotheses. For instance, Aplin et al. (2015b), though confronted with  
206 similar limitations due to working with wild animal populations, obtained detailed  
207 records of birds responding to differently-sized majorities and incorporated their

208 majority numbers, in terms of individuals and behaviours, into statistical analyses to  
209 provide insight regarding whether the birds actually *used* the majority cue or merely  
210 obtained the most common strategy randomly. Without such analysis, our  
211 understanding of transmission biases is not furthered by the reporting of a correlation  
212 between two possible measures. Note that due to the very nature of “the majority” (i.e.  
213 comprising more than half of the sampled individuals) measures of for instance, skilful,  
214 conspicuous and high-ranking individuals will also coincide with the majority strategy.

215         Furthermore, we note that two cases of correlation between the number of  
216 individuals and behaviours indicating the use of a particular strategy (Aplin et al., 2015a  
217 and Whiten & van de Waal, this volume) do not constitute sufficient evidence in favour  
218 of the two measures being ‘functionally equivalent’. While scenarios in which the  
219 number of individuals and behaviours correlate are straightforward to envision, we  
220 could imagine other scenarios in which the two respective measures would diverge,  
221 either due to individual differences in performance rates (in conjunction with relative  
222 preferences for certain strategies) or population structure (increasing the likelihood of  
223 repetitively sampling the same individuals). Moreover, for reasons of informational  
224 accuracy, it may well matter if one individual “cries wolf” ten times, or if ten  
225 individuals (independently) do so once (e.g. see Wolf et al., 2013). We conjecture that  
226 the adaptive value of relying on indiscriminate sampling of behaviours versus relying  
227 on the aggregate knowledge of similarly poised, unpredictability-reducing conspecifics  
228 will differ to the extent that under certain conditions, one particular bias is expected to  
229 evolve (at the expense of the other). Formal modelling would be a constructive way  
230 forward in fuelling our understanding and expectations regarding this pending question,  
231 which was acknowledged by Aplin et al. (2015a). In the absence of such understanding,  
232 we fail to see how grouping two potentially distinct social learning biases (see Haun et

233 al., 2012) under one and the same denominator of “conformist transmission” could be  
234 beneficial to the (comparative) study of learning biases.

235

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

237 In addition to our conceptual arguments in favour of keeping separate the biases of  
238 relying on the majority of individuals versus the majority of behaviours (also see van  
239 Leeuwen et al., 2015), we now present a methodological argument in favour of this  
240 proposition. Specifically, we note that the gold standard to evidence conformist  
241 transmission has been to identify a sigmoidal relation between individuals’ probability  
242 to copy the majority and the proportional majority size (e.g., see Boyd & Richerson,  
243 1985; Chou & Richerson, 1992; Claidiere et al., 2012; Battesti et al., 2015; Aplin et al.,  
244 2015b; but see Acerbi et al., under review). A simple agent-based model may help  
245 illustrate one of the problems arising from considering the frequencies of *behaviours*,  
246 instead of the frequencies of *individuals*, in detecting this sigmoidal signature of  
247 conformist transmission.

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

258

259 FIGURE 1.

260

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

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

281           A slightly more complex model shows an analogous result, without the need to  
282 initialise the populations in the above way. In this set-up, populations start naïve, and  
283 the two possible behaviours are instead introduced through individual innovations (each  
284 behaviour – A or B – with the same probability). Note that this set-up reflects the

285 scenario in which conformist transmission is typically studied (e.g. Boyd & Richerson,  
286 1985; Henrich & Boyd, 1998; Morgan & Laland, 2012; van Leeuwen & Haun, 2014).  
287 The guiding copying mechanism is exactly the same as in the previous model, i.e.  
288 random copying remains the only form of copying. The only twist in our new model is  
289 that innovation rate decreases over time, mimicking individuals gradually converging  
290 on a certain variant preference (we believe this to be a realistic scenario). The results are  
291 analogous to the previous model: an analysis based on *individuals* shows perfect  
292 linearity in keeping with the random copying default, but an analysis based on  
293 *behaviours* reveals a sigmoidal relation between copying probability and the variant  
294 frequency in the population (see Figure 2). The reason for this result is that an initial  
295 innovation rate creates a situation in which both behaviours become present – similar to  
296 the random mixture of behaviours with which the populations were initialised in the  
297 first model – and, after that, populations again converge on one of the two behaviours,  
298 as innovation becomes less influential. Regardless, it is striking that even in the more  
299 typically studied scenario of naive individuals exploring a novel cultural landscape (the  
300 conformist transmission scenario), the illusion of conformist transmission can still  
301 emerge when analysis focuses on *behaviours* instead of *individuals*.

302

303 FIGURE 2.

304

305 In conclusion, for reasons of conceptual, empirical and methodological clarity,  
306 we propose to keep the study of conformity and conformist transmission restricted to  
307 the level of *individuals* and pursue the study of the effects of repetitive exposure to  
308 stimuli or behaviours, regardless of their executors, in its own right. Accordingly, we  
309 note that in the seminal conformity studies “the majority” did not consist of *behaviours*  
310 but *individuals*. For instance, in the Asch studies (1956), “the majority” was assembled

311 by a group of confederates each expressing one opinion, not by one confederate  
312 expressing his/her opinion multiple times (for studies on the (mere) exposure effect, see  
313 e.g. Bornstein, 1989; Zajonc, 1968).

314

315 *The pivotal role of observation records*

316 Finally, we wish to draw attention to the most prominent matter highlighted by van  
317 Leeuwen and colleagues (2015) in reference to the study of conformity in particular and  
318 social learning biases in general: observation records. Underlying all previous  
319 considerations, e.g. whether or not the social learning rule ‘copy high-rankers’ could  
320 explain the patterns described in van de Waal et al. (2013), lies the implicit assumption  
321 that the respective decision-makers have observed all available social information. We  
322 challenge this assumption and wish to emphasize that when it comes down to  
323 pinpointing (social) learning biases, it is essential that observation records are obtained  
324 and used in analysis, especially given that such data are accessible (e.g. see van  
325 Leeuwen et al., 2013; Kendal et al., 2015).

326         Whiten & van de Waal (this volume) respond to our previous criticism that in  
327 their original study (van de Waal et al., 2013) it was ‘unknown what and whom the  
328 immigrating males had observed prior to their preference switching’ (van Leeuwen et  
329 al., 2015, p.3) by stating that this is true for all studies, including experimental ones like  
330 that conducted by Haun and colleagues (2012). However, our criticism did not refer to  
331 the actual observations made by individuals – we agree that a certain level of  
332 assumption, ultimately even when using eye-tracking or more advanced technologies, is  
333 unavoidable. Instead, our criticism pertained to the assumption that the immigrants were  
334 somehow able to obtain knowledge of the available social information. The immigrant  
335 vervets’ observation records were entirely absent in the original study claiming to have  
336 identified conformity (van de Waal et al., 2013) and remain too imprecise for the

337 investigation of conformity in the follow-up analysis (Whiten & van de Waal, this  
338 volume). In the first instance, we refer to records of what/whom the vervets could have  
339 observed because they were *present* when the social information (which would need to  
340 be quantified per observation bout) was available. In the second instance, head  
341 orientation during the inadvertent demonstrations seems a crucial measure to report.  
342 Such measures provide the necessary information to link an individual's observational  
343 input (in this case: social information) to an individual's behavioural output (in this  
344 case: maintaining or adjusting food colour preference), and thus the relevant  
345 information to draw conclusions on individuals' specific learning biases.

346         Another example of individuals' observation records receiving insufficient  
347 consideration concerns the recent great tit study by Aplin and colleagues (2015b). While  
348 this study provides detailed analyses of the birds' tendencies to learn socially,  
349 including, importantly, their propensities to copy in response to different majority sizes,  
350 the very data central to their conformist transmission analyses rest on assumptions  
351 rather than observations. The authors derived an external measure of which birds  
352 typically flocked together and calculated an average 'group length' of flocking (i.e. 245  
353 seconds) that was subsequently used during the experiment in order to *assume* that all  
354 birds operating the experimental task in this time-window obtained knowledge of each  
355 other's choices. In other words, the authors did not score which birds were  
356 simultaneously present at the experimental task (or which birds observed each other),  
357 but instead relied on the assumption that the birds were in the vicinity of the  
358 experimental task at the same time as the birds that were considered to be  
359 "demonstrators", and the further assumption that they paid attention to those  
360 demonstrations (see Aplin et al., 2015b). We feel this to be an unfortunate caveat in an  
361 otherwise excellently conceived and conducted study. Regardless of the plausibility of  
362 such assumptions, observational input is the very measure from which we aim to derive

363 conclusions on individual's (social) learning biases, which, in our view, makes it  
364 imperative to be as accurate as possible. We wonder, for instance, whether the birds  
365 with the most extreme copying probabilities (0 and 100%) had observed that the entire  
366 sub-group of their sub-population had not converged on one particular strategy (see  
367 Figure 1 in Aplin et al., 2015a). These data seem crucial for the sigmoidal pattern to  
368 emerge, which was used to argue for conformist transmission in the birds' social  
369 learning patterns (Aplin et al., 2015b). Notably, new modelling insights show that this  
370 very sigmoidal pattern can emerge in the absence of individuals' being conformist  
371 biased (Acerbi et al., under review), making it even more pertinent to know what the  
372 birds observed exactly.

373



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375

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455 **Figure Legends**

456

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

464

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