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1 Complex nests but no use of tools: an investigation of problem solving in
2 weaverbirds (*Ploceidae*)

3

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13

14 **Abstract**

15 Few avian species use tools in the wild. Yet, several birds build nests of great complexity and
16 many aspects of tool use may also apply to nest building. It has long been hypothesised that
17 tool use may select for specialised cognitive adaptations or even general cognitive skills. This
18 might similarly pertain to species that build complex nests. In this study, we investigated the
19 problem-solving capacity of a complex nest builder, a weaverbird species, in a foraging context
20 that either required or did not require the use of tools. First, we tested the capacity of yellow-
21 crowned bishops (*Euplectes afer* ssp. *afer*) to use a tool for retrieving an out-of-reach reward
22 during three problem-solving tasks offering different nest/non-nest materials (Experiment 1).
23 Next, subjects were confronted with two problem-solving tasks that required no tools
24 (Experiment 2) to assess their problem-solving ability without tools. No subject was able to use
25 a tool in Experiment 1. However, 11 out of 12 subjects succeeded using their beak in the first
26 problem-solving task, and 9 in the second problem-solving task of Experiment 2. These results
27 suggest that weaverbirds showed flexible problem-solving if the use of tools was not required.

28

29 **Keywords:** ecological utility; nest building; problem solving; tools are not often useful
30 hypothesis; tool use; weaverbird

31

32 **1. Introduction**

33 The belief that tool use reflects complex cognition has long been enshrined in comparative
34 psychology (Bird and Emery, 2009; Brosnan, 2009; Emery and Clayton, 2004; Hansell and
35 Ruxton, 2008; van Schaik et al., 1999). However, tool use and complex cognition need to be
36 dissociated, as the former often arises from quite simple mechanisms (e.g. genetic influences,
37 Tebbich et al., 2001; Kenward et al., 2005). To examine the complexity of the processes
38 underlying tool use, one has to study *how* the tool is employed (Byrne, 1997). For instance, do
39 subjects comprehend the functional properties of a task (e.g. von Bayern et al., 2009), or those
40 of the tools they are using (e.g. Weir et al., 2002)? Is tool use only observed in a very specific
41 context or flexibly employed (e.g. Wimpenny, 2011)? Do subjects use tools depending on their
42 necessity (e.g. Danel et al., 2017)?

43 Whereas tool use in animals has received attention by various disciplines, nest building has
44 long been neglected with respect to cognitive evolution (Healy et al., 2008). The reason for this
45 may be the putative role tool use has played in human brain evolution (Byrne, 2004; Gibson et
46 al., 1994; Keller and Keller, 1996; Osiurak and Reynaud, 2020; Vaesen, 2012), whereas nest
47 building is a behaviour predominantly observed in birds and commonly assumed to be mainly
48 under genetic control (Raby and Clayton, 2009; Seed and Byrne, 2010).

49 Similarly to tool use, and as Alfred Russel Wallace pointed out more than a century ago,
50 nest building does not rely solely on instinct (Healy et al., 2008; Healy et al., 2015). This
51 affirmation is supported by recent circumstantial evidence of decision making and flexibility in
52 different bird species, ranging from choosing (i) *where* to build (given the environment's
53 unpredictability, e.g. the topography of the nest site; Hansell, 2000), by finding a suitable place
54 to incubate eggs or rear nestlings (Gauthier and Thomas, 1993; Reed et al., 2014); (ii) *what* to
55 build, by selecting and sometimes manufacturing nest materials with appropriate properties
56 (Muth and Healy, 2014); and (iii) *how* to build, by experiencing and learning how to improve
57 the construction behaviour over time (Borgia et al., 1985; Maxwell, 2004; Walsh et al., 2010).
58 Nest-building behaviour might therefore provide an opportunity to study cognition from an
59 ecologically relevant perspective in several avian species (e.g. planning ability, memory,
60 behavioural flexibility, Healy et al., 2008; Hansell and Ruxton, 2008), and to further understand
61 its evolution (Guillette and Healy, 2015).

62 Nest building also involves selection and manipulative components that resemble tool use
63 in many ways (e.g. great apes, *Pan*: Manrique et al., 2010; great tits, *Parus major*: Gosler et al.,
64 2020; capuchin monkeys, *Cebus apella*: Manrique et al., 2011; New Caledonian crows, *Corvus*
65 *moneduloides*: Chappell and Kacelnik, 2002; zebra finches, *Taeniopygia guttata*: Muth and

66 Healy, 2014). Noteworthy, similarly to some tool-using species (e.g. Brosnan, 2009;
67 Holzhaider et al., 2010; Visalberghi et al., 2009), the selection of suitable nest-building
68 materials is not entirely genetically determined but requires experience and learning in certain
69 non-tool using species (Bailey et al., 2017). Aspects of learning (e.g. trial-and-error learning)
70 during nest building have also been suggested to parallel tool material choice exhibited by
71 certain nonhuman primates (Muth and Healy, 2014). Considering the flexible object
72 manipulation observed in many nest-building species, holding a tool in order to access an out-
73 of-reach prey does not seem to be more difficult to perform than using various materials to
74 build a nest (Ruxton and Hansell, 2008). For instance, Duyck and Duyck (1984) reported the
75 case of a great tit using a pine needle as a tool to probe for prey in wood crevices. Transfer of
76 nest-building capacity to the context of tool use may have occurred in some other notable
77 builders that also use tools in the wild (e.g. beavers *Castor Canadensis*: Barnes, 2005;
78 chimpanzees *Pan troglodytes*: Pruetz and Bertolani, 2007).

79 However, it still remains unclear whether complex nest construction involves similar
80 cognitive capacities as those employed during flexible tool use (Muth and Healy, 2014). It is a
81 possibility that complex nest builders may be capable of harnessing the skills underpinning nest
82 building to problem-solving situations involving simple tools (e.g. sticks for reaching, rocks for
83 pounding, Johnson-Frey, 2004; Osiurak, 2017; Osiurak et al., 2017), especially when their
84 construction behaviours involve decision making, flexibility, and complex manipulative skills
85 (Hansell and Ruxton, 2008; Healy et al., 2008).

86 Weaverbirds (*Ploceidae*) stand out among birds for the intricacy of their nests (Hansell,
87 2010; Healy et al., 2008). In ploceids, males construct the majority of the nest while the females
88 line its inner part (Craig, 2017). Although nest structure varies considerably between species,
89 all constructions involve a particularly difficult technique of assembling materials (i.e. weaving:
90 Howman and Begg, 1995). When starting their nests, some weaverbirds are able to select the
91 appropriate green leaf strips, by tearing and pulling them from the substrate (e.g. village
92 weavers, *Ploceus cucullatus*: Collias and Collias, 1964). Males subsequently create a spiral
93 wrapping around the branch, sometimes by using both their feet and beak (e.g. the male red-
94 billed weaver, *Quelea quelea*: Chapin, 1954; Friedmann, 1922). To solidly secure this latter
95 attachment, weavers use loops, knots, or hitches of various kinds (e.g. half hitch, loop tuck, slip
96 knot, overhand knot: Collias and Collias, 1964), which may require skill learning (Hansell,
97 2010). When weaving, birds intertwine nest materials by, for instance, passing/pushing the
98 grass inside the developing nest, grasping its end, and pulling it through into the centre of the
99 gradually forming nest structure (Hansell, 2010; Hansell and Ruxton, 2008). In the few species

100 tested to date (e.g. Southern masked weavers, *Ploceus velatus*, and village weavers), the
101 weaving skill of individuals gradually develops with increasing experience (Collias and Collias,
102 1964; Walsh et al., 2010, 2011). Furthermore, when a deprivation method experimentally varied
103 the availability of green grass in captivity, two ontogenic studies found that nest-building skills
104 of naïve young male village weavers were affected, suggesting that learning and practice were
105 implicated (Collias and Collias, 1964; Collias and Collias, 1973). Yellow-crowned bishops may
106 therefore provide an excellent opportunity for testing the possibility that the cognitive abilities
107 (e.g. learning and flexibility) used during complex nest-building in some birds may be
108 transferable to the context of tool use (Muth and Healy, 2014).

109 The aim of this study was to examine problem solving in a tool/non-tool related context in a
110 weaverbird species building particularly complex nests, the yellow-crowned bishop (*Euplectes*
111 *afer afer*). This African weaverbird lives in open grassy valleys generally at low altitudes where
112 it forms mixed flocks and exhibits a polygynous mating system (Craig, 1980, 2017; Pryke et
113 Andersson, 2008; Winterbottom, 1971). During the breeding season, however, males become
114 territorial and build their nests in very wet areas (e.g., swamps or seasonally flooded habitats:
115 Craig, 1974, 2017; Lynes, 1924), which consist of woven oval ball structures with a side
116 entrance near the top (Howman and Begg, 1995). During nest building (sometimes repeatedly
117 in the same breeding season, e.g. the Southern masked weaver: Walsh et al., 2011), they engage
118 in various motor actions that may also be relevant when handling a tool, including tearing,
119 grasping, carrying, inserting, pulling, or pushing. One might therefore expect the weaverbirds
120 to exhibit sufficient motor as well as flexibility to use simple tools, requiring the grasping and
121 the inserting of a commonly used nest material in order to get a food reward.

122 For that purpose, we assessed the problem-solving ability of twelve male yellow-crowned
123 bishops in a foraging problem-solving context involving tool use and one that did not require
124 the use of tools. In Experiment 1, three tool-use tasks were presented that required the subjects
125 to use a tool to retrieve an out-of-reach food reward from an apparatus. In contrast, Experiment
126 2 required the use of the beak to get access to a food reward, either by pushing or lifting a short
127 straw (problem-solving task 1), or by pulling or pushing the opaque lid of a container (problem-
128 solving task 2). If complex nest-building shares with flexible tool-use similar cognitive
129 processes, we predict yellow-crowned bishops to perform equally well in both experiments. If,
130 on the other hand, flexible tool-use is more cognitively demanding than complex nest building,
131 we predict successful problem solving within the non-tool-related context only (i.e. Experiment
132 2: involving the use of the beak).

133 **2. Materials and methods**

134 2.1. Experiment 1: tool-use tasks

135 This experiment tested whether yellow-crowned bishops could use a tool to retrieve an out-of-
136 reach food reward from an apparatus. Three tasks, that shared the same functional properties
137 but had no visual features in common, were carried out, in order to assess whether the subjects
138 relied on functional rather than perceptual cues of the apparatus to solve the task. Tool-use tasks
139 1 and 2 aimed at testing the capacity of yellow-crowned bishops to show spontaneous tool use.
140 Tool-use task 3 examined the subjects' performance before and after experience (use and
141 manipulation) with a novel tool material through nest-building behaviour.

142 2.1.1. Subjects

143 Twelve adult yellow-crowned bishops (*Euplectes ssp. afer afer*) were tested at a professional
144 bird breeding centre in L'Isle-D'Abeau, Auvergne-Rhône-Alpes, France. All birds were males
145 (based on nuptial plumage coloration and nest-building behaviour) and had a minimum age of
146 1 year. At the onset of the experiment (i.e. during the breeding season: Aug-Oct, when bishops
147 normally engage in nest-building behaviour), bishops were housed momentarily in individual
148 wooden cages (39.5 cm x 42.5 cm x 43 cm), and were maintained under a 12:12h dark-light
149 cycle. Throughout the day, the subjects had *ad libitum* access to fresh water and food, which
150 consisted of an exotic seed mix (Versele Laga Prestige Tropical finches®). Tests took place
151 each morning before feeding (10 a.m.). Prior to this study, the subjects have been tested in an
152 unrelated social-learning task conducted by Danel et al. (2019).

153 2.1.2. Materials

154 The apparatus used for Tool-use task 1 consisted of a long and transparent deep-yellow box (13
155 cm in length; back: 5.4 cm in width x 3.5 cm in height; front: 5.7 cm in width x 3.8 cm in height)
156 with a slot at the front for tool insertion (1.1 cm in height; **Figure 1a**). In this task, the species'
157 usual nest-building material (fresh and long strands of grass: Collias and Collias, 1984) was
158 provided as potential tools and comprised twelve short grass stems (six dry ones: 'stiff', six
159 fresh ones: 'flimsy'; 7 cm in length), and twelve long grass stems (six 'stiff' and six 'flimsy'
160 ones; 15 cm in length). The food reward consisted of seeds filled onto the bottom of the box,
161 out of the birds' reach.

162 In Tool-use task 2, we used a rectangular box (9.5 cm x 6 cm x 2 cm) covered with a clear
163 Perspex top. The box contained seeds and had a slot on its front side (1.5 cm in height; **Figure**
164 **1b**). Subjects were provided with twelve toothpicks of different lengths (6 tools of 3.5 cm and
165 6.3 cm, respectively).

166 The apparatus of Tool-use task 3 was a small plastic cup (5.6 in length; back: 2.8 cm in width
167 x 2.1 cm in height; front: 4.2 cm x 4.1 cm in height; **Figure 1c**) with a front slot (1.3 cm in

168 height) into which a tool could be inserted. The cup was fixed horizontally on a rounded terra
169 cotta platform (9.8 in diameter, 2.3 in height) and slightly inclined with three sticks (9 mm in
170 length), allowing the subjects to see the seeds at the bottom of the cup. The birds were given
171 twenty raw coco fibres that varied in length (between 4 to 10 cm).

172 A camera (one Samsung HMX-F90, two Ordoro HDV-Z8 1080P) setup on a tripod in front
173 of each apparatus recorded the test trials.

174 < Insert Figure 1 about here >

175 **2.1.3. Procedure**

176 In all three tool-use tasks, the subjects were required to pick up a tool and insert it into a slot in
177 the front of the apparatus until reaching the reward, and then *pull/rake* the reward gradually out
178 of the apparatus. Subjects were first familiarized with the recording equipment and each
179 unrewarded apparatus for two hours.

180 2.1.3.1. Tool use task 1

181 Subsequently, fifteen test trials were administered per subject (15 min each, usually two trials
182 per day, inter-trial interval of 2 hours minimum). The order in which subjects participated
183 changed randomly from day to day.

184 2.1.3.2. Tool use task 2

185 The procedure was the same as in the Tool-use task 1, except that the tools were located in a
186 rounded terra cotta container on the right side of the cage and at a distance of about 15 cm from
187 the apparatus.

188 2.1.3.3. Tool-use task 3

189 Subjects were randomly assigned to two experimental groups. Prior to being tested, the six
190 individuals of group 1 (Asc., Ast., Coé., Hél., Océ., Pro.) were allowed to gain experience with
191 the properties of the novel tool material through nest building. For that purpose, bishops were
192 provided with coco fibres, a natural nest material they never encountered before (previously
193 they had only built nests with natural grass material) for six days until they had completed a
194 nest. The six subjects of group 2 (Cri., Cro., Jap., Lel., Mén., Oph.), in contrast, were not
195 allowed to use coco fibres for nest building. In the subsequent test phase, bishops were given
196 ten trials of fifteen min each (usually two trials per day, inter-trial interval of 2 hours minimum)
197 in which we assessed whether they were able to use the coco fibres to remove the food reward
198 from the foraging apparatus.

199 **2.1.4. Coding and analysis**

200 All test trials were video recorded and continuous second-by-second coding of the videos was
201 performed for all experiments. For the three tool-use tasks, we coded the behaviour of each

202 individual ($n = 12$) and in each trial (e.g. Tool-use task 1: 15 trials in total) following a coding
203 scheme including ten behaviours divided into three categories i.e., Ineffective (1 = perch on the
204 apparatus; 2 = insert beak in the apparatus), Exploratory (3 = look: head and eyes directed at
205 the apparatus from perch; 4 = look through apparatus's opening; 5 = touch box; 6 = touch tool;
206 7 = shake box), and Effective (8 = pick up a tool; 9 = lift a tool; 10 = insert a tool in the
207 apparatus). Based on this coding scheme, the number of behaviours exhibited by each bird was
208 counted by assigning a score of 1 when this behaviour lasted at least 1 s. For instance, when a
209 subject picked up a tool (Effective behaviour) during at least 1 s, this behaviour was coded as
210 1 (1 s). When no behaviour from the coding scheme was reported over trials, this was coded as
211 0 (0 s). The variable measured thus corresponded to the time each behaviour lasted in each trial
212 - or the count of each behaviour occurring during each trial (e.g. 15 trials in total, one trial: 15
213 min so 900 s).

214 In Experiment 1 (tool-use tasks), the use of Linear Mixed models was irrelevant as our
215 variable response involved count data (i.e. discrete variable) and the assumptions of normality
216 and homoscedasticity were violated. We therefore implemented Generalized Linear Mixed
217 models with a Poisson error structure or a negative binomial structure when overdispersion was
218 reported (see below).

219 Using preliminary data exploration, we did not report the same sampling variation between
220 the modalities *Effective*, *Exploratory*, and *Ineffective* of the variable *Category* (see **Figure S1**
221 in Supplementary Materials). As potential differences in interaction including the variable
222 *Category* may be due to an unbalanced sampling rather than a real ecological effect (Ieno and
223 Zuur, 2015), we implemented three GLMM models for each of the three modalities (*Effective*,
224 *Exploratory*, and *Ineffective*). The variable *Experiments* showed no variation between
225 modalities (Tool-use task 1, Tool-use task 2, and Tool-use task 3; see **Figure S2**). Therefore,
226 we did not add this variable in the statistical analyses.

227 In Model 1 (*Effective* behaviours), we used a GLMM with a Poisson error structure. *Test*
228 (count data i.e. number of *Effective* behaviours exhibited) was set as dependant variable, *Trials*
229 (1 vs 2 vs ...10) as fixed factor, and *Subject* (i.e. subject's identity) as random effect. In Model
230 2 (*Exploratory* behaviours) and Model 3 (*Ineffective* behaviours), Poisson GLMM showed
231 overdispersion (i.e. score: 9.28 and 16.53, respectively). Thus, we conducted a GLMM with a
232 negative binomial error structure for those two models. Same variables were used to carry out
233 these Model 2 and Model 3.

234 We used the packages *ggplot2* for plotting the data (Wickham, 2016), *lme4* for fitting
235 Generalized Linear Mixed-Effects Models (Bates et al., 2015). GLMM analyses were
236 conducted in R 3.6 (R Core Team 2019).

237 2.2. Experiment 2: problem-solving tasks (without tools)

238 2.2.1. Subjects

239 Same as in *Experiment 1*.

240 2.2.2. Materials

241 2.2.2.1. Problem-solving task 1

242 The reward was stuck into a short straw (8.5 cm in length, 8 mm in diameter) plugged at one
243 end. The seeds did not exceed 6.5 cm of the straw (**Figure 2a**).

244 2.2.2.2. Problem-solving task 2

245 The reward was located within a circular plastic container (6 cm x 3 cm) with a removable
246 opaque white lid on its top (**Figure 2b**). For stability, the box was fixed on a round cardboard
247 (13 cm in diameter).

248 < Insert Figure 2 about here >

249 2.2.3. Procedure

250 Problem-solving task 1 - In this task, the straw was placed at the centre of the cage and subjects
251 were tested in one single trial of 20 min.

252 Problem-solving task 2 - Subjects were first confronted with a pre-test phase, in which they had
253 to feed from the plastic container eight consecutive times before they were allowed to proceed
254 to the test phase. The latter consisted of a single trial of 30 min, during which a lid covered the
255 container. The subjects had to push or lift the lid with the beak to solve the task.

256 2.2.4. Coding

257 For the two problem-solving tasks, we scored each subject's latency (in s) to solve the task
258 as well as the technique displayed.

259 3. Results

260 3.1. Model 1: effective behaviours

261 No subject succeeded in inserting a tool within the foraging apparatus to get access to the reward
262 in this experiment. Among effective behaviours, *picking up a tool* (Tool-use task 1: $n = 8$, i.e.
263 Asc., Ast., Coé., Cri., Cro., Jap., Océ., Pro.; Tool-use task 2: $n = 3$, i.e. Asc., Océ., Pro.) and
264 *lifting a tool* (Tool-use task 1: $n = 2$, i.e. Asc., Océ.) were the two reported actions. Materials
265 used during effective behaviours consisted of short flimsy grass stems (*picked up* and *lifted* in
266 Tool-use task 1), and 3.5 cm in length toothpicks (*picked up* in Tool-use task 2).

267 There was a significant effect of *Trials* (0.14 ± 0.02 , $z = 7.11$, $p < .001$) during the experiment
268 (estimated parameters are provided in **Table 1**). Subjects indeed increased their effective
269 behaviours towards the tools along trials during tool-use tasks. This effect, although significant,
270 was moderate when we calculated the exponential of the coefficient (corresponding to an
271 increase of 1.15 per trial).

272 < Insert Table 1 >

273 3.2. Model 2: exploratory behaviours

274 All the panel of exploratory behaviours was reported among subjects during the experiment i.e.,
275 *look: head and eyes directed at the apparatus from perch* (Tool-use task 1 - $n = 11$: except Hél.;
276 Tool-use task 2 and Tool-use task 3 - $n = 12$), *look through apparatus's opening* (Tool-use task
277 1 - $n = 12$; Tool-use task 2 - $n = 11$: except Lél.; Tool-use task 3 - $n = 8$: except Asc., Coé., Lél.,
278 Pro.), *touch box* (Tool-use task 1: $n = 12$; Tool-use task 2: $n = 10$, i.e. except Coé., Mén.; Tool-
279 use task 3 - $n = 11$: except Lél.), *touch a tool* (Tool-use task 1 - $n = 3$: Hél., Jap., Lél.; Tool-use
280 task 2 - $n = 2$: Océ., Oph.; Tool-use task 3 - $n = 1$: Ast.), and *shake box* (Tool-use task 1 - $n =$
281 6: except Hél., Jap., Lél. Mén., Oph., Pro.; Tool-use task 2 - $n = 10$: except Ast., Asc.; Tool-use
282 task 3 - $n = 0$).

283 There was a significant effect of *Trials* (-0.11 ± 0.02 , $z = -7.13$, $p < .001$) during the
284 experiment (see **Table 1**), and subjects showed a moderate decrease of their exploratory
285 behaviours over trials.

286 3.3. Model 2: ineffective behaviours

287 Ineffective behaviours were widespread among subjects i.e., *put beak in the apparatus* (Tool-
288 use task 1 - $n = 8$: except Asc., Ast., Coé.; Tool-use task 2 - $n = 8$: except Hél., Jap., Lél.; Tool-
289 use task 3 - $n = 1$: Cri.), *perched on the apparatus* (Tool-use task 1 - $n = 12$; Tool-use task 2 -
290 $n = 12$; Tool-use task 3 - $n = 0$).

291 No significant effect of the variable *Trials* was reported (-0.03 ± 0.03 , $z = -1.04$, $p < .001$;
292 see **Table 1**).

293 3.2. Experiment 2: problem-solving tasks (without tools)

294 3.2.1. Problem-solving task 1

295 Eleven out of twelve subjects succeeded to solve the task by pushing the straw around
296 causing the seeds to move out, either at once or through repeated thrusts. One subject (Asc.),
297 however, used a different behavioural technique, by lifting the straw up with its beak (**Table**
298 **2**).

299 3.1.2. Problem-solving task 2

300 Nine out of twelve subjects were able to open the box, mostly by pushing the lid with the
301 beak (**Table 4**). Two of those individuals (Cro. and Pro.) additionally shuck the transparent
302 container with the beak.

303 < Insert Table 2 about here >

304 **4. Discussion**

305 Although all bishops failed to use simple tools in Experiment 1, the majority of subjects was
306 successful when the tasks required the use of the beak in Experiment 2. Although the birds were
307 capable of solving novel problems not involving tools and thus showed some form of
308 behavioural flexibility, they did not come up with tool use as the solution to a foraging problem.
309 Despite bishops' significant manipulative skills and nest-building sophistication, these results
310 suggest that tool use may require specific cognitive processes (Hunt et al., 2013; Visalberghi et
311 al., 2017) and that nest building is highly context-dependent in this species.

312 However, several potentially confounding factors may have masked the birds' actual
313 capacity to use tools, and these need to be discarded before discussing our results further. One
314 potential confound may be that, in all tool-use tasks, subjects were required to retrieve seeds
315 from the apparatuses by pulling the tool towards them. Problem-solving task 2 suggests that the
316 birds may have been better at pushing, as all subjects succeeded to open the box by pushing the
317 lid with the beak, whereas no subject has tried to pull the lid. If indeed pulling was not part of
318 the species' behavioural repertoire, our tasks would not have been ethologically valid (Seed et
319 al., 2006). Nevertheless, this possibility seems unlikely. Bishops, and weavers generally,
320 frequently pull grass materials when building their nests (Hansell, 2000), and this pulling
321 pattern is natural among passerines (Johnsson and Brodin, 2019). Moreover, pulling the reward
322 towards oneself with a tool (rather than pushing it away) is generally considered to arise easier,
323 because the perceptual feedback of the reward moving gradually closer towards the subject is
324 positively reinforcing its actions (Tebbich et al., 2007; Jacobs and Osvath, 2015; Mulcahy and
325 Call, 2006), and may act as a facilitator (Hare, 2001).

326 Another potential factor hindering the birds' success may be a morphological limitation i.e.,
327 the slight curvature of the beak. This feature may have prevented them from holding a straight
328 tool in alignment with their head properly, thus hindering them to solve the task. Although
329 skilled stick-like tool use may be facilitated by a straight beak and an extreme binocular vision
330 in some corvids (e.g., Hawaiian crow, *Corvus hawaiiensis*: Rutz et al., 2016; New Caledonian
331 crows *Corvus moneduloides*: Troscianko et al., 2012), some individuals of other bird species
332 with quite curved foraging apparatuses are able to use tools (e.g., great white pelicans,
333 *Pelecanus onocrotalus*: Danel et al., submitted work; keas, *Nestor notabilis*: Auersperg et al.,

334 2011) and manufacture tools in the laboratory (e.g., rooks, *Corvus frugilegus*: Bird and Emery,
335 2009). Further, as discussed before, weavers' nests are considered as the most behaviourally
336 demanding of all other types of avian construction identified to date (Hansell, 2000) and involve
337 important dexterity and the choosing of grass materials that vary significantly in terms of their
338 functional properties (e.g. substance, size, shape, malleability, strength). It seems unlikely that
339 simple tool use (i.e. in our case, picking up and inserting a stick-like tool inside the apparatus)
340 was too difficult for the birds to perform. Therefore, we consider it unlikely that beak
341 morphology has constrained tool use in yellow-crowned bishops.

342 One may argue that tool-use behaviour may not have been selected for in yellow-crowned
343 bishops, because this capacity does not seem to provide any foraging benefit in humid climates.
344 This 'tools are not often useful' hypothesis (Hansell and Ruxton, 2008) has been assumed to
345 apply to other bird species (e.g. parrots: Lefebvre et al., 2002) as well as to distantly animal
346 groups (e.g. regarding the variation in the use of 'fishing tools' between different populations
347 of chimpanzees, *Pan troglodytes*: Pruetz and Bertolani, 2007; or the use of sponge tools by
348 females in some populations of bottlenose dolphins, *Tursiops truncatus*: Smolker et al., 1997).
349 Following this line of reasoning, however, would imply that the birds may be able to use tools
350 when it is beneficial, such as in the present study (Visalberghi et al., 2017).

351 Our results do not support the assumption that flexible notable nest builders may be capable
352 of spontaneous stick-like tool-use when confronted with a problem-solving situation. Although
353 effective behaviours significantly increased over trials, subjects that lifted or picked up a tool
354 never directed their behaviours towards the foraging apparatus. Moreover, the decrease in
355 exploratory behaviours over trials is unlikely to mirror the understanding or acquisition of the
356 tasks (e.g. through learning processes). We rather believe that this pattern reflected a
357 progressive lack of motivation. Bishops' behaviours resemble those found in another passerine:
358 the wild-caught great tit (*Parus major*), which failed to use tools despite facilitation (Johnsson
359 and Brodin, 2019). Indeed, like yellow-crowned bishops, none of the great tits attempted to
360 insert tools into the foraging apparatus. The absence of association between the effective
361 behaviours reported (e.g. picking up a tool) and the foraging apparatus itself raises the
362 possibility that great tits and yellow-crowned bishops may lack specific cognitive capacities for
363 using tools. Comprehending the relationship between an object and the solving of a physical
364 task may require the initial physical understanding that some objects can be used as tools
365 (Amodio et al., 2018; Hunt, Gray, & Taylor, 2013; Visalberghi et al., 2017). Without this first
366 'cognitive step', species could not transfer their experience with objects (e.g. nest materials) to
367 a problem-solving situation where they would have served as a tool. It is a possibility that object

368 manipulation, although considered as a precursor to tool use in animals (Hayashi and
369 Matsuzawa, 2003; Johnsson and Brodin, 2019; Koops et al., 2015), may promote flexibility for
370 bishops' nest-building skills only. For instance, although inexperienced weaverbirds
371 manipulate and select functionally dissimilar nest materials during their first nest-building
372 attempts, they tend to develop preferences for more suitable materials with experience (Collias
373 and Collias, 1964).

374 Our results also lead us to evaluate the absence of tool use in bishops in light of the well-
375 discussed theory which posits that tool use is a by-product of domain general intelligence (e.g.
376 Kacelnik et al., 2009). Keas, for instance, that normally do not use tools in the wild, are able to
377 use several tools flexibly in captivity (e.g. stone-tools: Auersperg et al., 2010; Auersperg et al.,
378 2011). These findings, along with other studies on flexible tool-use in non-tool-using species,
379 may suggest that tool use is a by-product of domain general intelligence (e.g. Bird and Emery,
380 2009; Emery and Clayton, 2004; Kacelnik et al., 2009). Future studies, systematically
381 comparing the cognitive abilities and problem-solving performance (both involving tool use
382 and non-tool use) of habitually non-tool using species are necessary to test this hypothesis.
383 Moreover, we used transfer tasks to assess subjects' capacity to generalise - *transfer* -
384 previously learned rules across functionally equivalent tasks with different perceptual features
385 (e.g. van Horik and Emery, 2016; von Bayern et al. 2018). These tasks involved the same motor
386 actions i.e. inserting and then pulling a tool. Other tasks may be designed so that subjects need
387 to display different actions, such as pushing or dropping a tool down a platform apparatus to
388 release food (e.g. Bird and Emery, 2009; Logan, 2016). Along with the administration of many
389 more trials (*learning* to use tools), these investigations may allow us to firmly exclude the
390 possibility that yellow-crowned bishops may use tools spontaneously. As materials' handling
391 may be strongly context-dependent in bishops, future studies should also investigate whether
392 interaction with stick-like materials in these and other complex nest-builders may be restricted
393 to the breeding domain and/or the breeding season.

394 **5. Conclusions**

395 Although yellow-crowned bishops appear to be flexible problem solvers, they were not able
396 to use tools in our tests. It seems likely that their incapacity to use tools in a problem-solving
397 situation under controlled conditions relates to cognitive rather than methodological
398 constraints. However, conclusions should be drawn carefully as they originate from the
399 observation of only one weaverbird species. Further systematic cross species comparisons are
400 required to draw firm conclusions, which may compare tool-related/non-tool-related cognitive
401 abilities of species differing in their nest-building intricacy.

402 **Declarations**

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410 *Ethics* – The research conforms to the 'Guidelines for the use of animals in research' as
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625 **Table 1** - *GLMM estimates of Test by each Category (Effective, Exploratory, or Ineffective)*
 626 *and Trials*

Variable	Estimate	SE	z	Pr(z)
<i>GLMM Effective</i>				
Intercept	-5.24	0.69	-7.64	< .001
<i>Trials</i>	0.14	0.02	7.11	< .001
<i>GLMM Exploratory</i>				
Intercept	1.49	0.20	7.33	< .001
<i>Trials</i>	-0.11	0.02	-7.13	< .001
<i>GLMM Ineffective</i>				
Intercept	1.44	0.32	4.56	< .001
<i>Trials</i>	-0.03	0.03	-1.04	< .001

627

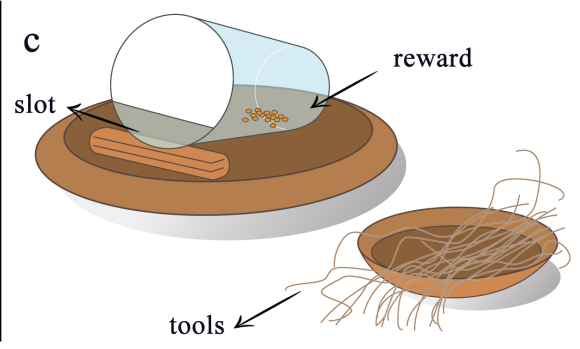
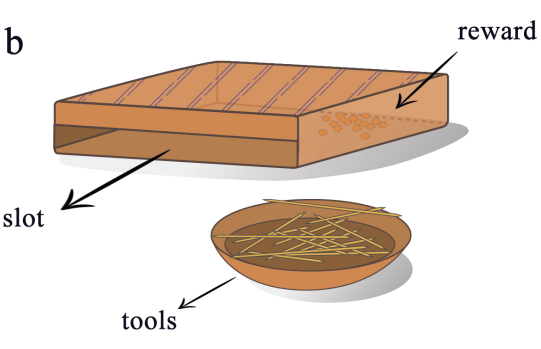
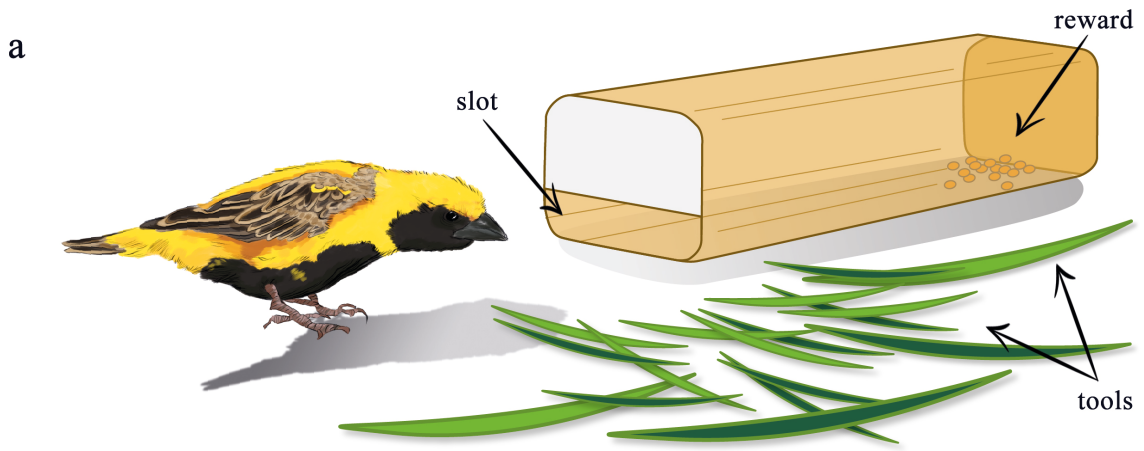
628 **Table 2** - Individual performance of subjects during both problem-solving tasks. The latency
 629 (in sec) and the technique used to access the reward are reported. (l) identifies the opaque lid
 630 of the box, (c) identifies the plastic container of the box.

Subjects	Problem-solving 1		Problem-solving 2	
	Latency time (sec)	Technique	Latency time (sec)	Technique
Asc.	36	lift	01:34	push (l)
Ast.	39	push	22:27	push (l)
Coé.	86	push	02:19	push (l)
Cri.	27	push	0	0
Cro.	35	push	01:37	push (l)/shake (c)
Hél.	0	0	03:04	push (l)
Jap.	75	push	0	0
Lél.	29	push	24:34	push (l)
Mén.	77	push	0	0
Océ.	22	push	02:13	pull (l)
Oph.	17	push	02:28	push (l)
Pro.	21	push	00:38	push (l)/shake (c)

631

632 **Figures**

633 **Figure 1.**



634
635
636

637 Figure 2.

a



b



638

639

640 **Figure captions**

641 **Figure 1.** Schematic representation of the apparatuses used during the 3 tool-use tasks in
642 Experiment 1. In order to access the out-of-reach reward inside each apparatus, subjects had to
643 pick up a tool on the ground and to insert it into the box's slot. Panel (A) represents the tool use
644 task 1, the apparatus consisted in a long and transparent deep-yellow box and the tools were
645 grass stems. Panel (B) represents the tool-use task 2, the apparatus was a horizontal box and the
646 tools were toothpicks. Panel (C) represents the tool-use task 3, the apparatus was a horizontal
647 little plastic cup and the tools were coco fibres. In this task, subjects were divided into two
648 groups. The group 1 was first allowed to experience nest building (by building a nest with coco
649 fibres), while the group 2 was not allowed to do so. After this experience phase 1, both groups
650 were subsequently confronted to the tool use task 3. Subjects were then presented with the
651 experience phase 2, in which the group 1 was now not allowed to build a nest, and conversely
652 for group 2. Both groups were once again tested with the tool use task 3.

653 **Figure 2.** Schematic representation of the problem-solving tasks used during Experiment 2.
654 Panel (A) shows the apparatus of the problem-solving task 1, the subjects can either lift/push a
655 one-side plugged straw with the beak to make the reward go out. Panel (B) shows the problem-
656 solving task 2, the subjects have to push the opaque lid of the box to get access to the reward.