

1 Running head: PUBLIC INFORMATION USE IN CHIMPANZEES

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8 PUBLIC INFORMATION USE IN CHIMPANZEES (*PAN TROGLODYTES*) AND

9 CHILDREN (*HOMO SAPIENS*)

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Author Footnotes

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Abstract

The discernment of resource quality is pertinent to many daily decisions faced by animals. Public information is a critical information source that promotes quality assessments, attained by monitoring others' performance. Here we provide the first evidence, to our knowledge, that chimpanzees (*Pan troglodytes*) use public information to guide resource selection. Thirty-two chimpanzees were presented with two simultaneous video demonstrations depicting a conspecific acquiring resources at a fast (resource-rich) or slow (resource-poor) rate. Subsequently, subjects selected the resource-rich site above chance expectation. As a comparison, we report evidence of public information use in young children. Investigation of public information use in primates is pertinent as it can enhance foraging success and potentially facilitate payoff biased social learning.

Keywords: public information; social information; social learning; social cognition.

76

77 Social learning denotes behavior or learning that is altered according to other organisms'
78 presence, behavior or behavioral products (Heyes, 1994). A large body of evidence indicates
79 that many animal species are capable of social learning (Brown & Laland, 2003; Galef &
80 Giraldeau, 2001; Reader & Biro, 2010; Reader & Laland, 2002), culminating in regional
81 variation in behavior, suggestive of tradition or culture (Perry, 2011; van Schaik et al., 2003;
82 Whiten et al., 1999). Wild chimpanzees, in particular, display one of the broadest cultural
83 repertoires recorded, with geographical variation in food extraction and processing methods
84 as well as social behavior, thought to be underpinned by social learning rather than genetic or
85 ecological factors alone (Whiten et al., 1999). Ancillary studies of captive chimpanzees
86 support claims that social learning plays a role in regional behavioral variation in the wild
87 (Horner, Proctor, Bonnie, Whiten, & de Waal, 2010; Whiten, Horner, & de Waal, 2005;
88 Whiten et al., 2007). Indeed, both arbitrary behavioral traditions (Bonnie, Horner, Whiten, &
89 de Waal, 2007) and foraging traditions (Horner, Whiten, Flynn, & de Waal, 2006) have been
90 shown to emerge through social learning in this species.

91 A trend exists in the social learning literature to document how chimpanzees socially
92 acquire foraging techniques (Hopper et al., 2007; Horner & Whiten, 2005) and, more
93 recently, from whom they learn (Horner et al., 2010). In particular, focus has been given to
94 the question of whether chimpanzees imitate (broadly defined as the copying of behavioral
95 actions) or rely on other social learning processes (Hopper, Lambeth, Schapiro, & Whiten,
96 2008; Tennie, Call, & Tomasello, 2006); a question that remains a topic of debate (Tennie,
97 Call, & Tomasello, 2009; Tennie, Call, & Tomasello, 2012). Additionally, work on model-
98 based biased social learning has begun to document selective copying with regard to whom it
99 is that chimpanzees attend to and from whom they copy. Chimpanzees, for example, have
100 been shown to preferentially copy dominant over low-ranking conspecifics, and selectively

101 attend to the food associated behavior of older or same-aged individuals (Biro et al., 2003;
102 Horner et al., 2010; Kendal et al., submitted).

103 One area of interest that has received relatively little attention addresses whether
104 social information influences chimpanzees' decisions of where to forage; whether the
105 foraging successes of others act as a cue to locating the most abundant food resources.
106 When animals feed, they produce information, often inadvertently, through their
107 performance, activity and decisions as well as in their by-products. This information can then
108 be used by others as cues to resource locations (Danchin, Giraldeau, Valone, & Wagner,
109 2004). Theoretical modeling suggests that social learning (resulting in joining feeding
110 conspecifics) outcompetes individual sampling in changing environments where resources
111 with high payoffs are associated with a high probability of samplers failing to find food
112 (Arbilly, Motro, Feldman, & Lotem, 2011). Thus, for species that experience a variable food
113 supply, where nutritional food sources can be devoid of food (e.g., seasonal fruits,
114 Basabose, 2004; Watts, Potts, Lwanga, & Mitani, 2012), attending to foraging conspecifics
115 may prove an adaptive strategy. While the question of whether graded foraging
116 performances cues resource quality judgments in primates remains understudied, evidence of
117 the capacity to source and use social information to locate food resources has been
118 documented in various primate species. The presence of a conspecific at one of two opaque
119 food containers (local enhancement), for instance, can act as a social cue used by
120 chimpanzees to locate a container baited with food (Itakura, Agnetta, Hare, & Tomasello,
121 1999). Similarly, Tonkean macaques (*Macaca tonkeana*) have been shown to use both
122 olfactory and visual residual signs, produced as a by-product of conspecific feeding, to locate
123 distant food sources of the same type (Drapier, Chauvin, & Thierry, 2002).

124 Social cue use has been documented in all four great ape species (*Pan troglodytes*,
125 *Pan paniscus*, *Gorilla gorilla gorilla* and *Pongo pygmaeus abelii*) (Buttelmann, Call, &

126 Tomasello, 2008). Specifically, various behavioral cues consistent with attempts to extract
127 hidden food from one of two locations were used by subjects to infer the location of the
128 hidden food sources. For example, a preference was displayed for baited containers, which
129 the experimenter smelled and attempted to bite open, compared to those that were only
130 smelled. Interestingly, Buttelmann and colleagues (2008) found that when subjects possessed
131 personal knowledge of the absence of food in both containers, despite differential behavioral
132 cues performed on the containers, subjects selected at random. Thus, social information use
133 was dependent on subjects' own knowledge states (i.e., personal information) and when
134 personal and social information conflicted, a preference was displayed for the reliable,
135 personal information; a “copy (only) when uncertain” strategy (Kendal, Coolen, & Laland,
136 2009; Kendal, Coolen, van Bergen, & Laland, 2005). More recently, chimpanzees have been
137 shown to remember (inaccessible) locations at which they observed a human hide food items,
138 and when eliciting the aid of a human to gain the hidden food items, they directed them first
139 to items of high quality (Sayers & Menzel, 2012). Thus, the chimpanzees were able to store
140 and use both personal information regarding resource quality and social information
141 regarding location of resources following a delay. What is novel about the current study is
142 an investigation of whether chimpanzees use social cues to assess resource *quality* (public
143 information *sensu* Valone, 1989) and use this to guide their choice of a resource location.

144 **Although** studies have shown that primate species use social cues to locate hidden
145 food (Buttelmann et al., 2008; Itakura et al., 1999) and that feeding conspecifics can socially
146 facilitate other animals food consumption (Visalberghi & Addessi, 2000), little is known
147 regarding whether primates are capable of discerning food abundance based on conspecifics'
148 foraging successes. One of the main daily decisions facing foragers is, of course, how to
149 optimize energetic returns. When social information acts as a cue to resource quality it is
150 termed ‘public information’ (Valone, 1989). Public information, specifically, is a term

151 derived from behavioral ecology, that, rather than referring to any information that is public
152 (available to others), is confined to social information sourced from others' performances
153 conveying cues regarding quality (Valone, 1989; Valone, 2007; Valone & Templeton, 2002).
154 This can include cues to abundant resources, successful breeding partners, habitats and
155 breeding sites and the quality of potential competitors (Valone, 2007). Public information
156 use does not necessitate complex social learning processes; it can occur via local
157 enhancement (Webster & Laland, 2012), feeding rate (Coolen, Bergen, Day, & Laland, 2003)
158 and food related collective commotion (Laidre, 2013).

159 Public information use has been assessed in the common marmoset (*Callithrix*
160 *jacchus*) (Voelkl & Huber, 2007). Marmoset pairs (demonstrator-observer) were presented
161 with four pairs of opaque containers filled with wood chips, some of which were baited with
162 food. The marmosets could forage simultaneously, with visual access to each other, but were
163 separated by wire mesh. Equally, paired containers were positioned adjacent to one another
164 but separated by mesh, so that resource sites matched for marmoset pairs. The
165 'demonstrator' marmoset was informed of food locations and thus, the 'observer' marmoset
166 could maximize its foraging success by synchronizing its search for food with that of the
167 demonstrator. Contrary to expectation, however, the availability of this social information
168 did not enhance foraging success.

169 In chimpanzees, auditory information can signal resource quality. Chimpanzees,
170 upon locating food, produce rough-grunt vocalizations that differ according to the producer's
171 food preferences (Slocombe & Zuberbühler, 2006), offering important resource quality
172 information. Slocombe and Zuberbühler (2005) showed that a chimpanzee altered his
173 foraging strategy according to playbacks of a high- versus low-quality food response,
174 suggesting rough-grunts served as a social signal to resource quality. Overall, food searching
175 behavior was found to be prolonged and more thorough upon hearing rough grunts produced

176 in response to the high-quality food. Food searching additionally tended to be longer at the
177 resource sites that were associated with the rough grunt played. Thus, rough grunts may
178 constitute an important source of auditory public information.

179 In Experiment 1, we aimed to examine whether chimpanzees use visual public
180 information - differential foraging behavior of a conspecific - to identify the most abundant
181 food source, in the absence of vocal signals. Public information is predicted to be widespread
182 in nature, promoting greater accuracy in environmental assessments (Valone & Templeton,
183 2002). Yet, research into public information use has largely been confined to species of birds
184 and fish (Valone, 2007). The study of public information in chimpanzees is vital for
185 understanding what social information contributes to the daily decisions made by this species,
186 including whether public information facilitates resource maximization. Public information
187 use was recently reported in chimpanzees (Martin, Biro, & Matsuzawa, 2011), where
188 observers used models' behavioral actions to solve a matching to sample task. However, as
189 the copying of behavioral decisions was not confined to resource quality (as required for the
190 strict use of 'public information' *sensu* Valone, 1989), to date, whether chimpanzees discern
191 patch profitability by monitoring the relative success of conspecifics is unknown.

192 We employed a variant of Coolen, van Bergen, Day and Laland's (2003)
193 methodology, to examine whether chimpanzees use graded information of a conspecific
194 foraging at a food-rich and food-poor site to inform their own foraging decisions.
195 Simultaneous videos of a conspecific acquiring resources at two locations, each differing in
196 terms of the rate at which food was gained (food-rich versus food-poor), were presented.
197 Subsequently, observer chimpanzees were given access to the resource sites, and their
198 selections recorded. Employing video-based social stimuli with chimpanzees (Hopper,
199 Lambeth, & Schapiro, 2012) offers the advantage of presenting the same unfamiliar model at
200 each foraging site, thus controlling for any model-based biases (Rendell et al., 2011). This is

201 important due to the established influence of social dynamics, age, and perhaps previous
202 track record of success (Biro et al., 2003; Horner et al., 2010; Kendal et al., submitted) to
203 whom it is that chimpanzees attend and from whom they learn. As bird and fish species use
204 public information (Valone, 2007), and given chimpanzees' sensitivity to behavioral cues in
205 foraging situations, their discerning auditory food signals (Slocombe & Zuberbühler, 2005)
206 and their ability to engage in observational learning (Martin et al., 2011), we predicted that
207 chimpanzees would display the ability to use public information.

208 We were additionally interested in the ability of 5-year-old children (*Homo sapiens*)
209 to use public information as, to our knowledge, whether children use public information to
210 discern reward quality has yet to be empirically investigated. In Experiment 2, we replicated
211 the chimpanzee study with 5-year old children (*Homo sapiens*), using a similar methodology.
212 This follows previous studies that have focused on the socio-cognitive skills of both
213 chimpanzees and children, finding that young children constitute an appropriate group to
214 which chimpanzees can be compared (Dean, Kendal, Schapiro, Thierry, & Laland, 2012;
215 Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007; Horner & Whiten, 2005).
216 Similar to chimpanzees, the feeding behavior of children shows susceptibility to social
217 context. Children's food preferences, for example, have been shown to alter in accordance
218 with peer preferences (Birch, 1980a). Similarly, children's food intake and preferences have
219 been documented to positively correlate with those of parents and other adults of the same
220 subculture (Birch, 1980b; Orlet Fisher, Mitchell, Wright, & Birch, 2002), while the amount
221 of food consumed has been shown to vary according to one's own size and social partner size
222 (Salvy, Romero, Paluch, & Epstein, 2007). Given the social influence on feeding behavior
223 and that children readily respond to social information (Lyons, Damrosch, Lin, Macris, &
224 Keil, 2011; Wood, Kendal, & Flynn, 2012), it is predicted that children would use public
225 information as a cue to resource quality.

Experiment 1: Chimpanzees

The purpose of this study was to establish whether individual chimpanzees would assess resource quality by monitoring the relative foraging success of a conspecific feeding, or retrieving stickers, at different rates (public information use).

Method

Subjects. Thirty-nine chimpanzees participated; three were discounted as they did not interact with the resource boxes during a pre-testing phase (see procedure) and four were discounted due to inattention to the demonstrations. The remaining 32 chimpanzees (16 male) ranged in age from 15 to 44 years ($M = 30$). Following previous studies, a dominant female (Hopper, Schapiro, Lambeth, & Brosnan, 2011), unfamiliar chimpanzee served as the demonstrator. Subjects were housed at the Michale E. Keeling Center for Comparative Medicine and Research (KCCMR) facility in Bastrop, TX USA. The KCCMR is fully accredited by the AAALAC-I. The chimpanzees were group housed with access to enriched indoor and outdoor enclosures with climbing facilities. Subjects had participated in previous video social learning tasks (Hopper et al., 2012) and had past exposure to video for enrichment. No food or water deprivation was used during this study which was approved by the Life Sciences Ethical Review Committee, Durham University and the Institutional Animal Care and Use Committee of The University of Texas MD Anderson Cancer Center.

[TABLE 1 AROUND HERE]

Video Stimuli. Video demonstrations showed a model acquiring rewards (peanuts) at different rates (rich: approximately every 12secs, poor: approximately every 84secs; see Table 1) from two boxes (21.5 H x 10 W x 30 L cm). To achieve this, the boxes had a small hole situated at the back through which the food items were dispensed by the experimenter.

251 The demonstrator could then retrieve the food items by reaching inside an opening at the
252 front of the box. Thus, the peanuts themselves were barely visible whilst the foraging/eating
253 actions of the demonstrator were. The two boxes, resource-rich and resource-poor, were
254 colored either yellow or black. To allow counterbalancing of the box color constituting the
255 rich resource sites during the test sessions, four video demonstrations were captured (yellow
256 rich; black poor; black rich; yellow poor, with the same demonstrator used in all
257 demonstrations). To ensure that the demonstrator sourced individual peanuts at the
258 predetermined rates, where appropriate video demonstrations were edited slightly using
259 Picture Motion Browser and Windows Live Movie Maker. Video editing consisted of cutting
260 and/or looping subsections of the demonstrations. All recordings were captured with a Sony
261 Handycam.

262 [FIGURE 1 AROUND HERE]

263 **Design and Procedure**

264 **Pre-tests.** As neophobic reactions to novel objects can occur in chimpanzees, a habituation
265 stage was performed to expose subjects to the resource boxes prior to running the experiment.
266 Chimpanzees were given sequential, color counterbalanced, exposure to the baited resource
267 boxes. Chimpanzees that did not retrieve a grape from both boxes during this session ($N=3$)
268 were eliminated from the study. This pretest identified subjects who lacked the motivation to
269 participate and/or those that would fail to select a resource box in test sessions due to
270 neophobic responses to the apparatus.

271 Color preference was assessed using a dichotomous preference paradigm (Hopper et
272 al., 2011). In 10 successive, counterbalanced and unrewarded trials, the experimenter
273 simultaneously held one cylindrical token (yellow/black) in each hand and chimpanzees
274 selected one via gesture. No color preferences were observed (yellow token selections from
275 10 trials $M = 4.81$, $SD = .90$; binomials, all $p > .05$, $N = 36$).

276

277 **Experimental Test.** Chimpanzees were tested individually and voluntarily within their
278 indoor compartments (ca. 2.4x2.4x1.8m³). Demonstrations were presented on two computer
279 monitors (48.26 cm) on separate trolleys (85 H x51 W x51 L cm) located adjacent to one
280 another (separated by cf. 40cm). The two opaque boxes (yellow/black), from which the
281 demonstrator retrieved resources, were positioned in front of the trolleys behind an occluding
282 barrier, and positioned (left/right) to match the box color depicted in the corresponding video.
283 The color (yellow/black) constituting the resource rich patch and the side (left/right) it was
284 presented were counterbalanced. All subjects received one trial only. Test sessions were
285 video recorded.

286 Following the demonstrations, the resource boxes were simultaneously revealed by
287 removal of the occluding barrier and pushed toward the subjects. The resource boxes were
288 designed such that the observers could not see the food rewards inside until they had placed
289 their hand inside the hole at the front. Resource selection was defined as the first resource
290 box the subjects touched. The unselected box was then removed by the experimenter to
291 prevent chimpanzees from gaining rewards from both boxes. Upon box selection,
292 chimpanzees could retrieve the food item from their chosen box. To reduce food intake, and
293 since only one trial was conducted with each subject, resource boxes were each baited with
294 one banana piece only, irrespective of box quality. This also prevented potential olfactory
295 cues arising from a large amount of food placed in one box only. Subjects were allocated up
296 to two minutes to make their selection, after which the trial would be terminated and the
297 subject discounted. In practice all selections were made in less than 13 seconds and no
298 individuals were discounted. Subjects' attention (head orientation) to the videos was noted at
299 10-second intervals, and those ($N = 4$) not meeting a criteria of attention at ≥ 6 10-second
300 intervals, were discounted.

301

302 **Statistical Analysis.** Due to the small sample size and dichotomous dependent variable, non-
303 parametric statistics were used. First we investigated whether the number of resource rich
304 selections differed from chance (50%) using the Binomial Test. Mann-Whitney U-Tests
305 were conducted to ascertain whether subject age, latency to box selection and attention levels
306 differed according to resource selection (rich/poor). Whether resource selection differed
307 according to sex, the video-sets viewed (yellow rich/black rich) and the sequential order of
308 box presentation during the pre-test habituation phase, was assessed using Chi Square and
309 Fisher's Exact (where contingency tables contained expected values of below 5) Tests.
310 Binomial Tests were additionally used to assess side and color biases in resource selections
311 (chance = 50%).

312

313

Results

314 As predicted, the majority (22 of the 32) chimpanzees selected the resource-rich box
315 following presentation of the demonstrations (binomial, $p = .03$, one tailed, 95% CI [.53, .84];
316 see Figure 2). The mean time taken to select a resource box was 4 seconds ($SD = 3$). No
317 significant differences were observed between age ($U = 74.50$, $N = 32$, $p = .15$), sex ($\chi^2(1) =$
318 2.33 , $p = .25$), latency to selection ($U = 94.50$, $N = 32$, $p = .54$) or attendance ($U = 95.50$, $N =$
319 32 , $p = .57$) as a function of the resource box selected.

320

321 There was no significant difference in resource box selection following the
322 demonstration as a function of the box presented first during the box exposure pretest ($\chi^2(1,$
323 $32) = 2.32$, $p = .25$). Resource box selections did not differ according to the different video-
324 sets needed to counterbalance color and resource richness (FET: $N = 32$, $p = 1.00$).

325 Moreover, the chimpanzees displayed no side bias (binomial: $N = 32$, $p = .38$, left $N = 13$ and
right $N = 19$) nor color bias (binomial: $N = 32$, $p = .86$, black $N = 15$ and yellow $N = 17$).

326 [FIGURE 2 AROUND HERE]

327 **Experiment 2: Children**

328 Experiment 1 showed that chimpanzees discerned resource quality from video
329 demonstrations. We now turn to the question of whether children use public information to
330 assess resource quality. The child study methodology was identical to the chimpanzee study
331 except for changes, detailed below, to accommodate species differences.

332
333 **Participants.** Thirty-six 5-year-old children (17 male) were recruited from three primary
334 schools in the North East of England. A single female child, unfamiliar to the participants
335 (aged 5 years), acted as the demonstrator, via video, for all children.

336
337 **Video Stimuli.** Video presentations were shorter in duration (1 minute 40 seconds) than for
338 the chimpanzees and, due to retention of the overall resource quantities presented (rich 15
339 versus poor 3), the rate at which each reward was dispensed at the resource rich location was
340 increased (from every 12 to every 6 seconds; see Table 1). Stickers constituted the resource
341 due to the ethical considerations of provisioning consumables. The boxes consisted of two
342 opaque hemisphere-shaped plastic containers (total surface area 763.41 cm²). As children
343 display color preferences (Boyatzis & Varghese, 1994), the boxes were differentiated by
344 pattern (large or small black squares). Upon retrieving stickers, the demonstrator placed
345 them in an opaque cup. This prevented a stack of stickers accumulating which could have
346 served as an additional cue for the children, relative to chimpanzees where rewards were
347 immediately consumed by the demonstrator.

348
349 **Design and Procedure.** Testing was conducted in a quiet room at each child's school away
350 from the rest of their class. Each child participated in one trial only. Participants were told

351 by an experimenter (GV), “I would like you to watch videos of a girl getting stickers, and
352 then after the videos you will get a chance to find stickers” and given verbal prompts (“are
353 you watching the videos?”, “can you see what the little girl is doing?”) if attention lapsed. It
354 is noteworthy, that children were encouraged to attend to the videos by experimenter
355 prompting, with no verbal prompts given to the chimpanzees. Following the videos, the
356 occluding barrier was removed to reveal the resource boxes and children were instructed,
357 “You can have a look in the boxes now”. Participants were allocated up to one minute to
358 make a resource selection, defined as the first box touched or gestured toward. The chosen
359 box was then opened to retrieve the stickers. The number of baited stickers in the resource
360 rich and resource poor boxes matched the number obtained by the demonstrator in the
361 corresponding videos (15 and 3, respectively). As the data was derived from one trial only,
362 the number of stickers gained did not influence the study results.

363

364

Results

365 As predicted, 24 of 36 children selected the resource rich location, which is above that
366 predicted by chance alone (binomial test: $p = .03$, one tailed, 95% CI [.51, .82] see Figure 2).
367 Average time to box selection was 6 seconds ($SD = 5$). Resource selection was not related to
368 sex ($\chi^2(1) = .22, p = .73$) or box selection latency ($U = 95.50, N = 36, p = .10$). No side
369 (binomial test; $N = 36, p = .24$) or box pattern preferences (binomial test; $N = 36, p = .62$)
370 were observed. There was no significant difference in the species’ tendencies to choose the
371 ‘rich’ patch ($\chi^2(1) = .03, p = 1.00$).

372

373

Discussion

374

375 Chimpanzees and children are capable of social learning (Horner et al., 2006). Numerous

376 studies have documented that group specific traditions occur in these species through
377 differential copying of knowledgeable conspecifics (Flynn & Whiten, 2008; Whiten et al.,
378 2005; Whiten et al., 2007). Such studies have tended to concentrate on the copying of
379 behavioral methods, often using tools, of gaining a food reward i.e., (novel) food extractive
380 behavior. Less is known about whether social information relating to differential food
381 abundance guides primates' subsequent foraging decisions. The ability to discriminate
382 between resource qualities using public information allows profitable food sources to be
383 identified and visited with potentially greater accuracy than if using personal information
384 alone (Arbilly et al., 2011; Valone, 2007). Our results indicate that chimpanzees, and 5-year-
385 old children, possess this ability, interestingly showing high concordance in public
386 information use across species. Thus, in addition to attending to social cues to locate food
387 sources (Buttelmann et al., 2008; Itakura et al., 1999), chimpanzees and children were able to
388 select reward sources according to the graded acquisition (of food/stickers) performance of a
389 conspecific. Children and chimpanzees thus performed at comparable levels despite
390 methodological differences including verbal attention prompts for children and not
391 chimpanzees and the provisioning of stickers versus consumables.

392 Foraging decisions rely on various cognitive skills. Route planning, cognitive maps,
393 memory of food sources, travel time, competition for food and likelihood of patch depletion
394 can all influence decisions of where to forage (Noser & Byrne, 2010). Much of this
395 information is derived from personal experience; however, social foragers are afforded an
396 additional information source derived from others' activities (Dall, Giraldeau, Olsson,
397 McNamara, & Stephens, 2005). Our results suggest that public information sourced from
398 conspecific foraging success may, in addition to personal information (Beran, Evans, &
399 Harris, 2008) and auditory signals (Slocombe & Zuberbühler, 2006), aid in locating quality
400 resources in chimpanzees and hence constitute one more factor among many that could

401 contribute to foraging decisions

402 The use of public information has many implications. Primates may optimize
403 foraging efficiency through exploiting inadvertent social information manifested in the
404 foraging activity of conspecifics (Arbilly et al., 2011). In the present study, the relative
405 number of times or the rate at which the demonstrator reached inside each resource box to
406 acquire reward items, and the subsequent consumption activity for chimpanzees, could
407 constitute potential cues by which resource quality was determined. Future investigation
408 would benefit from control conditions to isolate the cues utilized to discern resource
409 abundance. The inclusion of consumption only and reward retrieval without consumption
410 would prove beneficial conditions in this regard.

411 Public information use can allow patch estimation to occur without engaging in
412 personal sampling (Coolen et al., 2003). Public information may therefore aid decisions of
413 food approach through an assessment of whether food sources will support additional
414 foragers without direct food contest. That is, use of public information could benefit foragers
415 through conflict avoidance by allowing a predetermination of whether approach would likely
416 result in conflict due to low resource abundance versus safer approach to more abundant non-
417 monopolizable food sources. When public information is derived from successful dominant
418 foragers, an ability to use it following the departure of that individual may prove beneficial
419 for subordinate observers (McQuoid & Galef, 1992). Chimpanzees have been shown to
420 remember, following a delay, locations they previously saw a human hide food and to ‘direct’
421 a human helper to hidden food of high quality first (Sayers & Menzel, 2012). This, along
422 with other numerous studies, show that chimpanzees are capable of delayed social
423 information use (Bering, Bjorklund, & Ragan, 2000; Bjorklund, Yunger, Bering, & Ragan,
424 2002). It is worth noting however that where food is markedly limited, public information
425 will be of little value, even after a delay, since due to depletion, food consumption depends

426 upon who discovers it first (Giraldeau, Valone, & Templeton, 2002). In this context,
427 reliance upon personal information would best serve the forager. Thus considerations of
428 public and personal information use are pertinent to chimpanzees, a species in which fission-
429 fusion dynamics are pronounced, as they allow assessment of resource distribution and
430 abundance, factors that can **underwrite** party size (Aureli et al. 2008).

431 Public information has the potential to aid foraging activity through signaling patch
432 depletion (Fraser, Ruxton, & Broom, 2006; Templeton & Giraldeau, 1995). It is of interest
433 that chimpanzees and children selected the resource box associated with the demonstrator
434 retrieving rewards at the fastest rate. This suggests that the faster feeding rates did not signal
435 patch depletion. While increased feeding rate can mark rapid food depletion, sustained high
436 rates should signal food abundance and slower (or reducing) rates should indicate limited
437 food supply. Finding that chimpanzees and children displayed a preference for the resource
438 supporting rapid food retrieval is in line with reports that species are attracted to food sites at
439 which feeding rate is faster (Coolen et al., 2003; Coolen, Ward, Hart, & Laland, 2005). To
440 investigate whether public information provides cues to patch depletion, it would be of
441 interest to examine the influence of demonstrator foraging success, varying success (x
442 retrieval attempts with no food obtained) and the feeding rate (gradual reduction versus
443 increase rate of food obtained) in addition to utilizing real-time demonstrations.

444 While chimpanzees in this study displayed a preference for the rich resource box, it
445 remains unclear whether this finding would hold in a group context. Video footage of a
446 foraging demonstrator, theoretically, could have alleviated any competitive foraging demands
447 that would otherwise occur in more naturalistic group settings, including dominance factors
448 (Emery Thompson, Muller, Kahlenberg, & Wrangham, 2010; Muller & Wrangham, 2004;
449 Sapolsky, 1992). This scenario is beneficial for the establishment of whether chimpanzees
450 *can* use public information, but nevertheless does not allow an assessment of whether they *do*

451 use public information more generally in the wild (Boesch, 2007, 2008). In groups, factors
452 such as the dominance rank of those already foraging, the number of foragers, food
453 distribution (monopolizable or not) and species level foraging strategies (e. g. contest and/or
454 scramble competition) will likely play a prominent role in foraging decisions (Murray,
455 Eberly, & Pusey, 2006; Murray, Mane, & Pusey, 2007).

456 Moreover, in chimpanzees, foraging strategies also differ according to sex and
457 reproductive status. Lactating females tend to visit fewer of the available high value
458 resources per day than do sexually receptive females and males, but stay at resource locations
459 longer (Bates & Byrne, 2009). Males, in contrast, have been shown to use linear daily
460 foraging paths, indicative of a strategy of combining foraging needs with territorial defense
461 (Bates & Byrne, 2009). Accordingly, **although** chimpanzees in this study showed public
462 information use, individual foraging strategies employed in the wild, including patch
463 departures, are mediated by optimizing food intake, and other factors such as sex specific
464 needs. Thus, foraging decisions in this species represents a complex process that may not
465 only rely on personal and public information, but one that is also variable according to
466 individual needs.

467 To understand decision making in chimpanzees (and children) it is important to
468 determine the information sources underpinning behavioral actions. In this study we
469 demonstrated that public information derived from differential foraging success can influence
470 subsequent foraging decisions. How human and non-human primates weight personal and
471 public information, especially when they conflict (Kendal et al., 2005), and how social
472 dynamics (CoussiKorbel & Frigaszy, 1995), such as dominance rank, influence public
473 information use, represent further important questions. Moreover, the pertinence of PI,
474 especially in species displaying traditions (Laland & Galef, 2009), lies in its use enabling
475 payoff assessments of resources without participating in personal sampling which can be

476 costly in terms time and energy losses (Valone, 2007). To this end, PI has the potential to
477 facilitate informed payoff biased copying decisions, whereby individuals adopt behaviors in
478 proportion to their profitability. One aspect of import to cumulative culture, in which cultural
479 traits and behaviors become more complex and efficient across generations such that a single
480 individual could never invent the trait within its lifetime (Tennie et al., 2009), is recognizing
481 when a behavioral option is a beneficial modification which should be incorporated into the
482 existing cultural trait (Laland, 2004). Public information may promote rudimentary ‘copy if
483 better strategies’ (Schlag, 1998, 1999), allowing the ‘ratcheting up’ (Tennie et al., 2009) of
484 cultural traits (e.g., technology) over generations. If quality assessments - made through
485 monitoring the relative payoffs gained by conspecifics, or one’s self, using different traits -
486 encourages the social acquisition of beneficial trait modifications (e. g. food processing
487 techniques), these could have potential consequences for cultural evolution. Specifically, it is
488 possible that cumulative culture, which is widely held to be responsible for humanity’s
489 success (Kendal, Rendell, Pike, & Laland, 2009), depends upon use of “payoff biased” social
490 learning strategies. Whether public information use may promote selectivity in what is
491 copied through facilitating such payoff biased social learning, and whether use of such
492 cultural transmission biases (Rendell et al., 2011) is instrumental in the observed cross-
493 species distribution of cumulative culture (Dean et al., 2012), requires further investigation.

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Table 1

Time (minutes, seconds) at which single rewards were dispensed during demonstrations

Pan		Homo	
Resource-Rich	Resource-Poor	Resource-Rich	Resource-Poor
0.05	0.05	0.06	0.06
0.17		0.12	
0.29		0.18	
0.41		0.24	
0.53		0.30	
1.05		0.36	
1.17		0.42	
1.29	1.29	0.48	0.48
1.41		0.54	
1.53		1.00	
2.05		1.06	
2.17		1.12	
2.29		1.18	
2.41		1.24	
2.53	2.53	1.30	1.30

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Figure 1. Model retrieving rewards from the resource boxes (video demonstrations stills)

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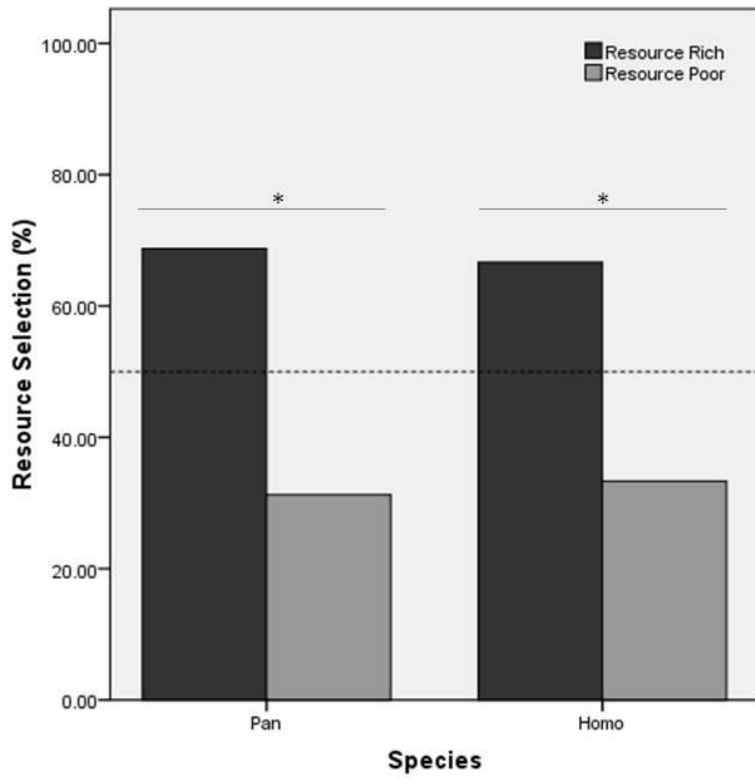
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Figure 2. Resource-rich and resource-poor selections (%) per species. Dotted line represents chance level, $*=p<0.05$.

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880 SHORT TITLE: Public information use in chimpanzees