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Diffusion of Novel Foraging Behaviour in Amazon Parrots through Social Learning

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## 26 Abstract

27 While social learning has been demonstrated in species across many taxa, the role it plays in  
28 everyday foraging decisions is not well understood. Investigating social learning during  
29 foraging could shed light on the emergence of cultural variation in different groups. We used  
30 an open diffusion experiment to examine the spread of a novel foraging technique in captive  
31 Amazon parrots. Three groups were tested using a two-action foraging box, including  
32 experimental groups exposed to demonstrators using different techniques and control birds.  
33 We also examined the influence of agonistic and pilfering behaviour on task acquisition. We  
34 found evidence of social learning: more experimental birds than control birds interacted with  
35 and opened the box. The birds were, however, no more likely to use the demonstrated  
36 technique than the non-demonstrated one, making local or stimulus enhancement the most  
37 likely mechanism. Exhibiting aggression was positively correlated with box opening, whilst  
38 receiving aggression did not reduce motivation to engage with the box, indicating that  
39 willingness to defend access to the box was important in task acquisition. Pilfering food and  
40 success in opening the box were also positively correlated; however, having food pilfered did  
41 not affect victims' motivation to interact with the box. In a group context, pilfering may  
42 promote learning of new foraging opportunities. Although previous studies have  
43 demonstrated that psittacines are capable of imitation, in this naturalistic set-up there was no  
44 evidence that parrots copied the demonstrated opening technique. Foraging behaviour in wild  
45 populations of Amazons could therefore be facilitated by low-fidelity social learning  
46 mechanisms.

47

48 *Keywords:* social learning, open diffusion, two-action test, parrots, *Amazona amazonica*

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50

51 Discoveries of locale-specific, or group-typical, behavioural patterns among wild  
52 populations of animals have been the source of fascination and debate for several decades.  
53 Often referred to as ‘cultural variations’ or ‘traditions,’ regional variations among wild  
54 populations have been found in a diversity of taxa, including mammalian, avian, and fish  
55 species (Laland and Hoppitt 2003; Swaddle et al. 2005; van de Waal et al. 2013; van Schaik  
56 et al. 2003; Witte and Ryan, 2002; Yurk et al. 2002). They are considered significant because  
57 of the insight they may provide into the evolution of culture. These discoveries have led to  
58 speculations about the parallels that may exist between the development of animal ‘traditions’  
59 and the emergence of human culture (Galef 1992; Heyes 1993; Laland and Hoppitt 2003).  
60 By conducting research aimed at understanding the spread of novel behaviour in animals, we  
61 may gain insight into the cognitive and socio-ecological processes that supported and shaped  
62 the evolution of human culture (Galef 1992; Laland and Hoppitt 2003).

63 Social learning provides a way of transmitting a novel behaviour, such as an effective  
64 foraging technique, that is more rapid than genetic transmission and can be more efficient  
65 than individual trial-and-error learning. Social learning can occur via a variety of different  
66 mechanisms, and may involve high or low fidelity copying; in the former, the details of an  
67 action are precisely replicated, while in the latter behaviour is replicated with some  
68 modification or variation in the action sequence (Lewis and Laland 2012; Whiten and Ham  
69 1992). Identifying which social learning mechanisms are available to (and used by) different  
70 species has important consequences for whether new behaviours are faithfully transmitted  
71 and maintained within a population. The development and maintenance of human culture is  
72 believed by many to rely upon high-fidelity social learning underpinned by imitation, or  
73 ‘action learning’ (seen when individuals copy motor patterns they have observed) (Legare  
74 and Nielson 2015; Tennie et al. 2009; Whiten and Mesoudi 2008; Whiten et al. 2009). This is  
75 distinct from mechanisms that may result in low-fidelity transmission, such as stimulus or

76 local enhancement, which occurs when an observer's attention is drawn to a particular area or  
77 object due to another individual's presence. This increases their chances of learning  
78 something valuable about that object or area, such as the availability of food in a specific  
79 location (Caldwell and Whiten 2002). An observer may also gain information about the  
80 function or affordances of an object as a result of another's actions, referred to as emulation  
81 (Whiten et al., 2004). In such cases, an observer achieves the same goal as the observed  
82 individual, but may do so by engaging in a different behaviour (Caldwell and Whiten 2002;  
83 Heyes and Saggerson 2002; Tennie et al. 2006). In order to fully understand how animal  
84 traditions emerge and are sustained, it is necessary to identify which types of social learning  
85 mechanisms are involved in the acquisition and spread of novel behaviour.

86         The two-action test is one of the most widely used paradigms in the experimental  
87 investigation of social learning mechanisms (e.g. Aplin et al. 2013, 2015; Campbell et al.  
88 1999; Dindo et al. 2008; Galef et al. 1986; Huber et al. 2001; Whiten et al. 2005). In this  
89 paradigm, subjects are presented with a baited apparatus containing a manipulandum that can  
90 be operated using two alternative methods (e.g. pull or push) to gain access to food (Dindo et  
91 al. 2009). If subjects are found to use the method they observed being employed by  
92 demonstrators significantly more than the alternate (non-observed method), it would suggest  
93 that they learned something about the technique, either by imitating the actions used or  
94 emulating their effects.

95         Testing demonstrator-observer dyads on two-action foraging tasks has provided  
96 evidence of social learning in avian, primate, and reptile species. Evidence has been found of  
97 task acquisition by means of imitation or possible emulation learning (European starlings:  
98 Akins and Zentall 1998, Campbell et al. 1999; pigeons: Zentall et al. 1996; budgerigars:  
99 Heyes and Saggerson 2002; capuchins: Dindo et al. 2009; chimpanzees: Horner et al. 2006;  
100 bearded dragons: Kis et al. 2015; kea: Huber et al. 2001). However, while tightly controlled

101 dyadic tasks may reveal species' social learning capacities, this experimental approach does  
102 not reveal anything about the social factors that may influence learning processes within a  
103 natural foraging context. In many species, natural foraging parties involve several observers  
104 being simultaneously exposed to the same event, who can all then react to the demonstration  
105 and potentially become demonstrators themselves. Additionally, behaviours such as  
106 aggression or scrounging are highly relevant to the diffusion of novel foraging behaviour in a  
107 natural group context. Willingness to enter into aggressive encounters, for instance, may  
108 ensure sufficient exploration opportunity to acquire behaviour that was previously observed  
109 (Schnoell and Fichtel 2012). Further, gaining rewards from the actions of others (scrounging)  
110 may either inhibit social learning (Giraldeau and Lefebvre 1987) or help focus individuals'  
111 attention on demonstrators' actions (e.g., nut cracking behaviour in sub-adult chimpanzees;  
112 Inoue-Nakamura and Matsuzawa 1997). Experimental designs that provide conditions that  
113 more closely resemble species' natural social environment are therefore vital for  
114 understanding how different types of social learning may function in a more natural foraging  
115 context.

116         The open diffusion design, involving the simultaneous exposure of a group of naive  
117 subjects to trained conspecifics engaging in novel behaviour, has greater ecological validity  
118 than dyadic testing (Whiten and Mesoudi 2008), and has provided further evidence of high  
119 fidelity copying in chimpanzees and capuchins (Dindo et al. 2009; Whiten et al. 2005). Only  
120 a few studies have used two-action tests to investigate transmission of behaviour through  
121 open diffusion in birds (Aplin et al. 2013, 2015). We believe it is important to do so in order  
122 to adequately understand the transmission of behaviour in birds that are social foragers. This  
123 approach not only makes it possible to investigate the social learning mechanisms that are in  
124 operation, but also allows for investigation of various social factors that may influence  
125 behaviour acquisition in natural conditions. Studies of captive and wild tits reveal that

126 experimental birds were significantly more likely to use the solution demonstrated by trained  
127 birds than the alternate one (Aplin et al. 2013, 2015). Furthermore, the foraging techniques  
128 that were introduced into wild tit populations were found to be stable over two generations  
129 (Aplin et al. 2015). This suggests that high fidelity copying could have adaptive value for  
130 these birds.

131         The occurrence of group-specific behaviours in wild avian populations, along with  
132 experimental findings that provide evidence of social learning capacities in a range of birds,  
133 suggest that this group can make a significant contribution to the development of a broad  
134 comparative framework aimed at understanding the emergence of culture. In discussions of  
135 primate and avian cognitive convergence, parrots are often cited alongside corvids as  
136 examples of birds that possess high-level, ‘primate-like,’ cognition (Emery and Clayton  
137 2004; Emery et al. 2007; van Horik et al. 2012). Like primates and corvids, parrots are highly  
138 social, long lived, and have large relative brain sizes (Seibert 2006; Shultz and Dunbar 2010),  
139 yet they remain comparatively understudied in most aspects of cognition and behaviour; only  
140 a small proportion of more than 350 extant parrot species have been the subject of any field  
141 or laboratory research.

142         Parrots are widely known for their capacity to engage in vocal learning, a trait that  
143 relies on social learning mechanisms. Vocal imitation has been documented in various  
144 species, such African greys, yellow-naped Amazons, budgerigars, and orange-fronted  
145 conures (Balsby et al. 2012; Bradbury 2004; Cruickshank et al.1993; Hile et al. 2000;  
146 Pepperberg 2006; Rowley and Chapman 1986; Wright 1996). However, evidence for  
147 imitation of motor patterns, such as those associated with foraging, is less abundant. Moore  
148 (1992) reports imitation of both words and actions by a captive African grey housed in a  
149 laboratory by itself. After regular exposure to a keeper engaging in repetitive word-behaviour  
150 sequences, the bird began to replicate these vocal and motor patterns in the absence of social

151 or food rewards. In the foraging domain, kea have been found to be capable of learning  
152 through stimulus enhancement and likely emulation in a dyadic transmission experiment that  
153 required subjects to manipulate a series of locking devices on a baited apparatus (Huber et al.  
154 2001). Experimental birds showed significantly shorter latency to approach locking devices,  
155 greater persistence in manipulation of the apparatus, and greater success in opening the locks,  
156 than control birds. Evidence of imitative capacities have been found in budgerigars (Dawson  
157 and Foss 1965; Heyes and Saggerson 2002). Heyes and Saggerson tested subjects using a  
158 two-action/two-object test. They were presented with baited boxes containing lids with two  
159 holes; holes were obstructed by distinctly coloured plugs, which could be removed by pulling  
160 or pushing. Subjects were found to remove the same coloured plug in the same manner as  
161 observed individuals, revealing evidence for imitation. A recent study with Goffin cockatoos  
162 showed that whilst they failed to learn to obtain food through novel tool use in a ghost control  
163 condition (whereby an observer is exposed to the movement of a manipulandum in the  
164 absence of a demonstrator), half the birds succeeded when observing a trained conspecific  
165 demonstrator. The tool-using techniques of demonstrators and observers, however, varied  
166 greatly, indicating that both stimulus enhancement and emulation were the most likely  
167 mechanisms underlying the successful performance (Auersperg et al. 2014). Psittacines seem  
168 to have the capacity to acquire novel motor and foraging behaviour from the observation of  
169 others; however, it is unknown what type of social learning occurs in the diffusion of a novel  
170 foraging technique in a naturalistic group setting.

171         The present study aimed to address this issue by investigating the transmission of a  
172 novel foraging technique in captive orange-winged Amazon (OWA) parrots (*Amazona*  
173 *amazonica*) using an open diffusion design. A Neotropical species, OWAs demonstrate  
174 characteristics typical of most parrots, including being highly social and having a long life  
175 history, a large relative brain size, and a monogamous breeding system (Hoppe 1992). In the

176 wild, OWAs rely on fruits and seeds that vary spatially and temporally and form foraging  
177 parties in order to locate food sources (Bonadie and Bacon 2000). They are also commonly  
178 regarded as agricultural pests because they tend to exploit novel food sources as their natural  
179 ones are replaced with farm land (Hoppe 1992). OWAs have vocal mimicry abilities (Hoppe  
180 1992) and their socio-ecology indicates that it is likely that learning to exploit novel foraging  
181 opportunities by observation of others would be highly adaptive in this species. It would  
182 likely provide a more efficient way of learning about suitable food sources (e.g., location,  
183 types, extraction methods) than individual learning.

184         We tested social transmission of foraging behaviour in OWAs using a two-action  
185 foraging box based on the design used by Dindo and colleagues (2008, 2009). Two OWA  
186 groups were exposed to a group member who was trained to open the apparatus, each using a  
187 different technique (slide or pull the door). As a third group of OWAs was not available to  
188 use as a control group, we used one OWA group as both a control and an experimental group  
189 (control trials were completed prior to experimental trials). If stimulus or local enhancement  
190 occurred, we would expect birds to approach and make physical contact with the foraging  
191 box more often in experimental trials (after seeing the trained demonstrator interact with it),  
192 than during control trials.

193         We could not use the OWA amazon control group to assess whether observing a  
194 skilled demonstrator increased the likelihood of an animal solving the task because the  
195 apparatus was locked during the control trials (locks were invisible to the birds) to ensure that  
196 the first exposure that group had to solving the novel foraging task would be as a result of the  
197 trained demonstrator's behaviour during experimental trials. We therefore used a group of  
198 blue-fronted Amazons (BFA; *Amazona aestiva*) to assess how likely the box was to be  
199 successfully opened in the absence of a trained demonstrator. BFAs are closely related to  
200 OWAs, and share various socio-ecological traits with OWAs (including habitat, diet, and

201 social composition; Hoppe 1992). If imitation, emulation or individual learning following  
202 stimulus enhancement occurred after observation of a trained demonstrator we expected more  
203 birds in the OWA experimental groups to solve the task than the BFA group.

204 We then investigated whether experimental subjects that successfully opened the box  
205 showed evidence of imitation of the door-opening method (slide or pull) that they had  
206 observed or if they used the same body parts used by the demonstrator to manipulate the door  
207 (beak or beak and foot). If imitation was occurring, then we expected the method and body  
208 part to match that of the trained demonstrator the birds had observed. If birds discovered and  
209 used both methods, we aimed to examine whether they were more likely to conform to the  
210 method of the trained demonstrator (using the same action as observed) when the  
211 demonstrator was present in the immediate vicinity of the foraging box. Conformity to an  
212 observed action, even when an alternative is discovered has been found in a number of  
213 species (chimpanzees: Whiten et al. 2005; vervet monkeys: van de Waal, Claidière et al.  
214 2013; tits: Aplin et al. 2015). Finally, we assessed whether subject engagement with or  
215 acquisition of the task was influenced by aggression or ‘pilfering’ (scrounging behaviour  
216 consisting of taking food from the apparatus after another bird opened the apparatus or taking  
217 a food reward from another bird’s physical possession). Whilst scrounging has previously  
218 been shown to both inhibit (Giraldeau and Lefebvre 1987) and facilitate (Inoue-Nakamura  
219 and Matsuzawa 1997) learning in those who gain food in this manner, we predicted pilfering  
220 and aggression may decrease the victims’ motivation to engage with the box.

## 221 **Methods**

### 222 **Study groups**

223 Research was conducted at Lincolnshire Wildlife Park, UK: a parrot sanctuary and  
224 licensed zoo. Parrots were voluntarily surrendered by owners who were unable to continue to  
225 care for them. Aviary group composition varied regularly at the sanctuary as newly

226 surrendered parrots joined groups and thus it is highly unlikely that any individuals within a  
227 single group were related. We used three independent groups of captive parrots (two OWA  
228 groups, one BFA group); each group's composition was kept stable throughout data  
229 collection periods. One group of OWAs ( $N = 22$ ) served as the 'slide' experimental group,  
230 and the other OWA group ( $N = 15$ ) served as both the 'pull' experimental group and the  
231 OWA control group. The BFAs ( $N = 20$ ) were used in order to assess the likelihood that birds  
232 would solve the task in the absence of a trained demonstrator (a third group was necessary for  
233 this assessment as the box door was kept locked during OWA control trials and a third group  
234 of OWAs were not available). We collected data on the slide OWA group in July 2012 and  
235 both the pull OWA group and the BFA group in August 2013.

236 All subjects were believed to be adults, although their exact ages were unknown. Only  
237 the sexes of the OWA slide group were known (9 females and 14 males) due to their  
238 participation in an observational study on social behaviour. All subjects were identified by  
239 coloured leg rings.

240 Each of the three groups of parrots was housed in its own outdoor aviary (2.3 (h) x 2.4  
241 (w) x 5.5 m (l)) containing natural wood perches. The enclosures contained covered areas that  
242 provided shelter from wind and rain and could be freely accessed by birds. The enclosure  
243 OWAs were housed in had an indoor training compartment (1.2 (h) x 1.8 (w) x 2.2 m (l)); the  
244 OWA slide group were housed in that enclosure in 2012 and the OWA pull group were  
245 housed in it in 2013. Food and water were provided ad libitum. Subjects' diets consisted of  
246 approximately 70% fresh fruit (fed in afternoon after testing) and 30% seed (fed in morning  
247 after testing).

#### 248 **Experimental box**

249 The two-action task consisted of a baited opaque apparatus that could be opened using  
250 two alternate methods. A wooden box measuring 11.4 (h) x 30.5(w) x 20.3 cm (l) was used.

251 The back of the box contained an opening (9.5 (w) x 10cm (l)) through which food could be  
252 inserted, and the front contained a door (9 (w) x 9 cm (l)) with a handle (4 (h) x 1.75 (w) x  
253 1.75 cm(l)) that could be opened by either pulling it or by sliding it (see Fig. 1).

#### 254 **Procedure**

255 **Training.** Habituation to three cameras mounted on tripods (see Fig. 2), as well as an  
256 observing researcher occurred for two 30-minute periods daily in the two weeks prior to test  
257 trials starting. We selected one bird in each experimental group to be a demonstrator; the  
258 birds selected met the following criteria: they showed high levels of food motivation, social  
259 tolerance, willingness to remain in the training compartment and low levels of neophobia.  
260 We used a successive approximation procedure to train demonstrators to perform the task.  
261 Training took place in the training compartment, out of sight of other individuals. The  
262 foraging box was mounted on the outside of a wire cage (64.8 (h) x 53.3 (w) x 45.7 cm (l)). A  
263 T-perch mounted on a base was placed in front of the box door, allowing demonstrators to  
264 open the door while standing on the perch. During initial training, the alternate method was  
265 locked (locking mechanism was invisible to the birds). The demonstrators were required to  
266 successfully open the box using the desired method (slide or pull) in 10 consecutive trials  
267 with the alternate door locked; this prevented the demonstrators from accidentally  
268 discovering the alternate solution before fully mastering the desired method. They were then  
269 required to complete a further 10 consecutive trials using the desired method, with the  
270 alternate method unlocked.

271 **Testing.** Set up was the same for control and experimental trials. The foraging box  
272 was placed in the centre of the 'target zone' that extended 30.5 cm from all sides of the box.  
273 Target zone corners were marked with coloured plastic zip-ties or electrical tape so that the  
274 boundaries were clearly visible. The box was visually accessible to subjects perched outside  
275 the target zone. A U-perch (23.5 (w) x 43.8 cm (l)) was mounted underneath the box (see

276 Fig. 2). All trials were videoed from three angles using two Panasonic SDRH40 cameras and  
277 one Panasonic HCW570 camera (see Fig. 2). Trials began when the foraging box was  
278 mounted and baited inside the aviary target zone. Two experimenters stood outside the aviary  
279 and provided real time commentary of behaviour in the target zone onto the video recordings  
280 (including identifying which individuals entered and exited the target zone and made contact  
281 with the box, and describing the type of contact made with the box). One of the  
282 experimenters re-set and re-baited the box after every successful opening. The box door was  
283 also re-set after unsuccessful attempts (see Table 1). Peanuts and grapes, favoured food items,  
284 were used as rewards for all trials. The box was baited with one food item at a time. Birds  
285 could obtain a food reward by flying or climbing into the target zone and opening the box  
286 door (using a slide or pull action). As group members were simultaneously exposed to the  
287 box, it was also possible for birds to obtain food items by scrounging - either pilfering  
288 (retrieving food from the box after the door was opened by another bird or taking it from  
289 another bird's physical possession) or by retrieving food from the ground that was dropped  
290 by another bird.

291 Twelve peanuts and 12 grape halves were available in each experimental trial. Trials  
292 ended when (i) all 24 pieces of food were successfully retrieved from the foraging box or (ii)  
293 if 20 min elapsed since the last interaction with the box. In cases in which there was no  
294 interaction with the box at all, trials ended after 30 min. We ensured both experimental  
295 groups retrieved the same number of pieces of food from the box (216 pieces) across all their  
296 trials. It took the slide experimental group a total of nine trials and the pull experimental  
297 group a total of 13 trials to retrieve all pieces of food.

298 A total of nine control trials were run on both the OWA pull group and the BFAs. As  
299 experimental trials had to be conducted on the OWAs after control trials were completed, the  
300 foraging box door was kept locked for the OWA control trials. The locking device was

301 located on the inside of the box and was not visible to subjects; thus, the box's outward  
302 appearance was the same in control and experimental trials. As no OWAs attempted to open  
303 the box in control trials they did not learn that the box was un-openable prior to their  
304 experimental trials. Performance of the OWAs in control and experimental trials were  
305 compared to assess whether stimulus or local enhancement occurred after observation of a  
306 trained demonstrator. During BFA control trials the box was unlocked, as it was in OWA  
307 experimental trials, thus comparison of BFA and OWA experimental trials enabled  
308 assessment of how observation of a trained demonstrator influenced the likelihood of  
309 successfully opening the box. All control trials lasted 30 min.

310 All trials (experimental and control) were performed in the morning (between 7:30  
311 and 9:00 am) and the afternoon (between 4:30 and 6:00 pm) when the zoo was closed to  
312 visitors. A maximum of two trials (one in the morning; one in the afternoon) were performed  
313 per day. For the OWA pull group experimental trials started the day after the last control trial.

#### 314 **Video coding**

315 The Observer XT 10 program was used to code recorded subject behaviour that occurred  
316 within the target zone (see Table 1). Methods used for unsuccessful attempts that included  
317 both slide and pull actions were coded as 'slide-pull.' Methods used for successful attempts  
318 that included both slide and pull actions were coded according to whether subjects retrieved  
319 food through the opening that resulted from a pull or slide action. Subject attempts were  
320 coded as separate behaviours if a minimum of 3 s elapsed between behaviours. This rule also  
321 applied to agonistic behaviours involving the same individuals. In cases of unidirectional or  
322 mutual aggression (and only in these cases), subjects were considered observers if they were  
323 not in physical contact with the box door at the start of the aggression; any bird (trained or  
324 non-trained) that was in physical contact with the box door was considered a demonstrator.

325 To test the accuracy of video coding, a second independent individual blind to the  
326 experimental group coded a random sample of 6 (2 control and 4 experimental) of the 38  
327 trials (16%) with the full coding scheme (Table 1) in Observer XT, and a Cohen's kappa test  
328 was run to assess inter-observer reliability. The mean kappa score was 89.33, indicating a  
329 high level of agreement between coders and that the videos had been coded accurately.

### 330 **Data Analyses**

331 Analyses were conducted using data from nine OWA control trials and nine  
332 experimental trials from the OWA slide group. The OWA pull group completed 13  
333 experimental trials, but only 11 were analysed; in the two excluded trials no bird (neither  
334 trained demonstrator nor subject) entered the target zone. The IBM SPSS Statistics 21  
335 program was used to run the majority of analyses, which were nonparametric due to small  
336 sample sizes and because data were not normally distributed. Our analyses focussed on the  
337 behaviour of subjects which were defined as all birds in the aviary except the trained  
338 demonstrator. We used two-tailed Fisher's exact tests to compare the proportions of subjects  
339 that (i) entered the target zone and (ii) that made contact with the box in the OWA slide  
340 experimental group and the OWA control group. As the OWA control group also served as  
341 the pull experimental group, we also assessed whether they showed significantly more  
342 interest in the box during experimental trials than control trials; McNemar's tests were used  
343 to compare proportions of birds that entered the target zone and that made contact with the  
344 box in the two conditions. Focussing on the subjects that successfully opened the box, we  
345 used a two-tailed Wilcoxon signed-ranks test and a binomial test to assess if subjects used  
346 door opening methods that matched those of their trained demonstrator. We used two-tailed  
347 Wilcoxon signed-ranks tests to compare the number of subjects' attempts 1 min before and 1  
348 min after being victims of unidirectional aggression or pilfering. Kendall's tau tests were run  
349 to investigate possible relationships between attempts and agonistic or pilfering behaviour

350 across trials (for both victims and aggressors). As recommended by Field (2009), we report  $r$   
351 values as measures of effect sizes. We report Hodges-Lehmann and exact binomial 95%  
352 confidence intervals (CIs). A web-based calculator was used to calculate exact binomial CIs  
353 (Pezzullo 2009).

354 We also used a generalized linear mixed-effects model (GLMM) with a binomial  
355 error structure and a logit link function to investigate whether the subject door-opening  
356 method ( $N = 278$  full opens by non-trained birds) matched their respective trained  
357 demonstrator method or not (binary dependent variable) was influenced by the presence or  
358 absence (0/1) of the trained demonstrator in the target zone (categorical explanatory  
359 variable). We ran the GLMM in R Version 3.1 (R Core Team 2014) and used the package  
360 lme4 (Bates et al. 2015) to run random intercepts models. In order to control for  
361 pseudoreplication; subject ID ( $N = 10$ ) and trial number ( $N = 16$ ) were entered as random  
362 factors to account for multiple data points being taken from each individual and each trial. To  
363 assess the significance of the explanatory variable, we compared the model containing this  
364 variable with a null model, comprising only the intercept and random effects, using a  
365 likelihood ratio test.

## 366 Results

### 367 Trained demonstrator performance

368 Both of the trained demonstrators consistently used the trained method to open the  
369 foraging box during test trials, although overall the slide trained demonstrator provided more  
370 demonstrations than the pull trained demonstrator, particularly in the first two trials (see  
371 Table 2). All of the interactions with the box and successful opening attempts in the  
372 experimental groups occurred after demonstrations by the trained demonstrators (Table 3).

### 373 Is there evidence of local or stimulus enhancement?

374 To determine whether subjects' interest in the foraging box was influenced by  
375 exposure to trained demonstrators' successful manipulation of it, the number of OWAs that  
376 entered the target zone and made contact with the box in control and experimental trials were  
377 compared. Fisher's exact tests showed that significantly greater proportions of OWAs entered  
378 the target zone (20/22; proportion 0.91 with 95% confidence limits of .71 and .99) and made  
379 contact with the box (18/22; proportion .82 with 95% confidence limits of .60 and .95) in  
380 the experimental slide group than the proportions of birds that entered the target zone (3/16;  
381 proportion 0.19 with 95% confidence limits of .04 and .46;  $p < .001$ ) and made contact with  
382 the box (0/15; proportion 0.00 with 95% confidence limits of .00 and .22;  $p < .001$ ) in the  
383 OWA control group. OWAs ( $N=15$ ) that completed control trials, followed by experimental  
384 (pull) trials, also showed changes in their responses. McNemar's tests revealed there was a  
385 significant increase in the number of subjects that entered the target zone from control (3/16)  
386 to experimental trials (13/16;  $p = .039$ ), as well as a significant increase in the number of  
387 subjects that touched the box from control (0/15) to experimental trials (8/15;  $p = .008$ ). As  
388 can be seen in Figure 3, we found that as the frequency of trained demonstrator box door  
389 opens increased, as did the number of subjects that made contact with the box.

#### 390 **Comparison of box opens by OWA experimental birds and BFAs**

391 Seven slide experimental birds and three pull experimental birds successfully opened  
392 the box at least once (see Table 4). The total time it took for each successful bird to enter the  
393 target zone from the start of the first trial is listed in Table 5. The time that elapsed between  
394 subjects' first target zone entry and subjects' first box contact, and the time that elapsed  
395 between subjects' first box contact and first successful box open, can also be seen in Table 5.

396 As the box door was kept locked during the control trials the OWA pull group  
397 completed, we used a group of BFAs to assess the likelihood that subjects would open the  
398 box without exposure to a trained demonstrator. Similar to the OWA control trials, few BFAs

399 entered the target zone (8/20) and crucially whilst 10/37 experimental OWA subjects opened  
400 the box at least once, 0/20 BFAs opened the box and no OWA attempted to do so during the  
401 control trials. A total of three BFAs made contact with the box; only one made contact with  
402 the door handle with the tip of its beak, but did not manipulate the door in anyway.

### 403 **Did subjects imitate the door opening methods they observed?**

404         The methods used by subjects who solved the task, in all successful openings  
405 (including those where the food was pilfered from the bird that opened the box) were  
406 compared to methods used by their group's trained demonstrators to determine whether they  
407 matched. A two-tailed Wilcoxon signed-rank test showed that subjects that successfully  
408 opened the box ( $N=10$ ) did not use the demonstrated method ( $Mdn = 5.50$ ,  $IQR = 22$ )  
409 significantly more than the non-demonstrated method ( $Mdn = 5.50$ ;  $IQR = 40$ ),  $z = -0.36$ ,  $p =$   
410  $.720$ ,  $r = -.11$ , 95% Hodges-Lehmann CI  $[-3, 17.5]$  (see Fig. 4); six subjects used both  
411 methods to open it. As individuals may have developed a preference for the alternative  
412 method through individual learning during the course of the experiment, subjects' initial  
413 attempts were also analysed; a binomial test (0.5) showed that the number of OWAs whose  
414 first successful open matched the demonstrator's method (6/10) was not above that expected  
415 by chance ( $p = .754$ ).

416         In this open diffusion setting, non-trained birds became demonstrators once they  
417 successfully opened the box. As such, we tested whether birds were influenced by the last  
418 demonstration they were exposed to before their successful attempts (or first successful  
419 attempt if they produced a sequence of attempts without intervening demonstrations from  
420 others). A Wilcoxon signed-rank test for the 10 birds that succeeded in opening the box  
421 showed that the number of attempts that matched ( $Mdn = 4.50$ ,  $IQR = 17$ ) the most recently  
422 used method by any (trained and non-trained) demonstrator did not significantly differ from  
423 the number of non-matching attempts ( $Mdn = 8$ ;  $IQR = 28$ ),  $z = -1.13$ ,  $p = .258$ ,  $r = -.36$ , 95%

424 Hodges-Lehmann CI [-6, 1]. We also examined whether the door-opening method that was  
425 used during an individual's first successful door-opening attempt matched the method that  
426 had been most frequently used up to the point those first solves were made (including across  
427 all previous trials). A Binomial test (.50) showed that the number of birds that used the  
428 dominant technique (6/10) was not significantly greater than chance,  $p = .754$  (see Table 4).

429 We investigated whether subjects replicated their trained demonstrators' pattern of  
430 body part use when opening the box. The trained demonstrators interacted with the apparatus  
431 in different ways, the slide trained demonstrator used only his beak and the pull trained  
432 demonstrator used both his beak and a foot in the majority of successful attempts. In  
433 contrast, subjects in both groups showed a similarly high preference for beak-only opens (see  
434 Table 6). Across both groups the beak only was used in 99% of opens that used the slide  
435 method opens and 92% of pull method opens. There was no instance in which a bird used  
436 only its foot to open the box door.

437 We conducted a GLMM to assess if subjects were more likely to use the trained  
438 demonstrator's method of box opening when he was present in the target zone. The GLMM  
439 indicated that the trained demonstrator presence in the target zone during or shortly before a  
440 subject's attempt did not affect the likelihood of the subject using the box-opening method  
441 that matched that of the trained demonstrator ( $X^2(1) = 0.09, p = .761$ ).

#### 442 **Did aggression influence subjects' interactions with the box?**

443 As the presence of a food source that could be monopolized created a competitive  
444 social environment, we examined the role that aggression may have played in task  
445 acquisition. Agonistic behaviour was seen in the target zone in all slide experimental group  
446 trials and in 10 of 11 trials in the pull experimental group. Both groups displayed similar total  
447 instances of aggression (slide group  $N = 172$  agonistic events involving 15 individuals  
448 (including the trained demonstrator); pull group  $N = 178$  agonistic events involving seven

449 individuals (including the trained demonstrator); see Fig. 5); no aggression was observed in  
450 control groups. A total of 19 experimental subjects were the victims of unidirectional  
451 aggression, with each victim receiving aggression from an average of 2.74 birds ( $SD = 1.09$ ).

452 In order to determine whether subjects were less likely to make contact with the box  
453 immediately (up to 1 min) after being the victims of aggression, we focused on the 19  
454 subjects who received unidirectional aggression in the target zone (not including trained  
455 demonstrators or subjects that were in physical contact with the box at the start of the  
456 agonistic interaction). For each agonistic event, we calculated the number of victims'  
457 attempts to open the box (see Table 1: all categories were included except 'touch other part of  
458 box') 1 min before and 1 min after the aggression. For each victim ( $N=19$ ) we then took  
459 mean values across all instances where they received aggression. A Wilcoxon signed-rank  
460 test showed there was no significant difference between victims' mean number of contacts  
461 with the front of the box 1 min before the aggression ( $Mdn = 1.00$ ,  $IQR = 1.88$ ) and 1 min  
462 after the aggression ( $Mdn = 1.00$ ,  $IQR = 1.50$ ;  $z = -.18$ ,  $p = .859$ ,  $r = .04$ , 95% Hodges-  
463 Lehmann CI [-.25, .33]).

464 Although receiving aggression did not affect interactions with the box in the short  
465 term, we also examined whether the amount of aggression received was related to box  
466 interactions across trials. We focussed on subjects that were the victims of unidirectional  
467 aggression and/or touched any portion of the front of the box for this analysis. Only subjects  
468 that had data points for at least one of these two behaviours in seven trials or more were  
469 included in this analysis ( $N = 6$ ). We ran correlational analyses for each of these birds  
470 individually, and despite small sample sizes ( $N = \text{trials}$ ), Kendall's tau tests showed  
471 significant positive associations between the duration of unidirectional aggression received  
472 and the number of victims' attempts to interact with the front of the box for three birds (see  
473 Table 7). For those three OWAs, making more attempts to interact with the front of the box

474 was significantly correlated with receiving more aggression (see Table 7). We found no  
475 evidence on either a short or long term basis that receiving aggression reduced victims'  
476 motivation to interact with the box.

477 An additional analysis was conducted to determine whether there was a relationship  
478 between successfully opening the foraging box and giving aggression to other group  
479 members in the target zone. All subjects that displayed unidirectional aggression and/or  
480 successfully opened the box were included in this analysis ( $N = 14$ ), with the total number of  
481 successful openings and incidences of being aggressive to others were entered for each bird.  
482 A Kendall's tau correlation revealed a significant positive relationship between the frequency  
483 of directing aggression towards others and the frequency of successfully completing the  
484 foraging task ( $\tau = .52, p = .015, N = 14$  birds).

485 Insufficient win-lose agonistic interactions within each group were observed to calculate  
486 reliable dominance hierarchies, so it was not possible to assess the influence of dominance on  
487 performance in this task.

#### 488 **Did pilfering influence subjects' interactions with the box?**

489 As pilfering victims did not benefit from their successful door-opening attempts,  
490 while pilferers gained rewards as a result of others' successful door-opening attempts, we  
491 examined whether victims' and pilferers' motivation to interact with the box may have been  
492 impacted by this behaviour. A total of 83 instances of pilfering were recorded across both  
493 experimental groups (slide  $N = 39$ ; pull  $N = 44$ ) and the majority of these ( $n = 63$ ) involved  
494 the pilfering of food from inside the box (slide  $n = 33$ ; pull  $n = 30$ ). To assess whether having  
495 food stolen had a short term effect on the victim's motivation to engage with the box, for  
496 each pilfering event we calculated the number of times victim subjects (excluding trained  
497 demonstrators) successfully opened the box door in the 1 min before and 1 min after being  
498 pilfered. For each victim ( $N = 8$ ), we then took mean values across all instances where they

499 experienced pilfering. A Wilcoxon signed-rank test showed no significant difference between  
500 the mean number of times victims opened the box before they were pilfered ( $Mdn = 1.21$ ,  
501  $IQR = 1.00$ ) and after they were pilfered ( $Mdn = 1.75$ ,  $IQR = .62$ ;  $z = -1.36$ ,  $p = .176$ ,  $r = -$   
502  $.48$ , 95% Hodges-Lehmann CI [-.16, 1]).

503 All eight subjects that pilfered food from inside the box also opened the box. To  
504 assess whether successful pilfering food from another was related to successfully opening the  
505 box across trials, we conducted a correlational analysis. All subjects that pilfered from inside  
506 the box and/or successfully opened the box were included in this analysis ( $N = 10$ ). A  
507 Kendall's tau test showed that there was a significant positive relationship between total  
508 number of times subjects pilfered food from inside the box and total number of times they  
509 successfully opened the box ( $\tau = .87$ ,  $p = .001$ ,  $N = 10$  birds).

## 510 Discussion

511 Our study provides further evidence of social learning capacities in psittacines, and to  
512 our knowledge, is the first to present evidence of this capacity in OWAs in a foraging  
513 context. The results obtained indicate that OWAs benefit from stimulus and/or local  
514 enhancement. Significantly more birds in experimental trials were found to approach and  
515 make physical contact with the testing apparatus than in control trials. This suggests that  
516 subjects' interest in the foraging box was increased due to trained demonstrators' interactions  
517 with it. More subjects in the slide group were found to have approached and touched the box  
518 in the first few sessions as compared to the pull group. This is likely due to the greater  
519 number of learning opportunities provided by the slide trained demonstrator in the initial  
520 sessions compared to the pull trained demonstrator. However, some of this variation may also  
521 be attributable to the pull group's prior experience as a control group, where they may have  
522 learnt the box was an irrelevant stimulus, and thus needed more time to overcome this. It is  
523 important to note though, that none of the OWAs in the pull group made contact with the

524 locked box during control trials. As such, it was not necessary for them to overcome learning  
525 that the box door did not open.

526         Whilst none of the OWAs made contact with the box in control trials and 0/3 BFAs  
527 who made contact with the box in control trials solved the task, 10 OWA experimental birds  
528 acquired this novel foraging technique. Although the comparison of BFA and OWA  
529 performance needs to be considered with caution, due to the species difference, these findings  
530 are consistent with previous avian research, which commonly reports significant differences  
531 between performance in experimental and control conditions in social learning tests (Fritz  
532 and Kotrschal 1999; Huber et al. 2001; Langen 1996; Midford et al. 2000). It is possible that  
533 successful acquisition of the task was influenced by emulation in addition to stimulus/local  
534 enhancement. By observing skilled demonstrators, experimental OWAs could have learned  
535 about the affordances of the box, in that movement of the box door revealed food.  
536 Alternatively, successful performance by the birds that opened the testing apparatus may  
537 have relied on trial and error individual learning once they were attracted to the apparatus  
538 through stimulus/local enhancement. Unfortunately, it is not possible to distinguish between  
539 the influences of local/stimulus enhancement and emulation on subject performance in the  
540 present study: future studies could address this with a ghost control condition.

541         Interestingly, no evidence of imitation was found. Both door-opening techniques  
542 (slide and pull) were used by OWAs in both experimental groups, and no connection was  
543 found between methods used by subjects and methods used by their groups' trained  
544 demonstrators, either in their overall performance or in their very first successful opening  
545 (before individual reinforcement for that behaviour had occurred). In this open diffusion  
546 setting, other birds who acquired the task then became demonstrators, however, there was no  
547 evidence that birds copied the method they last observed (from a trained or non-trained  
548 demonstrator) before each attempt. Additionally, no evidence was found that birds used the

549 dominant method (technique that had been used most often by group members up to that  
550 point of subjects' first attempts) significantly more than the non-dominant method.  
551 Experimental subjects also showed no inclination to use the trained demonstrator's method  
552 when he was present with the subject in the target zone. As both trained demonstrators  
553 consistently and repeatedly obtained food from the testing apparatus using the method they  
554 were trained to use, it is unlikely that the absence of imitation was due to poor performance  
555 of the trained demonstrators. Overall, subjects used the pull method about a third more often  
556 than the slide method. Despite efforts to have two actions that were equally easy to execute, it  
557 may be that this motion, pulling with the beak, is more similar to actions required for natural  
558 foraging such as the extraction of seeds and nuts from hard shells, than the slide action. The  
559 slide action was, however, clearly within the capacity of OWA, as 9/10 birds (three from pull  
560 group) who learnt to open the box used this method at least once. In the future, it may be  
561 interesting to consider using novel actions that are not likely to be used in natural feeding  
562 behaviour, but are within the scope of subjects' motor capacities.

563         Compelling evidence of complex social learning capacities has been reported in  
564 several parrot studies (Auersperg et al. 2014; Heyes and Saggerson 2002; Moore 1992;  
565 Pepperberg 2006), it may therefore be surprising that the present study failed to find evidence  
566 of imitation. Although it is possible that OWAs lack the capacity for motor imitation, we  
567 suggest that these results are more likely explained by the experimental design used. The  
568 two-action task we used may have been too easy, allowing birds to mainly rely on individual  
569 learning to acquire the task. Tennie et al. (2006) identified this as potential explanation for  
570 failure to find imitation in great apes in a push-pull task. Furthermore, disparities in findings  
571 between field and laboratory research with kea parrots indicate that social learning capacities  
572 detected in highly controlled testing, may not be observed under more naturalistic conditions  
573 (Gajdon et al. 2004; Huber et al. 2001).

574 Across animal species, imitation has been most commonly observed in highly  
575 controlled dyadic experiments. Under such testing conditions, there is little to distract an  
576 observer's attention from the demonstrator and testing apparatus, and crucially, there is no  
577 social competition when the observer is given access to the apparatus. In contrast, our  
578 subjects were tested in their aviaries, with all group members being given simultaneous  
579 access to the foraging box, therefore several factors may have influenced what subjects  
580 ultimately learned about the foraging task. First, it is much more likely in an open diffusion  
581 set-up that subjects obtain less consistent information about the method used by  
582 demonstrators to obtain food. Subjects in our study were exposed to alternate task solutions  
583 as a result of group members' task acquisition. It is also difficult to know what aspects of  
584 each demonstration each subject could observe from their position in the aviary. Subjects also  
585 had many more competing stimuli to attend to, including a range of social interactions. It is  
586 possible, for instance, that patterns of social association may have influenced task acquisition.  
587 As studies have found that the spread of novel behaviour can be predicted by social networks  
588 (e.g., lobtail feeding in humpback whales, Allen et al. 2013), future studies that use the open  
589 diffusion experimental approach to study social learning may benefit from engaging in  
590 network-based analyses. Furthermore, in our study, social competition for access to the  
591 foraging box meant that subjects had limited time to interact with the box before being  
592 displaced or receiving aggression. This may have encouraged the rapid use of multiple  
593 strategies to gain access to the box, rather than careful copying of the demonstrator's  
594 technique. Equally, the positive relationship we found between observers displaying  
595 aggression to others and successfully opening the box suggests that the most successful birds  
596 directed a great deal of their attention towards individuals that came in close proximity to the  
597 apparatus. They may therefore have been more interested in displacing group members in the  
598 target zone, including the trained demonstrator, than in observing the trained demonstrator's

599 manipulation of the box door. Individual factors such as dominance, boldness and motivation  
600 to obtain food are also likely to have impacted on individual engagement in agonistic  
601 interactions and task acquisition in this experimental setting and we recommend that future  
602 researchers assess these factors to investigate their influence on task acquisition. This  
603 complex set of issues and factors are likely to also be present and constrain the types of social  
604 learning that influence the transmission of group-specific behaviours in the wild, so using  
605 open diffusion designs in experimental work is vital in order to better understand the social  
606 learning mechanisms underlying these cultural variants in animals.

607         Our analyses concerning the effect of aggression and pilfering on subjects'  
608 performance indicate that individual characteristics influence the likelihood of an individual  
609 acquiring a novel foraging technique from others. The positive relationship we found  
610 between observers displaying aggression to others and successfully opening the box indicates  
611 that willingness to defend access to the resource from others is important in a highly  
612 competitive social situation in terms of ensuring sufficient exploration opportunity to acquire  
613 the task solution. Equally, birds who successfully pilfered food from others who opened the  
614 box also had high levels of their own successful foraging attempts with the box. Pilfering  
615 may be an important scaffolding behaviour in the acquisition of novel foraging techniques.  
616 However, this relationship could also be a product of aggressive birds defending an area close  
617 to the box door, providing them with a lot of opportunities to open it themselves and pilfer  
618 from others. Related to pilfering behaviour, we also anecdotally observed that some  
619 individuals in the present study spent more time scrounging for dropped food rewards on the  
620 ground below the target zone, than they did attempting to open the box themselves. Thus, for  
621 some subjects, benefiting from group members' successful manipulation of the box may have  
622 had an inhibitory effect on their task acquisition, in line with previous studies (Beauchamp  
623 and Kacelnik 1991; Giraldeau and Lefebvre 1987; Munkenbeck Fragaszy and

624 Visalberghi 1990). Unfortunately, because this behaviour occurred outside the target zone, it  
625 was not captured on video and could not be systematically examined. Contrary to our  
626 predictions, receiving aggression or having food stolen did not appear to deter subjects'  
627 efforts to interact with the box. However, it could be that only the more socially confident  
628 birds that were relatively resilient to aggression and pilfering chose to regularly enter the  
629 target zone to interact with the box. The use of multiple foraging boxes in future studies may  
630 reduce aggression and social competition, possibly yielding different results.

631         In conclusion, the present study found that social facilitation occurred, but high  
632 fidelity imitation copying did not. This narrows the space of mechanisms that could account  
633 for the social learning observed (local/stimulus enhancement; emulation), but does not  
634 distinguish between these low-fidelity social learning mechanisms. In this open diffusion set  
635 up experimental birds who could watch a trained demonstrator were more likely than control  
636 birds to approach the box and successfully extract food from it; however, we found no  
637 evidence that they imitated the method used to open the box. Aggression was relatively  
638 frequent as individuals competed to gain access to the monopolisable food source.  
639 Surprisingly, subjects were not deterred from making physical contact with the box as a result  
640 of receiving aggression from or having food stolen by group members; however, subjects that  
641 frequently displayed aggression towards others and pilfered food from others also had high  
642 numbers of successful box opens. This indicates that propensity for aggression may play a  
643 role in the extent to which birds are able to capitalise on opportunities to learn about, and  
644 compete for, monopolisable food, and that imitation is not necessary for the spread of  
645 exploitation of a novel food source when relatively basic extractive behaviours are required.  
646 While some species may show greater reliance on high fidelity copying (e.g., great tits; Aplin  
647 et al. 2015), which would allow adaptive behaviour to spread more rapidly through  
648 populations, others may rely more heavily on individual learning and thus may show greater

649 propensity for innovative behaviour. A trade-off may therefore exist between innovative  
650 behaviour and social learning. Our open diffusion study highlights important social and  
651 individual factors that constrain and promote learning from others in a naturalistic context, as  
652 well as the possibility that although tightly controlled dyadic social learning paradigms have  
653 shown many animals to be capable of imitation, group-specific behavioural variations  
654 observed in the wild could result from lower-fidelity copying processes.

655

656 **Ethical approval:** All applicable international, national, and/or institutional guidelines for  
657 the care and use of animals were followed. All procedures performed in studies involving  
658 animals were in accordance with the ethical standards of the University of York. Approval  
659 for this study was obtained by the Department of Biology Ethics Committee (Case  
660 KS230512), at the University of York.

661

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801 Figure legends

802

803 **Fig. 1** Photographs illustrate the foraging box and both methods of opening it - the slide  
804 method (a) and the pull method (b)

805

806 **Fig. 2** Representations of the experimental setup. A top view of the aviary (a) illustrates the  
807 position of the cameras in relation to the box. The camera in the aviary was protected with a  
808 camera box. A front view of the experimental box from the parrots' perspective (b) illustrates  
809 the position of the U-shaped perch and target zone boundary markers on the mesh in relation  
810 to the box

811

812 **Fig. 3** Number of demonstrations by trained demonstrators (TD) and number of subjects that  
813 made contact with the box in each trial for experimental groups

814

815 **Fig. 4** Total number of times subjects successfully opened the foraging box using each  
816 technique. Total number of successful opens in the slide group were 121 and 156 in the Pull  
817 group

818

819 **Fig. 5** Frequency of each type of aggression in each experimental group

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