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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
34 group 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
45 the most useful information. One way to obtain the best information may be to selectively copy
46 certain individuals based upon individual characteristics, such as age, sex or past successes. It is
47 also likely that animals may exhibit biased social learning based upon the social organisation of a
48 group (directed social learning, Coussi-Korbel & Fragaszy, 1995); greater time spent in
49 proximity to certain individuals may increase the likelihood that they will become models for
50 social learning. Research with a variety of nonhuman animals has yielded evidence for a range of
51 biases based upon the identity of the model in social learning, including age (Duffy, Pike &

52 Laland, 2009; Choleris, Guo, Liu, Mainardi, & Valsecchi, 1997), sex (Katz, & Lachlan, 2003;
53 van de Waal, Renevey, Favre, & Bshary, 2010), position in social network (Claidière, Messer,
54 Hoppitt & Whiten, 2013; Allen, Weinrich, Hoppitt, & Rendell, 2013) and kinship (van de Waal,
55 Bshary & Whiten, 2014). Findings of multiple social learning biases in the same species (Kendal
56 et al., 2015) 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,
60 although see Henrich & Gil-White, 2001). However few empirical studies have examined this
61 issue. Dindo and colleagues (2011) found no evidence of dominance-based biases in social
62 learning or social attention in captive tufted capuchin monkeys during an extractive foraging
63 task. By contrast, two studies with captive chimpanzees found that chimpanzees preferred to
64 copy a higher rather than lower ranked individual using tasks requiring both object manipulation
65 (Kendal et al., 2015, although see Watson et al. 2017) and token exchange (Horner, Proctor,
66 Bonnie, Whiten & de Waal, 2010), although dominance in the latter was confounded with age
67 and past success on tasks. On the basis of these findings with chimpanzees, it has been
68 suggested that such a bias towards copying dominant individuals could, in a similar way to
69 conformist transmission (Boyd & Richerson, 1985), constrain intra-group variation and enhance
70 the between-group variation found in wild chimpanzees (Kendal et al., 2015). However, such a
71 bias has not yet been assessed in wild populations.

72 The aim of the current study was, accordingly, to examine whether a dominance-based
73 bias 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 &

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

81 To provide an experimental test for a bias to copy high-ranking, over low-ranking,
82 models in a wild primate, we trained two models of differing rank within each of three groups to
83 use alternative methods to open an ‘artificial fruit’ to gain a reward inside and gave both models
84 the opportunity to demonstrate their method to their groupmates. We investigated whether a
85 certain rank of model was attended to more in an experimental setting and whether the method
86 they 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
95 exposed to the demonstration phase in the three two-model groups, whilst 42 monkeys
96 participated in the 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
99 (AK, NH and BD, see Table 1) and trained to demonstrate alternative methods for opening a
100 baited artificial fruit. Model rank was determined by the outcome of dyadic conflicts recorded
101 ad libitum and through regular observations of order to access of food provided to the group by
102 researchers since the habituation of the groups (between two and five years for each group).
103 During this time the female hierarchies have remained highly stable, as is usual for vervet
104 monkeys (Cheney & Seyfarth, 1990). Models defined as ‘dominant’ were ranked #1 of females
105 in their group, whilst ‘low rank’ models were taken from the bottom half of the female hierarchy
106 (positions 6 of 10 (AK), 11 of 12 (BD) and 7 of 11 (NH)). All researchers collecting data at IVP
107 were tested on monkey identification and interobserver reliability prior to data collection.
108 Individual rank for all group members was calculated using the EloRating package in R
109 (Neumann et al., 2011). In the control group (LT), no models were trained. In the fourth
110 experimental group, KB, only a low-ranking model (a sub-adult female model who had her first
111 offspring early on in the test and was then ranked 5 of 8 females) was trained to test the effects of
112 a single model. Demonstrations and test sessions were conducted by JB and MG, with the
113 assistance of one or more trained field assistants, comprising volunteers and students at IVP.

114 Apparatus

115 To create two alternative behaviours in the two models, an ‘artificial fruit’, a
116 polycarbonate box designed to mimic the characteristics of natural items that need to be opened
117 to gain the edible fraction inside (hereafter simply ‘box’) was used. Access to the food reward
118 inside required the opening of a small door on one side. The sides and top were painted black
119 with only the door left transparent, to funnel the monkeys’ attention to this part of the box. The
120 base of the box tilted it back at a roughly 30 degree angle and two metal hooks allowed the box
121 to be secured by 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
126 in place, so they could not be accidentally opened. A manual lock prevented one method of
127 opening 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)
130 video cameras.

131 Training

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

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

146 Demonstration and social attention

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

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

158 Test protocol

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

177 Statistical analyses

178 Analyses were performed using the statistical software ‘R’ version 1.0.136 (R Core
179 Team, 2013). Generalized linear mixed models (GLMMs, Bolker et al., 2009) were used to

180 analyse the majority of the data using the package ‘lme4’ (Bates, Maechler, Bolker & Walker,
181 2014). To analyse whether dominant or low-ranking models received differing levels of social
182 attention, the total number of observations made of each model during demonstration were
183 compared using a Wilcoxon test. GLMMs with Poisson error structure were fitted with the
184 outcome variables of “number of demonstrations seen of each model”. Observer age (adult or
185 juvenile), sex (male or female), rank (a continuous score between 0 and 1) and kinship to the
186 model (a categorical variable with three levels; “kin of dominant model”, “kin of low-ranking
187 model” or “non-kin”) were added as fixed effects. There were too few data points to use ID
188 nested within group as random factors and thus ID was entered as a random intercept into the
189 models as it led to a better fitting model than group (as judged by a lower AIC score which
190 represents the best fitting and simplest model, Akaike, 1974). To analyse whether groups
191 preferentially displayed the method of their dominant model, Fisher’s exact tests were used to
192 compare the first method used by each individual from the D-push and D-pivot conditions. A
193 series of GLMMs were then used to analyse whether fixed effects such as age, sex, rank, kinship
194 and proportion of dominant to low-ranking demonstrations observed had effects upon
195 participation and the method used by individuals. For all analyses with GLMMs, the full models
196 are reported containing all fixed effects and only interactions that had a significant effect. Full-
197 null model comparisons are reported using the package ‘MuMIn’ (Burnham & Anderson, 2002).

198 **Results**

199 *Social attention during demonstrations*

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

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

217 *Model Behaviour*

218 Prior to the test phase, the models had all successfully used their assigned methods at
219 least 120 times during the training and demonstration phase combined. All three dominant
220 females maintained a significant preference for their trained method (Gaga, $N=97$, $P<0.001$, 95%
221 CI [0.60, 0.79], Gene, $N=83$, $P<0.001$, 95% CI [0.92, 1.00], Ouli, $N=182$, $P=0.001$, 95% CI
222 [0.55, 0.69]), whereas the low-ranking models in the two-model groups did not maintain a
223 preference for their trained method and one low-ranking model showed a significant preference
224 for her non-trained method (Nkos, $N=132$, $P<0.001$, 95% CI [0.65, 0.81]). The low-ranking
225 model in BD opened the box only once, using her trained method, so a preference could not be
226 calculated. The low-ranking model in KB, where there was no dominant model demonstrating
227 another action, maintained a significant preference for her trained method (Ness, $N=260$,
228 $P<0.001$, 95% CI [0.92, 0.97]).

229 Whether the models used their trained or untrained method at each opening was entered into a
230 GLMM with a binomial error structure as the outcome variable with the fixed effect of model
231 rank, group and the observations they had made of the other model in their group during the
232 demonstration phase. Individual trial number was nested within ID and entered as a random
233 factor. Significant effects of model rank and group were found (see Table 3); dominant models
234 were significantly more likely to persist in their trained method than low-ranking models (see
235 Figure 2) and AK models were significantly less likely to stick to their trained method than NH
236 or BD.

237 *Participation*

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

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

250 *Method of Opening*

251 In the no-model control group (LT), six individuals opened the box. No significant
252 preference for either method was found for the first method used (binomial test, $N=6$, $P = 0.69$).
253 Of the three individuals who opened the box more than six times throughout the five tests, one
254 showed a significant preference for push (binomial test, $N=149$, $P<0.001$, 95% CI [0.68, 0.82]),
255 another a significant preference for pivot (binomial test, $N=12$, $P=0.04$, 95% CI [0.52, 0.98]) and
256 the other showed no preference for either method (binomial test, $N= 7$, $P=0.45$).

257 In the one-model group (KB), only three individuals opened the box, all using the
258 model's method of push on their first opening, including the dominant female of the group. Two
259 of the three openers also displayed a significant preference for the model's method over the
260 course of the 10 tests (binomial tests; Lif, $N=32$, $P=0.04$, 95% CI [0.53, 0.86]; Tang, $N=9$,
261 $P=0.04$, 95% CI [0.52, 1.0]), whilst the third showed no preference for either method (Avo,
262 $N=30$, $P>0.99$). All three individuals had seen at least one demonstration by the model (see
263 Table A2).

264 Given the small sample sizes, Fisher's exact tests were used to assess whether the method
265 of opening (pivot or push) differed across the conditions in the two-model groups. When the first
266 method used was analysed there were no significant differences between the D-pivot and D-push
267 conditions (Fisher's exact test, $N=33$, $P=0.30$). To assess whether there was an effect of
268 condition upon method used throughout the tests, all openings made by non-models in the three
269 two-model groups throughout the 10 test sessions were then collated ($N=1637$). A GLMM with
270 binomial error structure was used with individual trial number nested within monkey ID as a
271 random effect and with the method used at each opening entered as the outcome variable. The
272 condition and the proportion of pivot to push demonstrations witnessed by each individual within
273 5 at the demonstration phase and within 10 metres during the test phase, were entered into the

274 model as fixed effects. No significant effects were found for either condition or proportion of
275 demonstrations observed (see Table 5).

276 A comparison of the control group, LT, with the two-model groups was conducted using a
277 GLMM with a binomial error structure, random effect of trial number nested within ID and fixed
278 effect of condition. A significant main effect of condition was found; individuals in the D-pivot
279 condition were more likely to use the pivot method than individuals from the control group
280 (estimate = 2.54, SE = 1.02, $z = 2.5$, $P = 0.01$, 95% CI [0.55, 4.53], see Figure 3). The full model
281 differed significantly from the null model ($\chi^2 = 8.80$, $P = 0.01$).

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

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

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

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

294 *Latency to retrieve the reward*

295 To assess whether one method (push or pivot) could be considered ‘easier’ than the other,
296 time taken to successfully extract the food reward from the box using each method was
297 compared using the three two-model groups (BD, AK and NH). The time taken to open the box
298 was recorded for each opening as the time from when the monkey first touched the box, to the
299 moment when the apple was removed from the box. Only instances in which both the time that
300 the box was touched and the time that the apple was removed from the box could be accurately
301 recorded were used ($N=1358$, 1172 pivots, 186 pushes). The average time to open the box using
302 the push method across all three groups with models removed was 8.25 seconds ($SE = 0.82$),
303 whereas the average time to open using the pivot method was 7.62 seconds ($SE = 0.25$). A
304 GLMM with Gaussian error structure and a random intercept of ID was run with fixed effect of
305 opening method. When the three two-model groups were analysed together there was no
306 significant effect of method used upon the time taken to open ($t = -0.89$, $P = 0.37$). When only
307 the first test session was analysed, there remained no significant effect of method upon the time
308 taken to access the reward ($t = 0.71$, $P = 0.47$). However, when individuals from the one-model
309 group (KB) were analysed, the latency to open was significantly longer for the pivot method,
310 which was the method not modelled in this group (estimate = -7.21, $SE = 2.79$, $t = -2.59$, $P =$
311 0.01 , 95% CI [-12.7, -1.75]). No significant effect of whether the monkeys matched the dominant
312 method was found upon their latency to retrieve the reward ($t = -0.49$, $P=0.62$). Overall, BD
313 group were slower at opening the box than both LT (estimate = -5.68, $SE = 2.80$, $t = -2.03$, $P =$
314 0.042 , 95% CI [-11.2, -0.19]) and AK (estimate = -4.81, $SE = 2.36$, $t = -2.04$, $P = 0.042$, 95% CI
315 [-9.43, -0.18]).

316 *Discussion*

317 The primary aim of this experiment was to ascertain whether wild vervet monkeys
318 display a bias to attend to and copy a dominant model in an extractive foraging task. There was
319 no overall preference for group members to attend to the dominant females' demonstrations
320 more than the low-ranking models' demonstrations and no significant bias towards the dominant
321 females' versus the low ranking females' method was exhibited in the first method used on the
322 box by each individual, nor did any consistent bias emerge over the course of the ten test
323 sessions. When all sessions were collated, there was a significant effect of condition upon
324 likelihood of the dominant female's method being matched. This suggests a preference for the
325 pivot action over the push action, by comparison with which a model's rank had little enduring
326 effect upon the method adopted by group members.

327 This finding is consistent with an earlier experiment with captive capuchin monkeys
328 (Dindo et al., 2011) and findings of social attention in wild vervet monkeys which showed no
329 effect of rank upon levels of social attention received (Renevey, Bshary & van de Waal et al.,
330 2013). However it contrasts with reports of dominance-based biases in captive chimpanzees
331 (Horner et al., 2010; Kendal et al., 2015, although see Watson et al. 2017). It is possible, and not
332 implausible, that artificial social groupings could have influenced the captive studies; for
333 example, animals that have to remain in close proximity to all group mates may exhibit different
334 attentional biases compared to those living in their natural, fission-fusion state (Goodall, 1986;
335 Murray, Mane & Pusey, 2007). There may also be different perceptions of others' success (or
336 different levels of ability to judge success) between species. It has been shown that wild
337 dominant female chimpanzees are able to acquire higher quality resources than lower ranking
338 females and, as such, may achieve higher reproductive success (Pusey, Williams & Goodall,
339 1997). By contrast this does not always appear to be the case for female monkeys in the vervet

340 populations sampled thus far (Cheney, Lee & Seyfarth, 1981; Cheney & Seyfarth, 1987;
341 Wrangham, 1981). Therefore whilst for chimpanzees dominance might be a proxy for judging
342 the success of potential models, and thus invite a bias towards copying these individuals, this
343 may not be the case in vervet monkeys. This would then limit the adaptive value of copying a
344 dominant female. Indeed, vervet monkeys have already been shown to copy female, but not
345 male, models in extractive foraging tasks (van de Waal et al., 2010), ostensibly because females
346 are the philopatric sex and thus most knowledgeable about the local environment. Therefore,
347 females of all ranks may have similar and relevant local knowledge. The preference for the pivot
348 method almost exclusively in groups where it was modelled and the preferences for the push
349 method shown in the one-model group suggest that the models did influence individuals'
350 learning, but there appeared to be no enduring effect of the models' ranks upon method chosen.

351 Though there was no overall bias for group members to attend to, or copy, particular
352 models based upon the model's rank, there were biases in both attention and behaviour based
353 upon individual level variables and the observer's relationship with the model. Chance (1967)
354 suggested that individuals should attend more to higher-ranked individuals than lower-ranked
355 individuals, but this was not found in the current study. Instead the rank of the observers
356 significantly affected the demonstrations they observed by females of different rank; higher-
357 ranking individuals attended to more demonstrations by the dominant female than did lower-
358 ranking individuals. This effect of rank was also shown in the test phase where high-ranking
359 females were more likely to match the dominant than low-ranking females. It may be that all
360 individuals have a preference to attend to, and match the behaviour of, the dominant female, but
361 this can only be expressed in higher-ranking monkeys who may be more tolerated in proximity
362 to the dominant female (e.g. Seyfarth, 1977). However, we suggest that kinship may play a role

363 in this finding. Whilst kinship was not a significant predictor of method used, rank is maternally
364 determined in vervet monkeys (Cheney & Seyfarth, 1990) and thus can serve as an indicator for
365 kinship in females and juveniles. Indeed, it may be possible that in our study, rank was a better
366 predictor of kinship than our kinship variable. Since genetic data were not available, kinship was
367 recorded only for direct offspring born since the monkeys were habituated and reliably identified
368 five years ago; sibling relationships between adult females were unknown and could not be
369 included in our measure. However, given that sisters are usually adjacent in rank in vervet
370 monkeys (Cheney & Seyfarth, 1990), the rank variable likely captured these relationships. The
371 low ranking models' kin watched more of her demonstrations than the kin of the dominant model
372 (but not non-kin overall). Therefore, it may be that the tendency of high-ranked individuals to
373 preferentially attend to and copy the behaviour of the dominant female reflects a kinship bias to
374 some extent. Previously only infants have been shown to exhibit a kinship bias in social learning
375 in vervet monkeys (van de Waal et al., 2014). However, to confirm that a kinship bias goes
376 beyond infancy in vervet monkey social learning, more complete data on relatedness are
377 required.

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

384 Previous research found adult male vervet monkeys to be extraordinarily receptive to the
385 preferences of their new group following dispersal (van de Waal et al., 2013), showing a strong

386 tendency to adopt their new group's food colour preference. There has been considerable debate
387 about alternative explanations for such apparent conformity in this outcome and related findings
388 in birds (Aplin et al., 2015; van Leeuwen, Kendal, Tennie & Haun, 2015; van Leeuwen, Acerbi,
389 Kendal, Tennie, & Haun, 2016; Aplin et al. 2016; Whiten & van de Waal, 2016; Acerbi, van
390 Leeuwen, Haun & Tennie, 2016). A further study on vervet monkeys found stable
391 experimentally seeded dietary preferences in low-ranking females after group fission which,
392 along with the initial study, could be explained by a bias to either copy the dominant or conform
393 to the preferences of the origin group (van de Waal, van Schaik and Whiten, in press). As in the
394 current study we found no group level preference emerging for the method demonstrated by the
395 dominant female in each group, the latter explanation for the low-ranking females' behaviour
396 appears more parsimonious. Only four males who had transferred from another group managed
397 to open the box during the test phases of the present study and while all showed a preference for
398 the dominant models' method, this is too small a number from which to draw meaningful
399 conclusions.

400 This study also revealed a significant effect of age in attention to the models; juveniles
401 were more likely than adults to attend to the demonstrations of the dominant models. When
402 juveniles alone were analysed, they did not show a significant preference to attend to the
403 dominant models more than the low-ranking models. Therefore it seems likely that the observed
404 age differences in attention stem from a higher tolerance for juveniles in dominant models. Some
405 primate species show high levels of tolerance towards even unrelated juveniles (Hirata & Celli,
406 2003; Boinski et al., 2003) and thus it seems likely that the juveniles were able to be in closer
407 proximity to the dominant females' demonstrations than were adults. However, age was not a
408 significant predictor of method used in the test phase.

410 The behaviour of the models during the unrestrained test phase provided interesting
411 findings; whereas all three dominant models showed a sustained preference for their trained
412 action, none of the low-ranking models in the two-model groups did (although the low-ranking
413 model from BD was able to open the box only once). The finding that neither method was more
414 efficient than the other suggests that these models likely switched method after viewing others
415 performing the alternative action. However, since the number of observations of the other model
416 during the demonstration phase was not a good predictor of method used, it is likely that the low-
417 ranking models were influenced by other group members as well. The sole, low-ranking model
418 in KB maintained her preference for her trained, push action in the absence of a dominant model
419 performing the alternative action. This is consistent with findings that dominant individuals seem
420 to take less account of social information than lower-ranking individuals (Kendal et al., 2015;
421 Pongrácz, Vida, Bánhegyi & Miklósi, 2008), perhaps due to their ability to monopolise resources
422 and scrounge from others. The group level differences in models' adherence to their trained
423 method may have been due to individual variation or group level differences in social
424 relationships, as has been shown in our three experimental groups of vervet monkeys (Borgeaud,
425 Sosa, Bshary, Sueur & van de Waal, 2016), and thus potentially in social information use.

426 Finally, this study revealed a preference for one of the two alternative actions (pivot), an
427 issue that often arises when using multiple-option artificial fruits to test for social learning
428 (Claidière, et al., 2013; Tennie, Call & Tomasello, 2006). However, this preference was only
429 exhibited when the pivot was modelled (no preference was found in the control group), thus
430 suggesting that some actions may lend themselves more to social learning than others. This has
431 also been suggested for certain innovations in orangutans (van Schaik, van Noordwijk & Wich,

432 2006). The pivot method involved a bigger range of motion and was noisier than the more
433 discrete push action. We suggest that such differences in ease of transmission should be
434 investigated further as they may play a significant role in which behaviours are preferred and
435 likely to become traditions.

436 Some limitations in this initial attempt to address the issue of model bias experimentally
437 in the wild should be acknowledged. Our sample size was relatively small due to the low number
438 of individuals from each group who opened the box during the test phase. This should be borne
439 in mind particularly when interpreting the class-level biases revealed here, such as effects of age
440 and sex, as they may have been influenced by number and sex of individuals within the group.
441 Further investigation is required to assess the strength of these biases and whether they are seen
442 in other contexts. As in other studies of a similar nature (Lonsdorf et al., 2016), the open nature
443 of the test phase meant that some high-ranking individuals were able to monopolise the boxes
444 first, so monkeys would be likely to see more demonstrations from higher-ranking individuals
445 during the test phase than from lower-ranking individuals. Although we did incorporate the
446 number of pushes and pivots seen at this phase into our analyses and found them not to be
447 significant predictors, it is still possible that an individual other than a demonstrator may have
448 influenced the choice of method of the other monkeys.

449 To conclude, this experiment revealed that several biases appear to exist in vervet
450 monkey social attention and social learning based upon individual characteristics, such as rank,
451 sex and age, and the relationship between observer and model. Overall though, no group-wide
452 bias was found for individuals to copy a model of higher rank. These results highlight the
453 complex nature of social learning and social attention in primates, including factors such as
454 tolerance, the ease with which a certain behaviour lends itself to copying, and a multitude of

455 individual-level biases. Further research is needed to fully understand these biases and how they
456 might contribute to the spread of behaviours in wild primates.

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593

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609 **Appendix**

610 Table 1: Allocation of groups to conditions, group sizes and number of individuals who opened
 611 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

612 Numbers of individuals in the groups (excluding infants) are given as they were on the first day
 613 of the experiment, (in parentheses) numbers of adult males (AM), adult females (AF) & juveniles

614 (J). The number of individuals from each group who opened the box during the test phase are
 615 listed with a description of each condition.

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622 Table 2: Factors affecting the probability of individuals observing a demonstration from within 5
 623 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	-

624 Analyses are separated for demonstrations by the dominant and low-ranking female models.
 625 Significant predictors are presented in **bold**. Only significant interactions were included in the
 626 full model.

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

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

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636 Significant predictors are presented in **bold**. The final model was significantly different from the
 637 null model containing only the random effects of Test and Individual trial nested within ID
 638 (likelihood ratio test: $\chi^2=12.2$, $P=0.016$).

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649 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	-

650 Significant predictors are presented in **bold**. Only significant interactions were included in the
651 full model.

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

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

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664 The full model differed significantly from the null model with only the random effect of trial
665 number nested within ID ($\chi^2= 12.3, P=0.002$).

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678 Table 6: Factors affecting the probability that individuals matched the method of their dominant
679 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	-

680 Significant predictors are presented in **bold**. The full model was significantly different from the

681 null model containing only the random effects of individual trial nested within ID (likelihood

682 ratio test: $\chi^2= 35.2, P < 0.001$).

683 Table A1: All demonstrations watched by all individuals during the demonstration phase, with participation and associated individual
 684 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	Lhassa	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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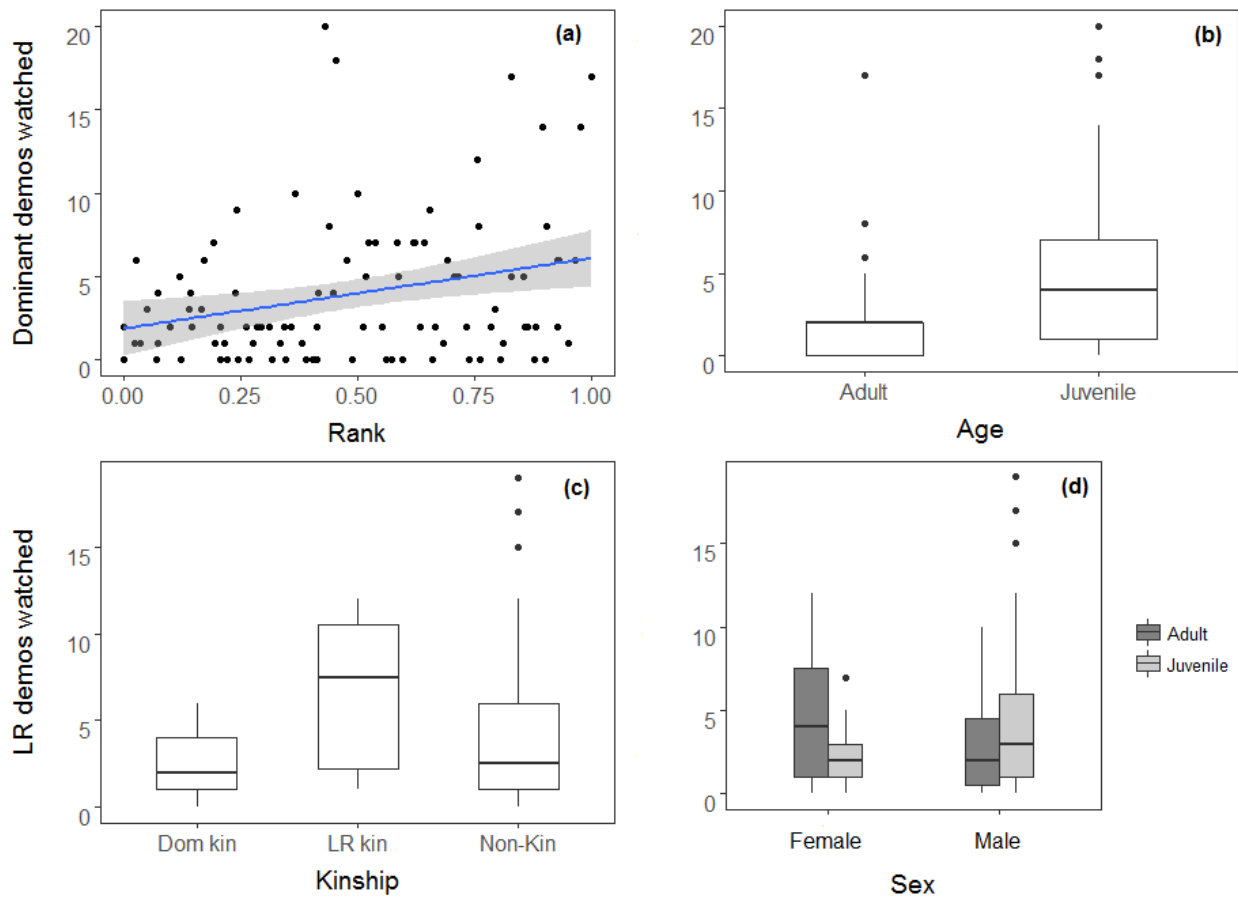
692 Table A2: All openings made by all individuals across the five groups using each method with all individual variables

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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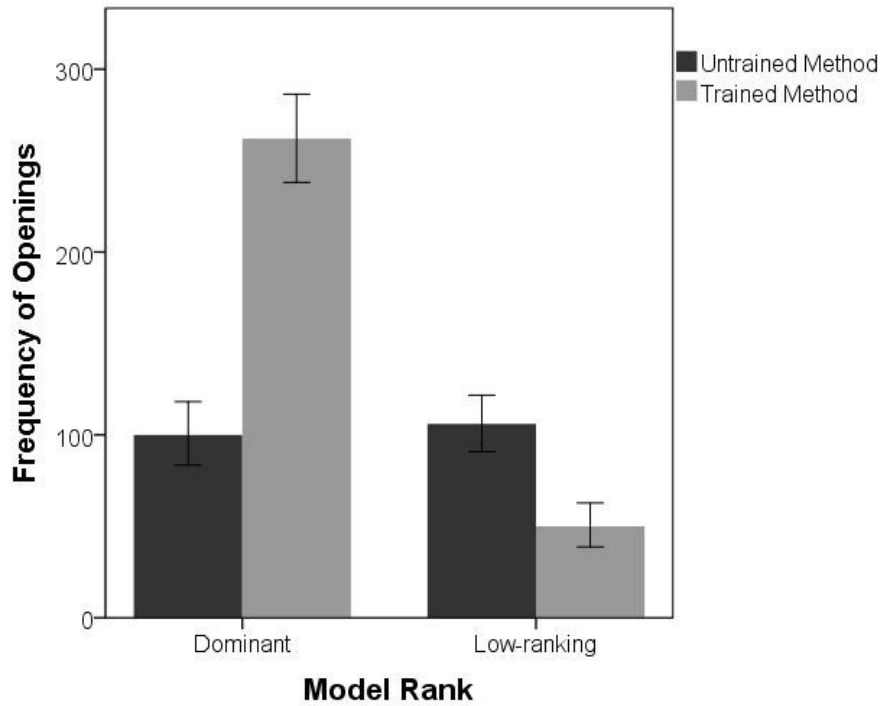
694 **Figures**



695

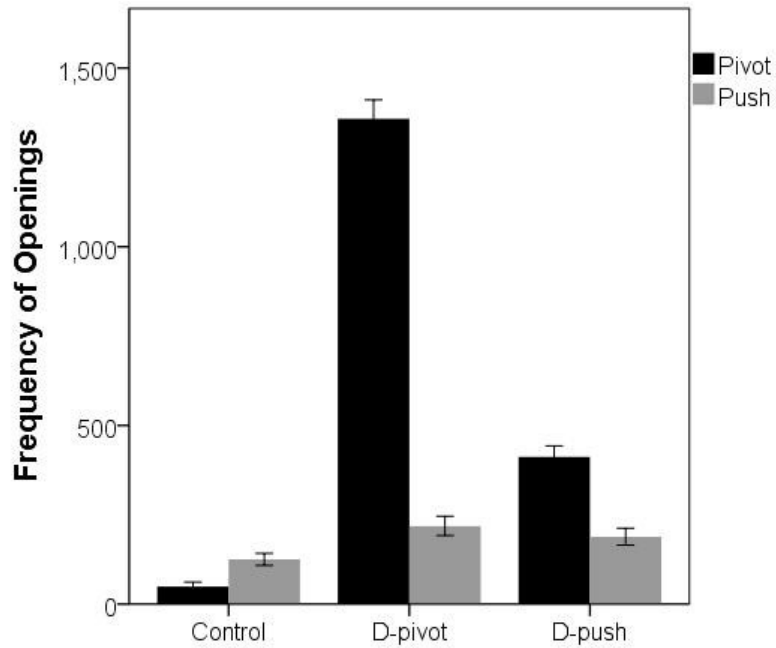
696 Figure 1: The average number of demonstrations for which observers were watching within 5
 697 metres of the (a & b) dominant demonstrators and (c & d) low-ranking demonstrators, as shown
 698 by the observer's (a) rank, (b) age, (c) kinship to the models (d) sex and age. Shaded area
 699 represents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

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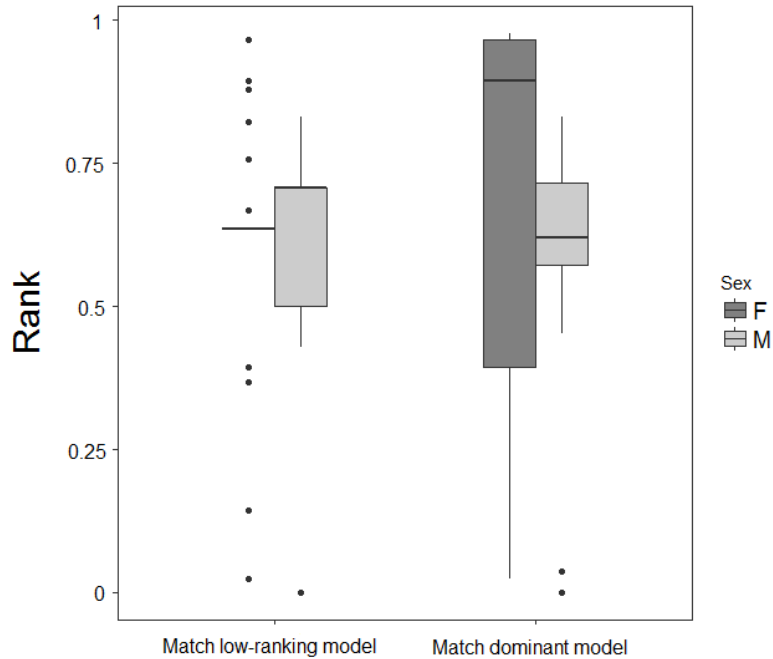
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703 Figure 2: The total frequency of box openings in which the dominant and low-ranking models
 704 used their trained and untrained methods from the three two-model groups. Error bars represent
 705 95% confidence intervals.



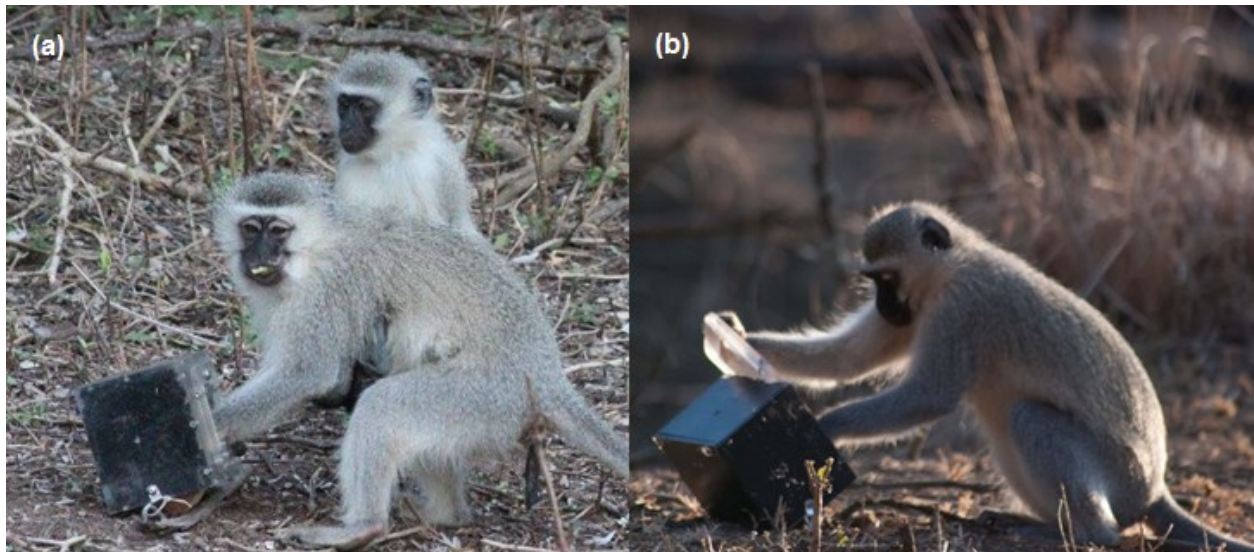
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707 Figure 3: Total frequency of openings across the two-model and control conditions which used
708 the pivot (black) or the push method (grey) throughout the 10 tests. Error bars represent 95%
709 confidence intervals.



710

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



713

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

715 Image credit: Jennifer Botting & P. Stoebener.