

1 **Forum**

2 **A reappraisal of ‘conformity’**

3

4 Edwin J. C. van Leeuwen^{1,2*}, Alberto Acerbi³, Rachel L. Kendal⁴, Claudio Tennie⁵,
5 Daniel B. M. Haun⁶

6

7 ¹ School of Psychology & Neuroscience, University of St Andrews, Fife, U.K.

8 ² Max Planck Institute for Psycholinguistics, Nijmegen, The Netherlands

9 ³ Eindhoven University of Technology, Department of Industrial Engineering & Innovation Sciences,
10 Eindhoven, The Netherlands

11 ⁴ Centre for the Coevolution of Biology and Culture, Department of Anthropology, Durham University,
12 U.K.

13 ⁵ School of Psychology, University of Birmingham, Birmingham, U.K.

14 ⁶ University of Leipzig, Department of Early Child Development and Culture and Leipzig Research
15 Center for Early Child Development, Leipzig, Germany

16

17 * Correspondence: E. J. C. van Leeuwen, School of Psychology & Neuroscience, University of St
18 Andrews, Westburn Lane, Fife KY16 9JP, U.K.

19

20 E-mail address: ejcvanleeuwen@gmail.com

21

22 **Keywords:** comparative psychology, conformist transmission, conformity, cultural
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

396 **References**

397

398 Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon,

399 B. C. (2015a). Counting conformity: evaluating the units of information in

400 frequency-dependent social learning. *Animal Behaviour*, *110*, e5-e8.

401 doi:10.1016/j.anbehav.2015.09.015

402 Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon,

403 B. C. (2015b). Experimentally induced innovations lead to persistent culture via

404 conformity in wild birds. *Nature*, *518*, 538-541. doi:10.1038/nature13998

405 Asch, S. E. (1956). Studies of Independence and Conformity .1. A Minority of One

406 against a Unanimous Majority. *Psychological Monographs*, *70*(9), 1-70.

407 Battesti, M., Moreno, C., Joly, D. & Mery, F. (2014). Biased social transmission in

408 *Drosophila* oviposition choice. *Behavioral Ecology and Sociobiology*, *69*, 83–

409 87.

410 Bornstein, R. F. (1989). Exposure and affect: Overview and meta-analysis of research,

411 1968-1987. *Psychological Bulletin*, *106*, 265-289.

412 Boyd, R., & Richerson, P. (1985). *Culture and the Evolutionary Process*. Chicago:

413 University of Chicago press.

414 Chou, L. S. & Richerson, P. J. (1992). Multiple Models in Social Transmission of Food

415 Selection by Norway Rats, *Rattus-Norvegicus*. *Animal Behaviour*, *44*(2), 337-

416 343.

417 Claidière, N., Bowler, M. & Whiten, A. (2012). Evidence for weak or linear conformity

418 but not for hyper-conformity in an everyday social learning context. *PLoS One*,

419 7, e30970.

- 420 Hastie, R., & Kameda, T. (2005). The robust beauty of majority rules in group
421 decisions. *Psychological Review*, *112*(2), 494-508. doi:10.1037/0033-
422 295x.112.2.494
- 423 Haun, D. B. M., Rekers, Y., & Tomasello, M. (2012). Majority-biased transmission in
424 chimpanzees and human children, but not orangutans. *Current Biology*, *22*, 727-
425 731. doi:10.1016/j.cub.2012.03.006
- 426 Haun, D. B. M., Rekers, Y., & Tomasello, M. (2014) Children conform to the behavior
427 of peers; other great apes stick with what they know. *Psychological Science*, *25*,
428 2160 - 2167. doi:10.1177/0956797614553235.
- 429 Haun, D. B. M., van Leeuwen, E. J. C., & Edelson, M. G. (2013). Majority influence in
430 children and other animals. *Developmental Cognitive Neuroscience*, *3*, 61–71.
- 431 Henrich, J., & Boyd, R. (1998). The evolution of conformist transmission and the
432 emergence of between-group differences. *Evolution and Human Behavior*,
433 *19*(4), 215-241.
- 434 Heyes, C. (2016). Blackboxing: social learning strategies and cultural evolution.
435 *Philosophical Transactions of the Royal Society B-Biological Sciences*, *371*,
436 20150369.
- 437 Kendal, R. L., Coolen, I., & Laland, K. N. (2009). Adaptive trade-offs in the use of
438 social and personal information. In R. Dukas & R. J. (Eds.), *Cognitive ecology*
439 *II*. (pp. 249-271). Chicago: University of Chicago Press.
- 440 Kendal, R. L., Hopper, L. M., Whiten, A., Brosnan, S. F., Lambeth, S. P., Schapiro, S.
441 J., & Hoppitt, W. (2015). Chimpanzees copy dominant and knowledgeable
442 individuals: implications for cultural diversity. *Evolution and Human Behavior*,
443 *36*, 65-72.
- 444 Laland, K. N. (2004). Social learning strategies. *Learning & Behavior*, *32*(1), 4-14.

445 Mesoudi, A. (2009). How Cultural Evolutionary Theory Can Inform Social Psychology
446 and Vice Versa. *Psychological Review*, 116(4), 929-952. doi:10.1037/0017062

447 Morgan, T. J. H., & Laland, K. N. (2012). The biological bases of conformity. *Frontiers*
448 *in Neuroscience*, 6(87). doi:10.3389/fnins.2012.00087

449 Morgan, T. J. H., Laland, K. N. & Harris, P. L. (2014). The development of adaptive
450 conformity in young children: effects of uncertainty and consensus.
451 *Developmental Science*, 18(4), 511–524.

452 Tennie, C., Fischer, J., Haun D. B. M., & Galef, B. G. (2013). Conformity in wild
453 vervet monkeys? Possibly not. *Online comment* on "Potent social learning and
454 conformity shape a wild primate's foraging decisions" by van de Waal et al.
455 2013. <http://comments.sciencemag.org/content/10.1126/science.1232769>

456 van Leeuwen, E. J. C., Cronin, K. A., Schütte, S., Call, J., & Haun, D. B. M. (2013).
457 Chimpanzees flexibly adjust their behaviour in order to maximize payoffs, not to
458 conform to majorities. *Plos One*, 8(11). doi:10.1371/journal.pone.0080945

459 van Leeuwen, E. J. C., & Haun, D. B. M. (2013). Conformity in primates: fad or fact?
460 *Evolution and Human Behavior*, 34, 1-7.

461 van Leeuwen, E. J. C., & Haun, D. B. M. (2014). Conformity without majority? The
462 case for demarcating social from majority influences. *Animal Behaviour*, 96,
463 187-194.

464 van Leeuwen, E. J. C., Kendal, R. L., Tennie, C. & Haun, D. B. M. (2015) Conformity
465 and its look-a-likes. *Animal Behaviour*, 110, e1-e4.
466 doi:10.1016/j.anbehav.2015.07.030

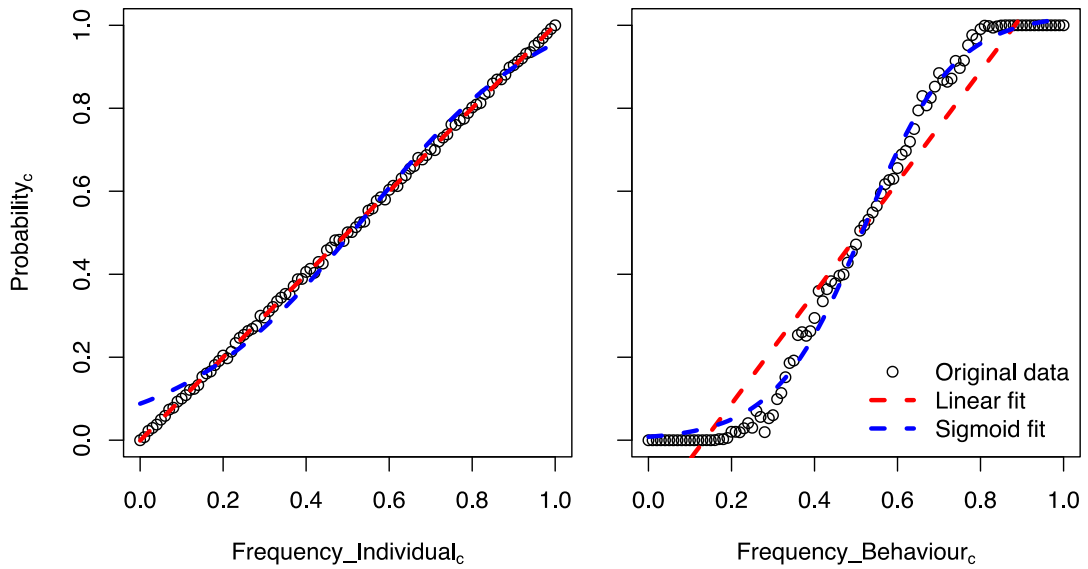
467 van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent Social Learning and
468 Conformity Shape a Wild Primate's Foraging Decisions. *Science*, 340, 483-485.
469 doi: 10.1126/science.1232769

470 Whiten, A. & van de Waal, E. (2016). *Animal Behaviour*. THIS VOLUME.

- 471 Wolf, M., Kurvers, R. H. J. M., Ward, A. J. W., Krause, S., & Krause, J. (2013).
472 Accurate decisions in an uncertain world: collective cognition increases true
473 positives while decreasing false positives. *Proceedings of the Royal Society B-*
474 *Biological Sciences*, 280. doi: 10.1098/rspb.2012.2777
- 475 Zajonc, R. B. (1968). Attitudinal effects of mere exposure. *Journal of Personality and*
476 *Social Psychology Monographs*, 9, 1-27.

477 **Figure Legends**

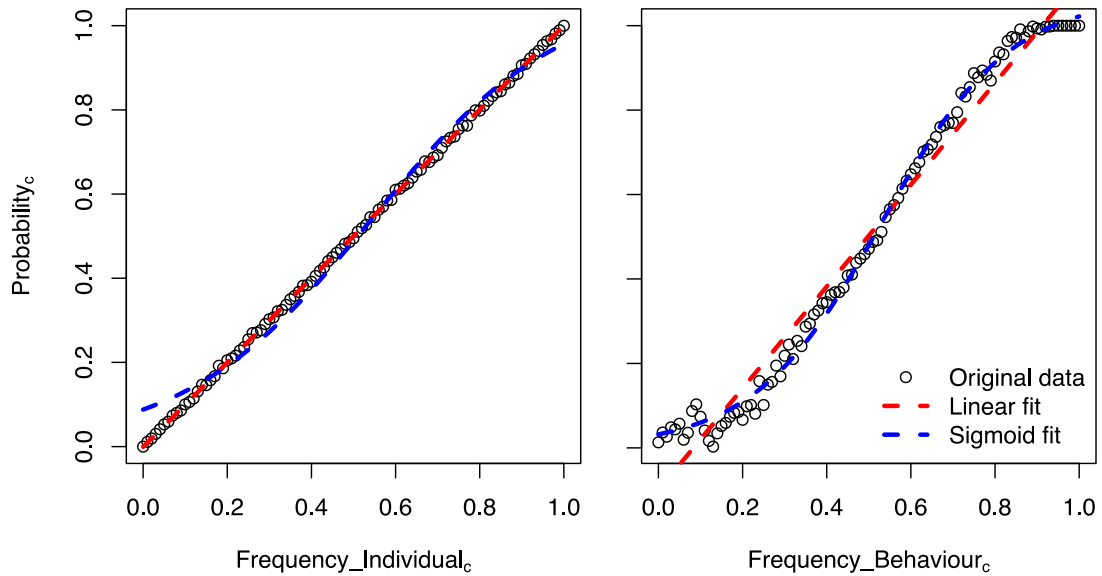
478



479

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

487



488

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