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2 Field experiments with wild primates reveal no consistent dominance-based bias in
3 social learning
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20

21 **Abstract**
22

23 Directed social learning suggests that information flows through social groups in a non-
24 random way, with individuals biased to obtain information from certain conspecifics. A bias to
25 copy the behaviour of more dominant individuals has been demonstrated in captive chimpanzees,
26 but has yet to be studied in any wild animal population. To test for this bias using a field
27 experiment, one dominant and one low-ranking female in each of three groups of wild vervet
28 monkeys was trained on alternative methods of opening an ‘artificial fruit’. Following 100

29 demonstrations from each model, fruits that could be opened either way were presented to each
30 group and all openings were recorded. Overall, the dominant females were not attended to more
31 than low-ranking females during the demonstrations, nor were their methods preferentially used
32 in the test phase. We conclude that these monkeys show no overall bias to copy high-ranking
33 models that would lead to a high-ranking model's behaviour becoming more prevalent in the group
34 than a behaviour demonstrated by a low-ranking model. However by contrast, there were
35 significant effects of observer monkeys' rank and sex upon the likelihood they would match the
36 dominant model. Additionally we found that the dominant models were more likely to stick to
37 their initially learned method than were low-ranking models.

38

39 **Introduction**

40

41 Research has increasingly revealed evidence for social learning abilities in a variety of
42 animal taxa. Social learning can be highly beneficial, allowing an animal to avoid the costs
43 associated with asocial learning (Laland, 2004). However, maladaptive information may also be
44 transmitted (Laland & Williams, 1998) and therefore animals could benefit from copying only the
45 most useful information. One way to obtain the best information may be to selectively copy certain
46 individuals based upon individual characteristics, such as age, sex or past successes. It is also likely
47 that animals may exhibit biased social learning based upon the social organisation of a group
48 (directed social learning, Coussi-Korbel & Fragaszy, 1995); greater time spent in proximity to
49 certain individuals may increase the likelihood that they will become models for social learning.
50 Research with a variety of nonhuman animals has yielded evidence for a range of biases based
51 upon the identity of the model in social learning, including age (Duffy, Pike & Laland, 2009;

52 Choleric, Guo, Liu, Mainardi, & Valsecchi, 1997), sex (Katz, & Lachlan, 2003; van de Waal,
53 Renevey, Favre, & Bshary, 2010), position in social network (Claidière, Messer, Hoppitt &
54 Whiten, 2013; Allen, Weinrich, Hoppitt, & Rendell, 2013) and kinship (van de Waal, Bshary &
55 Whiten, 2014). Findings of multiple social learning biases in the same species (Kendal et al., 2015)
56 also suggest that biases may work in concert.

57 In addition to the aforementioned biases, it has been proposed that copying successful
58 individuals may be an adaptive strategy (Boyd & Richerson, 1985; Henrich & Gil-White, 2001)
59 and that social rank may be used as a proxy for this in nonhuman animals (Laland, 2004, although
60 see Henrich & Gil-White, 2001). However few empirical studies have examined this issue. Dindo
61 and colleagues (2011) found no evidence of dominance-based biases in social learning or social
62 attention in captive tufted capuchin monkeys during an extractive foraging task. By contrast, two
63 studies with captive chimpanzees found that chimpanzees preferred to copy a higher rather than
64 lower ranked individual using tasks requiring both object manipulation (Kendal et al., 2015,
65 although see Watson et al. 2017) and token exchange (Horner, Proctor, Bonnie, Whiten & de Waal,
66 2010), although dominance in the latter was confounded with age and past success on tasks. On
67 the basis of these findings with chimpanzees, it has been suggested that such a bias towards
68 copying dominant individuals could, in a similar way to conformist transmission (Boyd &
69 Richerson, 1985), constrain intra-group variation and enhance the between-group variation found
70 in wild chimpanzees (Kendal et al., 2015). However, such a bias has not yet been assessed in wild
71 populations.

72 The aim of the current study was, accordingly, to examine whether a dominance-based bias
73 exists in a wild population of primates. Vervet monkeys (*Chlorocebus aethiops pygerythrus*)
74 provide an ideal species to examine this issue as they have linear hierarchies (Cheney & Seyfarth,

75 1990) and have previously been shown to learn socially in experimental contexts (van de Waal et
76 al., 2010; van de Waal, Borgeaud & Whiten, 2013; van de Waal, Claidière & Whiten, 2015).
77 Whilst a previous study revealed a bias for individuals to preferentially attend to and copy female,
78 rather than male, conspecifics (van de Waal et al., 2010), both sexes of models used in that study
79 were dominant and so the effect of demonstrator rank upon social learning remains to be tested in
80 this species.

81 To provide an experimental test for a bias to copy high-ranking, over low-ranking, models
82 in a wild primate, we trained two models of differing rank within each of three groups to use
83 alternative methods to open an ‘artificial fruit’ to gain a reward inside and gave both models the
84 opportunity to demonstrate their method to their groupmates. We investigated whether a certain
85 rank of model was attended to more in an experimental setting and whether the method they
86 displayed was preferred over the other in an extractive foraging task.

87

88 **Material & methods**

89 Study site and participants

90 The research was conducted at the Inkawu Vervet Project, located in the Mawana Game
91 Reserve in KwaZulu-Natal, South Africa (S 28° 00; E 031° 12). Experiments were conducted
92 between May and December 2015 with five groups of vervet monkeys at the field site. Four were
93 assigned to experimental conditions: Ankhase (AK), Baie Dankie (BD), Noha (NH) and Kubu
94 (KB) and one acted as a control group (Lemon Tree (LT)). A total of 100 monkeys were exposed
95 to the demonstration phase in the three two-model groups, whilst 42 monkeys participated in the
96 test phase of the experiment from all five groups.

97 General Protocol

98 Two models of differing rank were selected for each of the three ‘two-model’ groups (AK,
99 NH and BD, see Table 1) and trained to demonstrate alternative methods for opening a baited
100 artificial fruit. Model rank was determined by the outcome of dyadic conflicts recorded ad libitum
101 and through regular observations of order to access of food provided to the group by researchers
102 since the habituation of the groups (between two and five years for each group). During this time
103 the female hierarchies have remained highly stable, as is usual for vervet monkeys (Cheney &
104 Seyfarth, 1990). Models defined as ‘dominant’ were ranked #1 of females in their group, whilst
105 ‘low rank’ models were taken from the bottom half of the female hierarchy (positions 6 of 10
106 (AK), 11 of 12 (BD) and 7 of 11 (NH)). All researchers collecting data at IVP were tested on
107 monkey identification and interobserver reliability prior to data collection. Individual rank for all
108 group members was calculated using the EloRating package in R (Neumann et al., 2011). In the
109 control group (LT), no models were trained. In the fourth experimental group, KB, only a low-
110 ranking model (a sub-adult female model who had her first offspring early on in the test and was
111 then ranked 5 of 8 females) was trained to test the effects of a single model. Demonstrations and
112 test sessions were conducted by JB and MG, with the assistance of one or more trained field
113 assistants, comprising volunteers and students at IVP.

114 Apparatus

115 To create two alternative behaviours in the two models, an ‘artificial fruit’, a polycarbonate
116 box designed to mimic the characteristics of natural items that need to be opened to gain the edible
117 fraction inside (hereafter simply ‘box’) was used. Access to the food reward inside required the
118 opening of a small door on one side. The sides and top were painted black with only the door left
119 transparent, to funnel the monkeys’ attention to this part of the box. The base of the box tilted it
120 back at a roughly 30 degree angle and two metal hooks allowed the box to be secured by
121 hammering pegs into the ground.

122 One of two methods could open the door. First, the door was attached via a bolt in its top
123 centre, allowing it to be pivoted around this bolt ('Pivot'). Second, the door contained a smaller
124 section which was attached with hinges at the top, so this could be pushed inwards and upwards
125 as an alternative means of opening ('Push') (see Figure A1). Magnets held both door elements in
126 place, so they could not be accidentally opened. A manual lock prevented one method of opening
127 during training. Only one non-model attempted and failed to open the box during the
128 demonstration phase and this individual later successfully opened the box in the test phase. All
129 training, demonstration and tests were recorded using handheld Panasonic HD (HC-X920M) video
130 cameras.

131 Training

132 The dominant female and a mid- to low-ranking female (hereafter low-ranking) from each
133 of groups AK, NH and BD, and one low-ranking female from KB, were trained as demonstrators.
134 Some females had been trained to approach boxes with patterned covers for a food reward during
135 a previous study at the site (Borgeaud & Bshary, 2015). In the present study these covers were
136 placed on top of the boxes during the training and demonstration phase to encourage the target
137 females to approach the boxes; however not all models had been trained on a cover, so covers were
138 not used with Riss (low-ranking model, BD) and Ness (low-ranking model, KB).

139 Training was conducted over a period of 7-9 days on an opportunistic basis. Both models
140 were usually trained on each day of training, in no particular order. The food reward used for each
141 opening was a small piece of apple. The criterion for demonstration, which all models reached,
142 was the successful opening of the box 10 times during two consecutive sessions, totalling 20
143 successful openings. The training was opportunistically conducted when there were few other
144 monkeys in the area to minimise the observations of the models being trained.

145 Demonstration and social attention

146 One hundred demonstrations by each model were engineered on an opportunistic basis over
147 6-8 days, with no more than 20 demonstrations conducted per model, per day. Demonstrations
148 were completed with both models each day in no particular order. A session began with the
149 experimenter placing the baited box within 10 metres of the model and walking away. A successful
150 demonstration consisted of the model successfully opening the box and obtaining the food with at

151 least one other individual within 10 metres and with a clear line of sight. All individuals judged
152 by two experimenters as either within 5 metres or 10 metres and as either attending or not attending
153 to the box during the opening, based on head orientation, were identified and called aloud for the
154 video record. For the analyses, only individuals within five metres of the box and attending were
155 coded as ‘observers’. Following demonstrations, the box was removed.

156 Test protocol

157 Ten test sessions were conducted following the demonstration phase. The control group,
158 LT, saw no demonstrations and five test sessions were conducted due to time constraints. The
159 groups were located shortly after sunrise at their sleeping site and food calls were used, as with
160 past experiments which involved food with this study population, to alert the monkeys to the
161 presence of available food from the experiments. In the first test session, five unlocked boxes
162 were presented to the group (for test sessions 2-10, six boxes were used). Boxes were secured to
163 the ground in two rows perpendicular to an imagined line between the experimenters and at least
164 five metres apart. The boxes were placed with the doors facing outwards and less than 5 metres
165 between the boxes in the rows. At each interaction with the box by any monkey, the monkey was
166 identified and all individuals within 10 metres were identified by commentary recorded onto the
167 cameras. At each opening, the method of opening was identified in this way, as well as the success
168 of the opening. Once all the boxes were emptied, they were rebaited (the experimenter’s bodies
169 blocked most visual access during rebaiting and if the door needed to be re-opened to rebait, it was
170 done so using the method in which the door was most recently opened). An upper limit of 30 pieces
171 of apple per day was set for each monkey. The boxes were continuously rebaited until the group
172 moved away or an individual attained 30 pieces. If the latter occurred, no rebaits occurred until
173 that individual had moved out of sight. The test session ended when all monkeys had moved away
174 from the boxes and out of sight.

175 Statistical analyses

176 Analyses were performed using the statistical software ‘R’ version 1.0.136 (R Core Team,
177 2013). Generalized linear mixed models (GLMMs, Bolker et al., 2009) were used to analyse the
178 majority of the data using the package ‘lme4’ (Bates, Maechler, Bolker & Walker, 2014). To
179 analyse whether dominant or low-ranking models received differing levels of social attention, the

180 total number of observations made of each model during demonstration were compared using a
181 Wilcoxon test. GLMMs with Poisson error structure were fitted with the outcome variables of
182 “number of demonstrations seen of each model”. Observer age (adult or juvenile), sex (male or
183 female), rank (a continuous score between 0 and 1) and kinship to the model (a categorical variable
184 with three levels; “kin of dominant model”, “kin of low-ranking model” or “non-kin”) were added
185 as fixed effects. There were too few data points to use ID nested within group as random factors
186 and thus ID was entered as a random intercept into the models as it led to a better fitting model
187 than group (as judged by a lower AIC score which represents the best fitting and simplest model,
188 Akaike, 1974). To analyse whether groups preferentially displayed the method of their dominant
189 model, Fisher’s exact tests were used to compare the first method used by each individual from
190 the D-push and D-pivot conditions. A series of GLMMs were then used to analyse whether fixed
191 effects such as age, sex, rank, kinship and proportion of dominant to low-ranking demonstrations
192 observed had effects upon participation and the method used by individuals. For all analyses with
193 GLMMs, the full models are reported containing all fixed effects and only interactions that had a
194 significant effect. Full-null model comparisons are reported using the package ‘MuMIn’ (Burnham
195 & Anderson, 2002).

196 **Results**

197 *Social attention during demonstrations*

198 A total of 100 monkeys from the three two-model groups were recorded to observe at least one
199 demonstration from a model during the test phase (out of a potential 116 group members, excluding
200 infants). The dominant models’ demonstrations did not receive significantly more observations
201 overall than the low-ranking models’ demonstrations (Wilcoxon Signed-Rank Test, mean
202 observations of dominant female = 5.0; mean observations of low-ranking female = 4.82, $W =$
203 5028, $P = 0.95$). When the GLMM was fitted with the outcome variable as the number of dominant
204 female demonstrations viewed, rank and age of observer were significant predictors; rank had a
205 significant positive relationship with demonstrations viewed and juveniles observed more
206 demonstrations than adults (see Table 2, Figure 1). When juveniles were analysed separately, they

207 did not watch significantly more of the dominant models' demonstrations than the low-ranking
208 models' demonstrations (Wilcoxon Signed-Rank Test, mean observations of dominant models =
209 5.69, mean observations of low ranking models = 3.52, $W = 2466$, $P = 0.19$). When the outcome
210 variable was the number of low-ranking demonstrations viewed, kinship was a significant
211 predictor, with kin of the low-ranking model viewing significantly more of her demonstrations
212 than kin of the dominant model (but not more than non-kin, see Table 2, Figure 1c). We also found
213 a significant interaction between sex and age, as shown in Figure 1d.

214 *Model Behaviour*

215 Prior to the test phase, the models had all successfully used their assigned methods at least
216 120 times during the training and demonstration phase combined. All three dominant females
217 maintained a significant preference for their trained method (Gaga, $N=97$, $P<0.001$, 95% CI [0.60,
218 0.79], Gene, $N=83$, $P<0.001$, 95% CI [0.92, 1.00], Ouli, $N=182$, $P=0.001$, 95% CI [0.55, 0.69]),
219 whereas the low-ranking models in the two-model groups did not maintain a preference for their
220 trained method and one low-ranking model showed a significant preference for her non-trained
221 method (Nkos, $N=132$, $P<0.001$, 95% CI [0.65, 0.81]). The low-ranking model in BD opened the
222 box only once, using her trained method, so a preference could not be calculated. The low-ranking
223 model in KB, where there was no dominant model demonstrating another action, maintained a
224 significant preference for her trained method (Ness, $N=260$, $P<0.001$, 95% CI [0.92, 0.97]).

225 Whether the models used their trained or untrained method at each opening was entered into a
226 GLMM with a binomial error structure as the outcome variable with the fixed effect of model rank,
227 group and the observations they had made of the other model in their group during the
228 demonstration phase. Individual trial number was nested within ID and entered as a random factor.

229 Significant effects of model rank and group were found (see Table 3); dominant models were
230 significantly more likely to persist in their trained method than low-ranking models (see Figure 2)
231 and AK models were significantly less likely to stick to their trained method than NH or BD.

232 *Participation*

233 Across all ten tests, 33 individuals from the three two-model groups opened the box.
234 However, only 25 of these individuals were successful in gaining a reward when they opened the
235 box. The remaining eight individuals either opened the box only when it was already empty or
236 were unable to retrieve the reward despite having opened the box due, for example, to the pivot
237 door closing, or food becoming trapped behind the push door.

238 Whether an individual who had seen at least one demonstration participated in the test
239 phase was entered into a GLMM with a binomial error structure and group as random intercept.
240 Observer rank, sex and age, along with the proportion of dominant to low-ranking demonstrations
241 they had observed were entered into the GLMM as fixed effects. A significant interaction between
242 proportion of dominant demonstrations seen and the age class of the individual was found (see
243 Table 4). The more demonstrations by a dominant model that juveniles witnessed, the more likely
244 they were to participate.

245 *Method of Opening*

246 In the no-model control group (LT), six individuals opened the box. No significant
247 preference for either method was found for the first method used (binomial test, $N=6$, $P = 0.69$).
248 Of the three individuals who opened the box more than six times throughout the five tests, one
249 showed a significant preference for push (binomial test, $N=149$, $P<0.001$, 95% CI [0.68, 0.82]),

250 another a significant preference for pivot (binomial test, $N=12$, $P=0.04$, 95% CI [0.52, 0.98]) and
251 the other showed no preference for either method (binomial test, $N=7$, $P=0.45$).

252 In the one-model group (KB), only three individuals opened the box, all using the model's
253 method of push on their first opening, including the dominant female of the group. Two of the
254 three openers also displayed a significant preference for the model's method over the course of the
255 10 tests (binomial tests; Lif, $N=32$, $P=0.04$, 95% CI [0.53, 0.86]; Tang, $N=9$, $P=0.04$, 95% CI
256 [0.52, 1.0]), whilst the third showed no preference for either method (Avo, $N=30$, $P>0.99$). All
257 three individuals had seen at least one demonstration by the model (see Table A2).

258 Given the small sample sizes, Fisher's exact tests were used to assess whether the method
259 of opening (pivot or push) differed across the conditions in the two-model groups. When the first
260 method used was analysed there were no significant differences between the D-pivot and D-push
261 conditions (Fisher's exact test, $N=33$, $P=0.30$). To assess whether there was an effect of condition
262 upon method used throughout the tests, all openings made by non-models in the three two-model
263 groups throughout the 10 test sessions were then collated ($N=1637$). A GLMM with binomial error
264 structure was used with individual trial number nested within monkey ID as a random effect and
265 with the method used at each opening entered as the outcome variable. The condition and the
266 proportion of pivot to push demonstrations witnessed by each individual within 5 at the
267 demonstration phase and within 10 metres during the test phase, were entered into the model as
268 fixed effects. No significant effects were found for either condition or proportion of
269 demonstrations observed (see Table 5).

270 A comparison of the control group, LT, with the two-model groups was conducted using a
271 GLMM with a binomial error structure, random effect of trial number nested within ID and fixed

272 effect of condition. A significant main effect of condition was found; individuals in the D-pivot
273 condition were more likely to use the pivot method than individuals from the control group
274 (estimate = 2.54, SE = 1.02, $z = 2.5$, $P = 0.01$, 95% CI [0.55, 4.53], see Figure 3). The full model
275 differed significantly from the null model ($\chi^2 = 8.80$, $P = 0.01$).

276 *Effects of demonstrations seen, rank, kinship, age and sex*

277 Whether an individual matched the method of the dominant model at each trial in the test phase
278 was entered as an outcome variable into a further GLMM with binomial error structure.

279 Condition (D-push or D-pivot) as well as participant sex, rank, age and kinship (to the models),
280 and the demonstrations they had witnessed were entered as fixed effects. As before, individual
281 trial number nested within ID was entered as a random variable. All openings over the 10 tests
282 from the three two-model groups (BD, AK and NH) were used.

283 A significant main effect of condition and an interaction between rank and sex were found. Those
284 individuals whose dominant female demonstrated push matched her method significantly less
285 often than those whose dominant female demonstrated a pivot (see Table 6), thereby demonstrating
286 a preference for pivot irrespective of condition, and rank had a significant positive relationship
287 with the likelihood of females to match the dominant method (see Figure 4).

288 *Latency to retrieve the reward*

289 To assess whether one method (push or pivot) could be considered ‘easier’ than the other,
290 time taken to successfully extract the food reward from the box using each method was compared
291 using the three two-model groups (BD, AK and NH). The time taken to open the box was recorded
292 for each opening as the time from when the monkey first touched the box, to the moment when
293 the apple was removed from the box. Only instances in which both the time that the box was

294 touched and the time that the apple was removed from the box could be accurately recorded were
295 used ($N=1358$, 1172 pivots, 186 pushes). The average time to open the box using the push method
296 across all three groups with models removed was 8.25 seconds ($SE = 0.82$), whereas the average
297 time to open using the pivot method was 7.62 seconds ($SE = 0.25$). A GLMM with Gaussian error
298 structure and a random intercept of ID was run with fixed effect of opening method. When the
299 three two-model groups were analysed together there was no significant effect of method used
300 upon the time taken to open ($t = -0.89$, $P = 0.37$). When only the first test session was analysed,
301 there remained no significant effect of method upon the time taken to access the reward ($t = 0.71$,
302 $P = 0.47$). However, when individuals from the one-model group (KB) were analysed, the latency
303 to open was significantly longer for the pivot method, which was the method not modelled in this
304 group (estimate = -7.21 , $SE = 2.79$, $t = -2.59$, $P = 0.01$, 95% CI [-12.7 , -1.75]). No significant
305 effect of whether the monkeys matched the dominant method was found upon their latency to
306 retrieve the reward ($t = -0.49$, $P=0.62$). Overall, BD group were slower at opening the box than
307 both LT (estimate = -5.68 , $SE = 2.80$, $t = -2.03$, $P = 0.042$, 95% CI [-11.2 , -0.19]) and AK (estimate
308 = -4.81 , $SE = 2.36$, $t = -2.04$, $P = 0.042$, 95% CI [-9.43 , -0.18]).

309 *Discussion*

310 The primary aim of this experiment was to ascertain whether wild vervet monkeys display
311 a bias to attend to and copy a dominant model in an extractive foraging task. There was no overall
312 preference for group members to attend to the dominant females' demonstrations more than the
313 low-ranking models' demonstrations and no significant bias towards the dominant females' versus
314 the low ranking females' method was exhibited in the first method used on the box by each
315 individual, nor did any consistent bias emerge over the course of the ten test sessions. When all
316 sessions were collated, there was a significant effect of condition upon likelihood of the dominant

317 female's method being matched. This suggests a preference for the pivot action over the push
318 action, by comparison with which a model's rank had little enduring effect upon the method
319 adopted by group members.

320 This finding is consistent with an earlier experiment with captive capuchin monkeys
321 (Dindo et al., 2011) and findings of social attention in wild vervet monkeys which showed no
322 effect of rank upon levels of social attention received (Renevey, Bshary & van de Waal et al.,
323 2013). However it contrasts with reports of dominance-based biases in captive chimpanzees
324 (Horner et al., 2010; Kendal et al., 2015, although see Watson et al. 2017). It is possible, and not
325 implausible, that artificial social groupings could have influenced the captive studies; for example,
326 animals that have to remain in close proximity to all group mates may exhibit different attentional
327 biases compared to those living in their natural, fission-fusion state (Goodall, 1986; Murray, Mane
328 & Pusey, 2007). There may also be different perceptions of others' success (or different levels of
329 ability to judge success) between species. It has been shown that wild dominant female
330 chimpanzees are able to acquire higher quality resources than lower ranking females and, as such,
331 may achieve higher reproductive success (Pusey, Williams & Goodall, 1997). By contrast this does
332 not always appear to be the case for female monkeys in the vervet populations sampled thus far
333 (Cheney, Lee & Seyfarth, 1981; Cheney & Seyfarth, 1987; Wrangham, 1981). Therefore whilst
334 for chimpanzees dominance might be a proxy for judging the success of potential models, and thus
335 invite a bias towards copying these individuals, this may not be the case in vervet monkeys. This
336 would then limit the adaptive value of copying a dominant female. Indeed, vervet monkeys have
337 already been shown to copy female, but not male, models in extractive foraging tasks (van de Waal
338 et al., 2010), ostensibly because females are the philopatric sex and thus most knowledgeable about
339 the local environment. Therefore, females of all ranks may have similar and relevant local

340 knowledge. The preference for the pivot method almost exclusively in groups where it was
341 modelled and the preferences for the push method shown in the one-model group suggest that the
342 models did influence individuals' learning, but there appeared to be no enduring effect of the
343 models' ranks upon method chosen.

344 Though there was no overall bias for group members to attend to, or copy, particular
345 models based upon the model's rank, there were biases in both attention and behaviour based upon
346 individual level variables and the observer's relationship with the model. Chance (1967) suggested
347 that individuals should attend more to higher-ranked individuals than lower-ranked individuals,
348 but this was not found in the current study. Instead the rank of the observers significantly affected
349 the demonstrations they observed by females of different rank; higher-ranking individuals attended
350 to more demonstrations by the dominant female than did lower-ranking individuals. This effect
351 of rank was also shown in the test phase where high-ranking females were more likely to match
352 the dominant than low-ranking females. It may be that all individuals have a preference to attend
353 to, and match the behaviour of, the dominant female, but this can only be expressed in higher-
354 ranking monkeys who may be more tolerated in proximity to the dominant female (e.g. Seyfarth,
355 1977). However, we suggest that kinship may play a role in this finding. Whilst kinship was not a
356 significant predictor of method used, rank is maternally determined in vervet monkeys (Cheney &
357 Seyfarth, 1990) and thus can serve as an indicator for kinship in females and juveniles. Indeed, it
358 may be possible that in our study, rank was a better predictor of kinship than our kinship variable.
359 Since genetic data were not available, kinship was recorded only for direct offspring born since
360 the monkeys were habituated and reliably identified five years ago; sibling relationships between
361 adult females were unknown and could not be included in our measure. However, given that sisters
362 are usually adjacent in rank in vervet monkeys (Cheney & Seyfarth, 1990), the rank variable likely

363 captured these relationships. The low ranking models' kin watched more of her demonstrations
364 than the kin of the dominant model (but not non-kin overall). Therefore, it may be that the tendency
365 of high-ranked individuals to preferentially attend to and copy the behaviour of the dominant
366 female reflects a kinship bias to some extent. Previously only infants have been shown to exhibit
367 a kinship bias in social learning in vervet monkeys (van de Waal et al., 2014). However, to confirm
368 that a kinship bias goes beyond infancy in vervet monkey social learning, more complete data on
369 relatedness are required.

370 The interaction of rank and sex suggests that, perhaps because females are the philopatric
371 sex, there may be informational and/or normative (Claidiere and Whiten, 2012) benefits for
372 females to match the behaviour of their female kin/fellow high-ranking monkeys that may not be
373 as relevant for males. It may be that all females are able to convey equally useful social and
374 environmental information that would negate a bias for males to attend to and copy the most
375 dominant female.

376 Previous research found adult male vervet monkeys to be extraordinarily receptive to the
377 preferences of their new group following dispersal (van de Waal et al., 2013), showing a strong
378 tendency to adopt their new group's food colour preference. There has been considerable debate
379 about alternative explanations for such apparent conformity in this outcome and related findings
380 in birds (Aplin et al., 2015; van Leeuwen, Kendal, Tennie & Haun, 2015; van Leeuwen, Acerbi,
381 Kendal, Tennie, & Haun, 2016; Aplin et al. 2016; Whiten & van de Waal, 2016; Acerbi, van
382 Leeuwen, Haun & Tennie, 2016). A further study on vervet monkeys found stable experimentally
383 seeded dietary preferences in low-ranking females after group fission which, along with the initial
384 study, could be explained by a bias to either copy the dominant or conform to the preferences of
385 the origin group (van de Waal, van Schaik and Whiten, in press). As in the current study we found

386 no group level preference emerging for the method demonstrated by the dominant female in each
387 group, the latter explanation for the low-ranking females' behaviour appears more parsimonious.
388 Only four males who had transferred from another group managed to open the box during the test
389 phases of the present study and while all showed a preference for the dominant models' method,
390 this is too small a number from which to draw meaningful conclusions.

391 This study also revealed a significant effect of age in attention to the models; juveniles
392 were more likely than adults to attend to the demonstrations of the dominant models. When
393 juveniles alone were analysed, they did not show a significant preference to attend to the dominant
394 models more than the low-ranking models. Therefore it seems likely that the observed age
395 differences in attention stem from a higher tolerance for juveniles in dominant models. Some
396 primate species show high levels of tolerance towards even unrelated juveniles (Hirata & Celli,
397 2003; Boinski et al., 2003) and thus it seems likely that the juveniles were able to be in closer
398 proximity to the dominant females' demonstrations than were adults. However, age was not a
399 significant predictor of method used in the test phase.

400 *Model behaviour*

401 The behaviour of the models during the unrestrained test phase provided interesting
402 findings; whereas all three dominant models showed a sustained preference for their trained action,
403 none of the low-ranking models in the two-model groups did (although the low-ranking model
404 from BD was able to open the box only once). The finding that neither method was more efficient
405 than the other suggests that these models likely switched method after viewing others performing
406 the alternative action. However, since the number of observations of the other model during the
407 demonstration phase was not a good predictor of method used, it is likely that the low-ranking
408 models were influenced by other group members as well. The sole, low-ranking model in KB

409 maintained her preference for her trained, push action in the absence of a dominant model
410 performing the alternative action. This is consistent with findings that dominant individuals seem
411 to take less account of social information than lower-ranking individuals (Kendal et al., 2015;
412 Pongrácz, Vida, Bánhegyi & Miklósi, 2008), perhaps due to their ability to monopolise resources
413 and scrounge from others. The group level differences in models' adherence to their trained
414 method may have been due to individual variation or group level differences in social relationships,
415 as has been shown in our three experimental groups of vervet monkeys (Borgeaud, Sosa, Bshary,
416 Sueur & van de Waal, 2016), and thus potentially in social information use.

417 Finally, this study revealed a preference for one of the two alternative actions (pivot), an
418 issue that often arises when using multiple-option artificial fruits to test for social learning
419 (Claidière, et al., 2013; Tennie, Call & Tomasello, 2006). However, this preference was only
420 exhibited when the pivot was modelled (no preference was found in the control group), thus
421 suggesting that some actions may lend themselves more to social learning than others. This has
422 also been suggested for certain innovations in orangutans (van Schaik, van Noordwijk & Wich,
423 2006). The pivot method involved a bigger range of motion and was noisier than the more discrete
424 push action. We suggest that such differences in ease of transmission should be investigated further
425 as they may play a significant role in which behaviours are preferred and likely to become
426 traditions.

427 Some limitations in this initial attempt to address the issue of model bias experimentally in
428 the wild should be acknowledged. Our sample size was relatively small due to the low number of
429 individuals from each group who opened the box during the test phase. This should be borne in
430 mind particularly when interpreting the class-level biases revealed here, such as effects of age and
431 sex, as they may have been influenced by number and sex of individuals within the group. Further

432 investigation is required to assess the strength of these biases and whether they are seen in other
433 contexts. As in other studies of a similar nature (Lonsdorf et al., 2016), the open nature of the test
434 phase meant that some high-ranking individuals were able to monopolise the boxes first, so
435 monkeys would be likely to see more demonstrations from higher-ranking individuals during the
436 test phase than from lower-ranking individuals. Although we did incorporate the number of pushes
437 and pivots seen at this phase into our analyses and found them not to be significant predictors, it
438 is still possible that an individual other than a demonstrator may have influenced the choice of
439 method of the other monkeys.

440 To conclude, this experiment revealed that several biases appear to exist in vervet monkey
441 social attention and social learning based upon individual characteristics, such as rank, sex and
442 age, and the relationship between observer and model. Overall though, no group-wide bias was
443 found for individuals to copy a model of higher rank. These results highlight the complex nature
444 of social learning and social attention in primates, including factors such as tolerance, the ease
445 with which a certain behaviour lends itself to copying, and a multitude of individual-level biases.
446 Further research is needed to fully understand these biases and how they might contribute to the
447 spread of behaviours in wild primates.

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584

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599 **Appendix**

600 Table 1: Allocation of groups to conditions, group sizes and number of individuals who opened
601 the box

Group	Condition	Group size (AM, AF, J)	Number of individuals opening box	Description of Condition
AK	D-pivot	30 (4:10:16)	9	Dominant models pivot, Low-ranking models push
NH	D-pivot	43 (6:12:25)	15	Dominant models pivot, Low-ranking models push
BD	D-push	43 (6:12:25)	9	Dominant models push, Low-ranking models pivot
KB	L-push	21 (5:6:10)	3	Low-ranking models push
LT	Control	32 (5:7:20)	6	No models

602 Numbers of individuals in the groups (excluding infants) are given as they were on the first day
603 of the experiment, (in parentheses) numbers of adult males (AM), adult females (AF) & juveniles
604 (J). The number of individuals from each group who opened the box during the test phase are
605 listed with a description of each condition.

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612 Table 2: Factors affecting the probability of individuals observing a demonstration from within 5

613 metres.

Fixed effects	Estimate	SE	z	P	2.5 % CI	95% CI	Odds ratio
<i>Dominant demonstrations</i>							
Intercept	-0.29	0.44	-	-	-0.94	1.39	1.25
Age	1.00	0.24	4.17	<0.001	0.46	1.43	2.57
Kinship (Dominant – Low)	0.08	0.53	0.15	0.88	0.95	1.12	1.09
Kinship (Dominant – None)	0.48	0.34	1.41	0.16	-1.15	0.19	1.62
Kinship (Low – None)	0.56	0.41	1.37	0.17	-0.24	1.37	1.76
Rank	1.44	0.41	3.49	<0.001	0.63	2.25	4.23
Sex	-0.13	0.21	-0.62	0.53	-0.55	0.27	0.87
<i>Low-ranking demonstrations</i>							
Intercept	0.70	0.74	-	-	0.19	2.57	3.97
Age	-1.57	0.78	-2.01	0.044	-3.10	-0.04	0.21
Kinship (Low-Dominant)	1.24	0.61	2.05	0.040	0.05	2.43	3.47
Kinship (Dominant-None)	0.68	0.44	1.54	0.12	-0.19	1.55	0.51
Kinship (Low – None)	0.56	0.44	1.28	0.20	-0.30	1.42	1.76
Rank	0.56	0.45	1.24	0.21	-0.32	1.43	1.74
Sex	-0.50	0.39	-1.29	0.20	-1.26	0.26	0.61
Sex*Age	1.03	0.49	2.10	0.036	0.07	2.00	-

614 Analyses are separated for demonstrations by the dominant and low-ranking female models.

615 Significant predictors are presented in **bold**. Only significant interactions were included in the

616 full model.

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624 Table 3: Factors affecting the probability that models used their trained method in the test phase.

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Fixed effects	Estimate	SE	z	P	2.5% CI	97.5% CI	Odd Ratio
Intercept	0.81	0.66	-	-	-0.49	2.10	2.24
Model rank	-1.60	0.48	-3.35	<0.001	-2.53	-0.66	0.20
Group (AK-BD)	1.20	0.42	2.89	0.004	0.39	2.02	3.33
Group (AK-NH)	2.47	0.67	3.69	<0.001	1.16	3.78	11.78
Group (NH-BD)	-1.26	0.73	-1.73	0.084	-0.17	2.70	3.54
Observations of other model	-0.14	0.23	-0.58	0.56	-0.60	0.32	0.87

626 Significant predictors are presented in **bold**. The final model was significantly different from the

627 null model containing only the random effects of Test and Individual trial nested within ID

628 (likelihood ratio test: $\chi^2=12.2$, $P=0.016$).

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639 Table 4: Factors affecting the probability that an individual participated in the test phase.

Fixed effects	Estimate	SE	z	P	2.5% CI	97.5% CI	Odds ratio
Intercept	0.01	1.00	-	-	-1.96	1.97	1.01
Age	-1.39	0.82	-1.68	0.092	-3.00	0.23	0.25
Kinship (Dominant – Low)	-1.32	1.14	0.94	0.35	-4.07	1.43	0.27
Kinship (None - Low)	-0.39	1.17	-0.33	0.74	-2.67	1.91	0.68
Kinship (None - Dominant)	0.93	0.82	1.14	0.25	-0.67	2.54	2.55
Proportion of dominant demos observed	-3.34	1.59	-2.10	0.036	-6.46	-0.22	0.04
Rank	0.99	1.00	1.00	0.32	-0.96	2.95	2.70
Sex	-0.36	0.50	-0.72	0.47	-1.34	0.62	0.70
Proportion of dominant demos observed*Age	4.17	1.78	2.35	0.019	0.69	7.66	-

640 Significant predictors are presented in **bold**. Only significant interactions were included in the full

641 model.

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652 Table 5: Factors affecting the probability that an individual used push or pivot in the test phase.

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Fixed effects	Estimate	SE	z	P	2.5% CI	97.5% CI	Odds ratio
Intercept	1.42	0.80	-	-	-0.15	3.00	4.15
Condition	-0.87	0.64	-1.37	0.17	-2.12	0.37	0.42
Proportion of demos observed	0.53	0.82	0.65	0.52	-1.08	2.14	1.70

654 The full model differed significantly from the null model with only the random effect of trial

655 number nested within ID ($\chi^2= 12.3, P=0.002$).

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668 Table 6: Factors affecting the probability that individuals matched the method of their dominant
669 female in the test phase.

Fixed effects	Estimate	SE	z	P	2.5% CI	97.5% CI	Odds ratio
Intercept	1.18	0.89	-	-	-0.27	4.54	3.25
Age	-0.40	0.80	-0.50	0.62	-1.97	1.17	0.67
Condition	-3.59	0.85	-4.20	<0.001	-5.26	-1.92	0.03
Kinship (Dominant – Low)	0.16	1.40	0.11	0.91	-2.58	2.89	1.17
Kinship (None - Dominant)	0.95	0.60	1.59	0.11	-0.22	2.13	2.59
Kinship (None - Low)	1.11	1.34	0.83	0.41	-1.51	4.71	3.03
Proportion demos seen	-1.31	1.21	-1.09	0.28	-3.68	1.05	0.27
Rank	1.61	1.59	1.01	0.31	-1.50	4.71	4.99
Sex	-2.03	1.23	-1.65	0.099	-4.45	0.38	0.13
Rank*Sex	4.89	1.85	2.65	0.008	1.27	8.51	-

670 Significant predictors are presented in **bold**. The full model was significantly different from the
671 null model containing only the random effects of individual trial nested within ID (likelihood
672 ratio test: $\chi^2= 35.2, P < 0.001$).

673 Table A1: All demonstrations watched by all individuals during the demonstration phase, with participation and associated individual
674 variables.

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Group	Individual	Participated	Kinship	Sex	Age	Rank	Dominant demos watched	Low-ranker demos watched	Total demos watched	Proportion of demos watched
BD	Aapie	No	Non-Kin	F	J	0.292683	2	0	2	1
BD	Afrikaans	Yes	Non-Kin	M	J	NA	3	0	3	1
BD	Akkedis	No	Non-Kin	M	J	0.536585	7	6	13	0.54
BD	Alsiende	Yes	Non-Kin	F	J	0.365854	10	5	15	0.67
BD	Bullebak	No	Non-Kin	M	J	0.243902	0	1	1	0
BD	Chernobyl	No	Non-Kin	M	A	0.95122	1	1	2	0.5
BD	Chouchou	Yes	Non-Kin	F	A	0.634146	2	6	8	0.25
BD	Dapper	No	Non-Kin	M	A	0.268293	0	4	4	0
BD	Dwergie	No	Non-Kin	M	J	0.804878	0	2	2	0
BD	Heerlik	No	Non-Kin	F	A	0.560976	0	10	10	0
BD	Hippie	No	Non-Kin	F	J	0.585366	7	2	9	0.78
BD	Kies	No	Non-Kin	M	J	0.682927	1	9	10	0.1
BD	Little Blind	No	Non-Kin	F	J	0.073171	4	0	4	1
BD	Madagascar	No	Non-Kin	M	A	0.902439	0	5	5	0
BD	Mevrou	No	Non-Kin	F	J	0.341463	2	0	2	1
BD	Mieles	Yes	Non-Kin	F	A	0.121951	0	8	8	0
BD	Mvula	No	Non-Kin	M	A	0.097561	2	1	3	0.67
BD	Neuchatel	No	Non-Kin	M	A	0.926829	6	6	12	0.5
BD	Noktober	No	Non-Kin	M	J	0.170732	6	2	8	0.75
BD	Nurk	No	Non-Kin	F	J	0.219512	0	4	4	0
BD	Ogies	No	Dom kin	M	J	0.853659	5	4	9	0.56

BD	Onbeskof	Yes	Dom kin	M	J	0.707317	5	1	6	0.83
BD	Pannekookie	No	Non-Kin	F	A	0.146341	2	8	10	0.2
BD	Pieperig	Yes	Non-Kin	F	J	0.756098	12	1	13	0.92
BD	Poeding	Yes	Non-Kin	M	J	0.829268	17	2	19	0.89
BD	Potjie	No	Non-Kin	F	J	0.390244	0	2	2	0
BD	Princess	Yes	Non-Kin	F	A	0.878049	0	4	4	0
BD	Rakker	No	LR kin	M	J	0.317073	0	11	11	0
BD	Rooikat	No	LR kin	M	J	0.439024	8	1	9	0.89
BD	Siele	No	Non-Kin	F	J	0.414634	4	7	11	0.36
BD	Spook	No	Non-Kin	M	J	0.658537	0	6	6	0
BD	Toronto	No	Non-Kin	M	A	0.512195	2	10	12	0.17
BD	Vakkie	No	Non-Kin	M	J	0.02439	6	6	12	0.5
BD	Vulcan	No	Non-Kin	M	J	0.195122	1	2	3	0.33
BD	Wolfy	No	Non-Kin	M	J	0.487805	0	3	3	0
BD	Wurm	No	Non-Kin	M	J	0	2	5	7	0.29
BD	Zurich	Yes	Non-Kin	M	A	0.731707	2	2	4	0.5
AK	Elton	No	Non-Kin	M	A	0.931034	6	8	14	0.43
AK	Geleza	Yes	Dom kin	F	J	0.896552	14	1	15	0.93
AK	Ghangaan	No	Dom kin	F	A	0.862069	2	2	4	0.5
AK	Ghozo	No	Dom kin	M	J	0.793103	3	5	8	0.38
AK	Gugu	Yes	Dom kin	F	A	0.965517	6	6	12	0.5
AK	Heye	No	Non-Kin	M	J	0.310345	2	11	13	0.15
AK	Hlo	No	Non-Kin	M	J	0.206897	0	3	3	0
AK	Hleka	No	Non-Kin	F	A	0.448276	4	0	4	1
AK	Hola	No	Non-Kin	M	J	0.344828	0	1	1	0
AK	Hwawaza	Yes	Non-Kin	M	J	0.758621	8	17	25	0.32
AK	Idwala	No	Non-Kin	F	J	0.275862	1	4	5	0.2
AK	Ijinga	Yes	Non-Kin	M	J	0.034483	1	12	13	0.08
AK	Ilonga	No	Non-Kin	F	J	0.413793	0	2	2	0
AK	Inhla	Yes	Non-Kin	F	J	0.827586	5	2	7	0.71
AK	Inkwazi	No	Non-Kin	F	J	0.655172	9	1	10	0.9

AK	Isilonda	Yes	Non-Kin	F	A	0.413793	2	8	10	0.2
AK	Mbas	No	Non-Kin	M	J	0.137931	3	3	6	0.5
AK	Mungunya	Yes	Non-Kin	M	J	0	0	19	19	0
AK	Mvula	No	Non-Kin	M	J	0.068966	0	1	1	0
AK	Ndonsa	No	LR kin	F	A	0.206897	2	1	3	0.67
AK	Nyone	No	LR kin	M	J	0.241379	9	6	15	0.6
AK	Ubu	No	Non-Kin	M	J	0.62069	7	7	14	0.5
AK	Umzali	No	Non-Kin	M	A	0.586207	5	0	5	1
AK	Unwabu	No	Non-Kin	M	J	0.517241	5	3	8	0.63
AK	Voldemort	No	Non-Kin	M	A	0.551724	2	0	2	1
NH	Boston	No	LR kin	M	J	0.119048	5	9	14	0.36
NH	Brasilia	Yes	LR kin	F	A	0.666667	2	12	14	0.14
NH	Cancun	No	Non-Kin	M	A	0.761905	0	1	1	0
NH	Ertjies	No	Non-Kin	M	A	0.928571	2	0	2	1
NH	Garroua	Yes	Dom kin	M	J	0.619048	7	0	7	1
NH	Gaya	No	Dom kin	F	J	0.97619	14	2	16	0.88
NH	Glastonbury	Yes	Dom kin	M	J	0.452381	18	0	18	1
NH	Govu	No	Non-Kin	M	A	0.857143	2	3	5	0.4
NH	Jakarta	No	Non-Kin	F	A	0.214286	1	0	1	1
NH	Jillin	No	Non-Kin	F	J	0.071429	1	3	4	0.25
NH	Jinka	No	Non-Kin	F	A	0.595238	0	1	1	0
NH	Jixi	No	Non-Kin	M	J	0.166667	3	0	3	1
NH	Juneau	Yes	Non-Kin	M	J	0.428571	20	0	20	1
NH	Lhasa	No	Non-Kin	F	A	0.404762	0	3	3	0
NH	Lome	Yes	Non-Kin	M	J	0.785714	2	6	8	0.25
NH	M30	Yes	Non-Kin	M	A	0.571429	0	4	4	0
NH	Paris	Yes	Non-Kin	F	A	0.738095	0	6	6	0
NH	Praia	No	Non-Kin	F	J	0.285714	2	7	9	0.22
NH	Pretoria	No	Non-Kin	F	A	0.904762	8	0	8	1
NH	Puerto	Yes	Non-Kin	M	J	0.714286	5	15	20	0.25
NH	Reeva	Yes	Non-Kin	F	J	0.02381	1	2	3	0.33

NH	Rennes	No	Non-Kin	F	J	0.047619	3	0	3	1
NH	Rheeban	No	Non-Kin	M	J	0	2	0	2	1
NH	Rio	No	Non-Kin	M	J	0.380952	1	0	1	1
NH	Styx	No	Non-Kin	M	A	0.261905	2	0	2	1
NH	Tallin	No	Non-Kin	M	J	0.142857	4	1	5	0.8
NH	Tirroan	No	Non-Kin	M	J	0.238095	4	0	4	1
NH	Troia	Yes	Non-Kin	F	A	0.333333	1	4	5	0.2
NH	Uji	No	Non-Kin	M	J	0.690476	6	1	7	0.86
NH	Ulundi	Yes	Non-Kin	M	J	0.5	10	1	11	0.91
NH	Upsala	No	Non-Kin	F	A	1	17	0	17	1
NH	Xaixai	No	Non-Kin	F	A	0.880952	2	7	9	0.22
NH	Xalapa	Yes	Non-Kin	F	J	0.190476	7	0	7	1
NH	Xeres	Yes	Non-Kin	M	J	0.52381	7	7	14	0.5
NH	Xian	No	Non-Kin	F	J	0.47619	6	2	8	0.75
NH	Yoogali	No	Non-Kin	F	J	0.642857	7	3	10	0.7
NH	Zanzibar	No	Non-Kin	M	J	0.357143	2	0	2	1
NH	Zion	No	Non-Kin	M	J	0.809524	1	6	7	0.14

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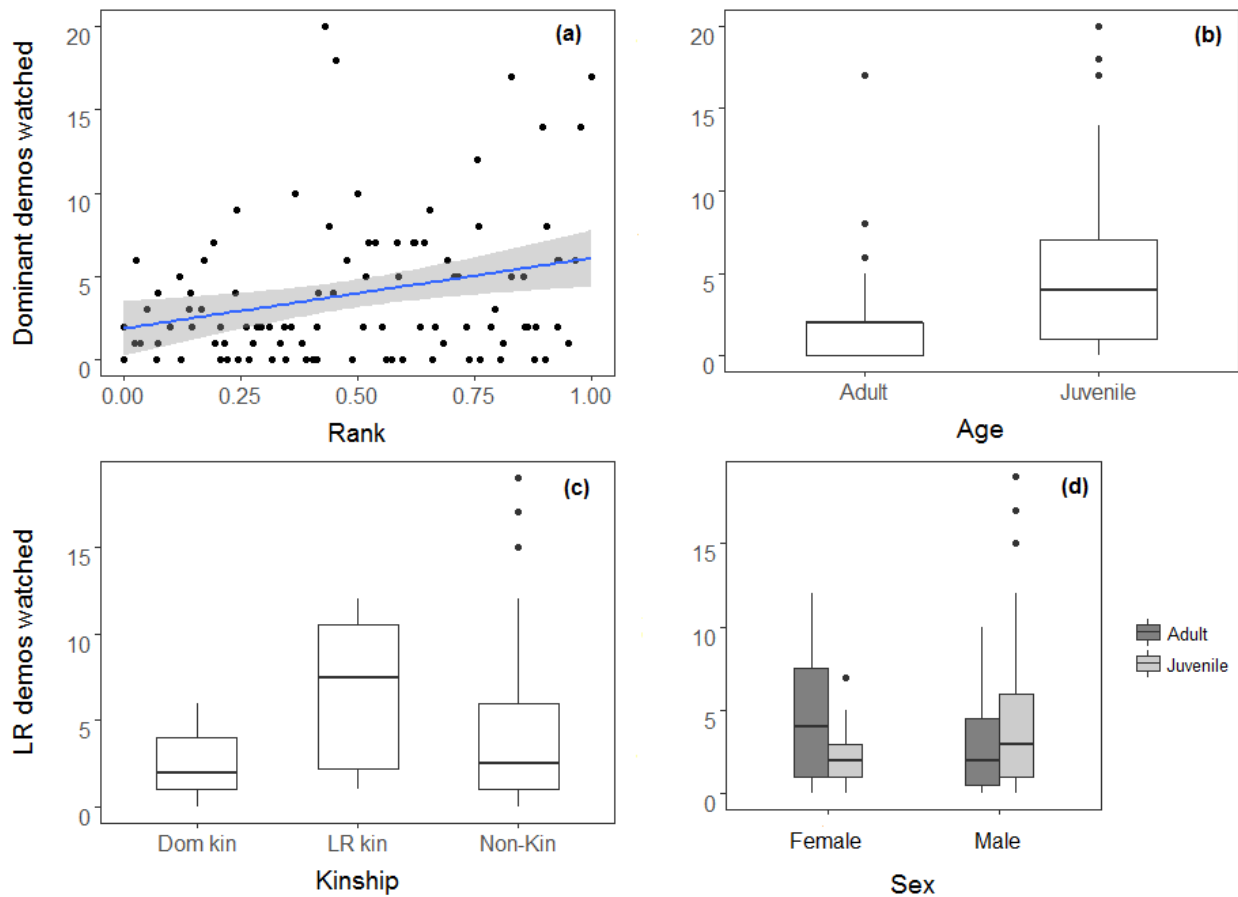
682 Table A2: All openings made by all individuals across the five groups using each method with all individual variables

ID	Group	Age	Sex	Kinship	Condition	First Method	Total Pivots Seen	Total Pushes Seen	Total Pivots at test	Total Pushes at test
Gele	AK	J	F	Dom	D-Pivot	Pivot	14	1	146	16
Gugu	AK	A	F	Dom	D-Pivot	Pivot	18	6	106	2
Hwa	AK	J	M	None	D-Pivot	Pivot	9	17	1	0
Isil	AK	A	F	None	D-Pivot	Pivot	7	9	105	24
Mun	AK	J	M	None	D-Pivot	Push	7	19	6	16
Afr	AK	A	M	None	D-Pivot	Pivot	0	3	174	4
Iji	AK	J	M	None	D-Pivot	Pivot	6	15	1	0
Inhl	AK	A	F	None	D-Pivot	Pivot	6	2	6	1
Mamo	AK	A	F	None	D-Pivot	Pivot	13	0	10	0
Asis	BD	A	F	None	D-Push	Pivot	3	0	0	1
Chou	BD	A	F	None	D-Push	Pivot	6	2	211	7
Poe	BD	J	M	None	D-Push	Push	3	24	16	10
Prin	BD	A	F	None	D-Push	Pivot	5	3	9	3
Zur	BD	A	M	None	D-Push	Push	2	4	1	10
Miel	BD	A	F	None	D-Push	Pivot	15	2	2	0
Onb	BD	J	M	Dom	D-Push	Pivot	1	9	102	21
Alsi	BD	J	F	None	D-Push	Pivot	4	13	2	0
Piep	BD	J	F	None	D-Push	Pivot	8	19	1	0
Gar	NH	J	M	Dom	D-Pivot	Pivot	7	0	81	11
M30	NH	A	M	None	D-Pivot	Pivot	2	4	185	18
Pari	NH	A	F	None	D-Pivot	Pivot	5	6	8	0
Pue	NH	J	M	None	D-Pivot	Pivot	12	15	201	2
Xer	NH	J	M	None	D-Pivot	Pivot	12	7	3	0
Gla	NH	J	M	Dom	D-Pivot	Pivot	21	0	5	0
Troi	NH	A	F	None	D-Pivot	Pivot	1	4	1	0
Xala	NH	J	F	None	D-Pivot	Pivot	7	0	1	0

Jun	NH	J	M	None	D-Pivot	Push	33	3	0	2
Pret	NH	A	F	None	D-Pivot	Pivot	8	0	1	0
Lom	NH	J	M	None	D-Pivot	Pivot	9	9	1	0
Ulu	NH	J	M	None	D-Pivot	Pivot	13	2	36	40
Bras	NH	A	F	Low	D-Pivot	Pivot	5	12	21	1
Reev	NH	J	F	None	D-Pivot	Pivot	6	3	3	1
Fluf	NH	A	M	None	D-Pivot	Pivot	0	0	1	0
Dar	LT	J	M	NA	Control	Push	NA	NA	1	3
Len	LT	J	M	NA	Control	Push	NA	NA	0	1
Liz	LT	A	F	NA	Control	Pivot	NA	NA	14	2
Mna	LT	A	M	NA	Control	Pivot	NA	NA	36	113
Noa	LT	J	M	NA	Control	Push	NA	NA	2	5
Vin	LT	A	M	NA	Control	Push	NA	NA	0	1
Avo	KB	J	M	None	L-Push	Push	NA	8	15	15
Lif	KB	A	M	None	L-Push	Push	NA	2	11	24
Tang	KB	A	F	None	L-Push	Push	NA	1	1	8

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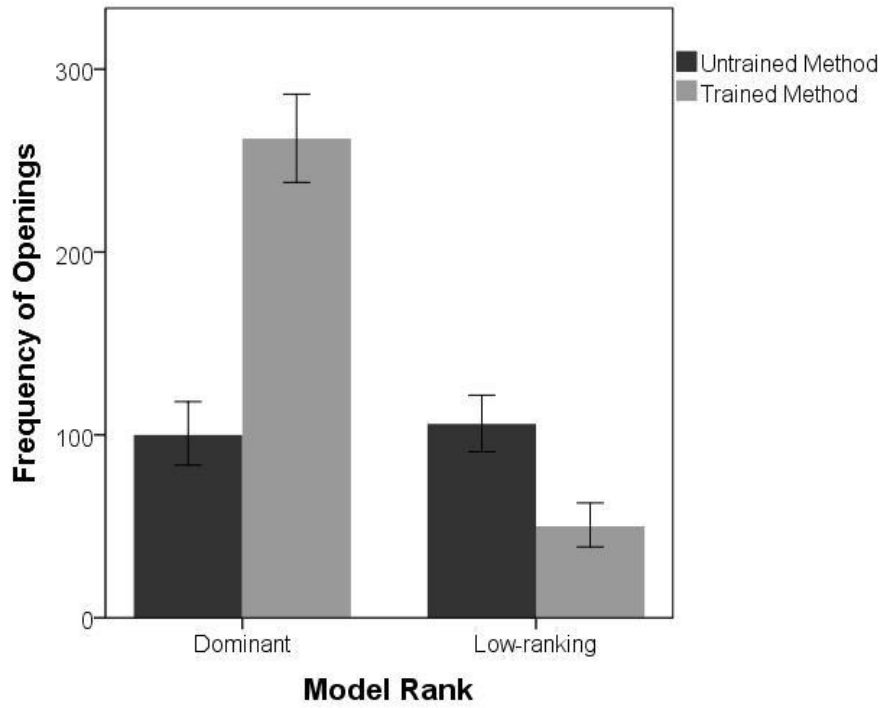
684 **Figures**



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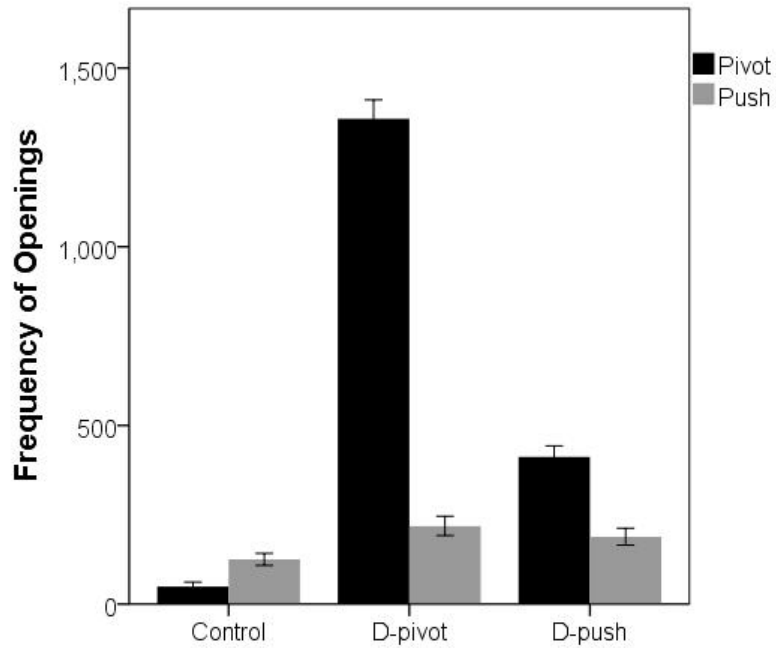
686 Figure 1: The average number of demonstrations for which observers were watching within 5
687 metres of the (a & b) dominant demonstrators and (c & d) low-ranking demonstrators, as shown
688 by the observer's (a) rank, (b) age, (c) kinship to the models (d) sex and age. Shaded area
689 represents 95% confidence interval. Boxplots show median, interquartile range, maximum and
690 minimum values and outliers represented by dots.

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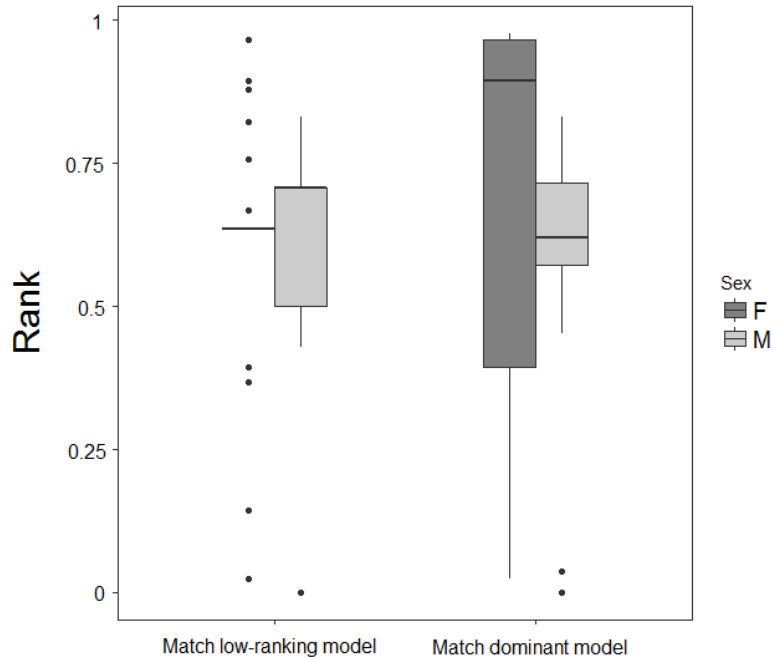
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693 Figure 2: The total frequency of box openings in which the dominant and low-ranking models
 694 used their trained and untrained methods from the three two-model groups. Error bars represent
 695 95% confidence intervals.



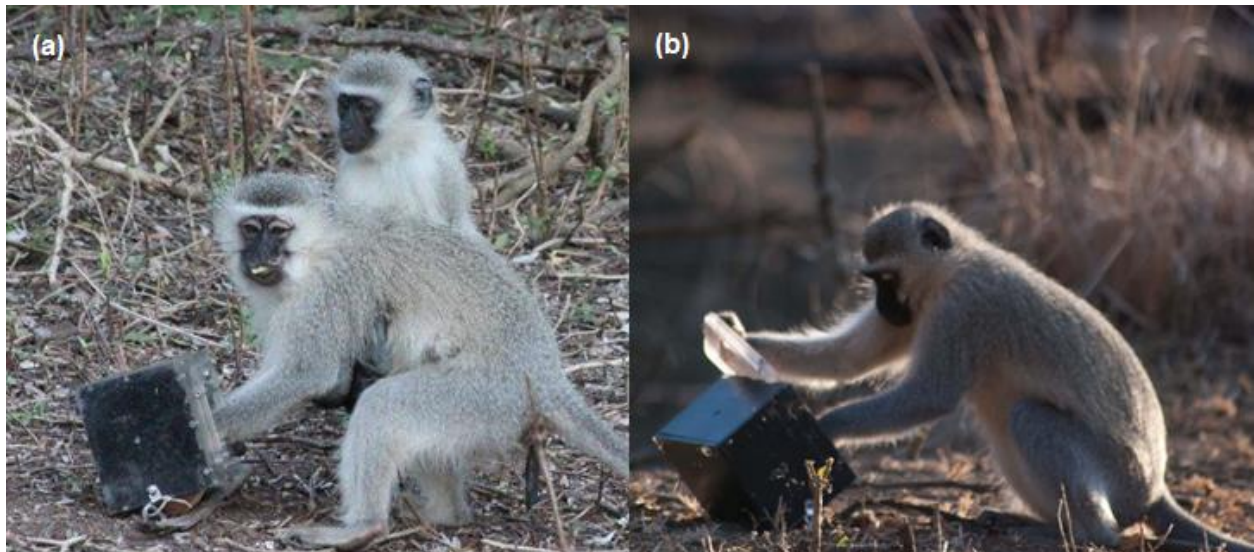
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697 Figure 3: Total frequency of openings across the two-model and control conditions which used
 698 the pivot (black) or the push method (grey) throughout the 10 tests. Error bars represent 95%
 699 confidence intervals.



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701 Figure 4: Individual rank compared to matching of the dominant females' method in the three
 702 two-action groups, as split by sex.



703

704 Figure A1: Individuals opening the box using the (a) push method and the (b) pivot method.

705 Image credit: Jennifer Botting & P. Stoebener.