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Samara Danel, Auguste M.P. von Bayern, François Osiurak. Great white pelicans (Pelecanus onocrotalus) fail to use tools flexibly in problem-solving tasks. Ethology, 2021, 128 (2), pp.99-110. 10.1111/eth.13243 . hal-04005949

HAL Id: hal-04005949 https://hal.science/hal-04005949v1

Submitted on 27 Feb 2023 $\,$

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1	Great white pelicans (Pelecanus onocrotalus) fail to use tools flexibly
2	in problem-solving tasks
3	Running title: Tool use in pelicans
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17	Acknowledgments of support:
18	This work was supported by grants from the Agence Nationale de la Recherche (ANR)
19	(Project "Cognition and tool-use economy", ECOTOOL, ANR-14-CE30-0015-01; to FO),
20	and was performed within the framework of the LABEX CORTEX (ANR-11-LABX-0042)
21	of the University of Lyon, within the program Investissements d'Avenir (ANR-11-IDEX-

of the University of Lyon, within the program Investissements d'Avenir (ANR-11-IDEX-

0007; to FO) operated by the ANR. We thank the Bird Park's (Ain, France) scientific board

for the authorization to provide environmental enrichments through non-invasive behavioural

experiments on captive pelicans. Samara Danel is very grateful to Sébastien Marcle for

helping in the experiments and general support, and to Fauna Stats for statistical training and

useful advice. We also thank two anonymous reviewers for their constructive comments.

27 Abstract

28 Although reports of animal tool-use are phylogenetically widespread, it remains rare in the 29 wild. From the perspective of human evolution, this rarity was first explained by the 30 cognitive demands associated with tool use. Recently, an alternative assumption, 'the tools 31 are not often useful' hypothesis, proposes that tool use is rare, because it is seldom more 32 useful than the species' anatomical adaptations. At the same time, several species that do not 33 use tools in the wild have shown the capacity for tool use in experimental problem-solving 34 settings, which suggests a certain level of cognitive flexibility. Investigating whether habitually non-tool using species are able to use tools flexibly is crucial to evaluate the 35 36 predictions of existing theories on the evolution of cognition. In this study, we tested whether 37 great white pelicans (*Pelecanus onocrotalus*), morphologically specialised fishers, for whose natural foraging tools are unlikely to be of use, were able to use tools in two problem-solving 38 39 situations. In two tasks, the subjects were required to drop tools into an apparatus to gain 40 access to a food reward. In Tool-use task 1, we tested the capacity of pelicans to show spontaneous tool-use behaviour. In Tool-use task 2, we assessed the birds' tool-using 41 42 performance, before and after providing them with different kinds of information about the task's solution, that is experience with the functional features of the apparatus ('platform-43 44 pushing group') and trial-and-error learning of tool-dropping behaviour ('stone-nudging group'). All subjects failed in using tools in Tool-use task 1 and only one individual in the 45 46 stone-nudging group learnt to use a tool in the training phase of Tool-use task 2. Despite 47 previous experience with the functional properties of the task, birds from the platform-48 pushing group did not exhibit tool-use behaviour or increased motivation towards the 49 apparatus and the tools during the test phase. Although pelicans were not inhibited by 50 morphological constraints to carry out the required tool behaviours, whether they lack the cognitive prerequisites for flexible tool-use remains to be further tested. 51

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53 Keywords: adaptive specialization; foraging ecology; *Pelecanus onocrotalus*; physical
54 cognition; problem solving; tool use

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61 Introduction

62 Initially considered a core feature of human evolution and intelligence (Washburn, 1959), 63 tool use is now reported in various animals, ranging from invertebrates to apes (for a review, 64 see Shumaker, Walker, & Beck, 2011). A widely used, standard definition of tool use is "The 65 use of an environmental object ... to alter more efficiently the form, position, or condition of 66 another object, another organism, or the user itself, when the user holds and directly 67 manipulates the tool during or prior to use" (Shumaker, Walkup, & Beck, 2011). For instance, a capuchin monkey (Cebus apella) uses a tool when hitting the ground with a stone 68 in search of insects, but does not use tools when engaging in object manipulations with no 69 70 apparent purpose (e.g. object play). Furthermore, according to this definition, tool use does 71 not include nest building as the manipulation of nest components involves *static* relations 72 (Visalberghi, Sabbatini, Taylor, & Hunt, 2017). In birds, numerous tool-use examples have been reported (Boire, Nicolakakis, & Lefebvre, 2002), with ever-growing evidence in the 73 74 wild (e.g. Camacho & Potti, 2018; Fayet, Hansen, & Biro, 2020, but see Farrar, 2020; Van Leeuwen, Cronin, & Haun, 2017). However, tool use remains rare in the animal kingdom 75 76 (Biro, Haslam, & Rutz, 2013; Visalberghi, Sabbatini, Taylor, & Hunt, 2017). Traditionally, this rarity was associated with the cognitive demands of exhibiting tool use i.e. the 'tools, 77 78 animal intelligence' hypothesis (Bird & Emery, 2009a; Brosnan, 2009; Van Schaik, Deaner, 79 & Merrill, 1999). In this context, numerous experimental studies have focused on large-80 brained accomplished tool users (e.g. chimpanzees, Pan troglodytes: Kühl et al. 2016, Pruetz 81 & Bertolani, 2007; New Caledonian crows, Corvus moneduloides: Hunt, 1996), and revealed 82 sophisticated cognitive capacities (e.g., Taylor, Hunt, Medina, & Gray, 2009; Povinelli, 2000; Wimpenny, Weir, Clayton, Rutz, & Kacelnik, 2009). 83

84 Nevertheless, as highlighted by Shumaker et al. (2011) in their second 'Myth', tool use does not always predict advanced cognition (Emery & Clayton, 2009; Hansell, 2000, 2007; 85 86 Mc Grew, 1993). Indeed, many instances of tool use or manufacture in animals possess a 87 significant inherited component (e.g. Kenward, Weir, Rutz, & Kacelnik, 2005; Tebbich, Taborsky, Fessl, & Blomqvist, 2001). Tool use seems also not directly associated with better 88 89 general cognitive capacities: woodpecker finches (Cactospiza pallida) and New Caledonian 90 crows do not outperform closely related, non-tool-using species in physical and general 91 cognitive tasks (Teschke, Cartmill, Stankewitz, & Tebbich, 2011; Teschke et al., 2013).

In their 'tools are not often useful' hypothesis, Hansell and Ruxton (2008) propose that *ecological utility* determines the emergence (or absence) of tool use in animals (Hunt, Gray,
& Taylor, 2013). The anhinga (*Anhinga anhinga*), for instance, forages in southern swamps

95 where it engages in a particular type of fishing, by using its specialized pointed bill as a 'harpoon' to spear prey (Davis, 2015). From an ecological perspective, foraging with a tool 96 97 does not seem to provide any selective advantage to this species, which already possesses a 98 tool-like morphological adaptation. Thus, according to this hypothesis, tool use is induced 99 when it is beneficial and practicable for the species in question given its morphological, 100 ecological, and/or behavioural features (Hansell & Ruxton, 2008; see also Bräuer, Hanus, 101 Pika, Gray, & Uomini, 2020). However, circumstances in which tool use is advantageous 102 may be actually more numerous than believed, suggesting that constraints, other than the lack 103 of ecological need, prevent tool use in birds and mammals in the wild (the 'excess-of-104 opportunity' problem: Hunt, Gray, & Taylor, 2013). Moreover, recently, an increasing 105 number of habitually non tool-using species (the 'facultative tool users') has been reported to 106 employ novel foraging tools flexibly in captivity (reviewed in Bentley-Condit & Smith, 2010; 107 Shumaker, Walkup, & Beck, 2011). This has led to the hypothesis that flexible tool-use - "the 108 production of innovative solutions to respond to challenging or new situations" (Call, 2013; 109 from Visalberghi, Sabbatini, Taylor, & Hunt, 2017) - is derivative of general-purpose 110 cognition in some species (e.g. Bird and Emery, 2009; Deaner, Van Schaik, & Johnson, 2006; see also the commentary of Kacelnik, 2009). 111

112 Providing a more complete taxonomic picture of tool-use skills in animals under 113 controlled conditions may significantly help elucidating why tool use is rare (Biro, Haslam, & 114 Rutz, 2013; Hunt, Gray, & Taylor, 2013). Among birds, for instance, in contrast to the 115 multifarious tool-use reports in the wild, captive Passeriformes have received considerable 116 attention, with much focus on habitual tool-users (e.g. corvids; reviewed in Kacelnik, 117 Chappell, Weir, & Kenward, 2006; Tebbich, Seed, Emery, & Clayton, 2007; finches: 118 Tebbich & Bshary, 2004; Teschke, Cartmill, Stankewitz, & Tebbich, 2011). Assessing tool-119 related capabilities in non-tool-using foragers that possess features generally associated with 120 flexible tool-use (e.g. brain size and innovation in birds: Lefebvre, Nicolakakis, & Boire, 121 2002; Lefebvre, 2013) is essential to comprehend to what extent ecology, cognition, and 122 morphology, influence species differences in tool use (Cheke, Bird, & Clayton, 2011; 123 Johnsson & Brodin, 2019).

The great white pelican (*Pelecanus onocrotalus*) is a highly specialised piscivorous forager (Bowker & Downs, 2008; Hatzilacou, 1996; Megaze & Bekele, 2013; Sibley, 2000) that possesses a beak functionally very similar to humans' hoop nets (Meyers & Myers, 2005; Mwema, de Ponte Machado, & Ryan, 2010; Redrobe, 2014). This sensitive feeding apparatus fulfils different functions (e.g. catching fish, stocking rain water, or ventilating the body

129 during heat; Elliott, 1992; Johnsgard, 1993; Wirtz, 1986) and has not changed during more than 30 million years, probably as a result of highly efficient adaptation to fishing (Louchart, 130 131 Tourment, & Carrier, 2011). Despite its seemingly unwieldy beak, this species shows basic 132 object manipulation outside the foraging domain. For instance, during the breeding season, 133 pelicans normally nest directly on the ground, from which they pile up natural materials 134 (grass, sticks, reeds, etc.) in order to form a nest (Brown & Urban, 1969). Object 135 manipulation is common in some captive populations, where one or more individuals take 136 and throw wood sticks on the ground, repeating this action sequence several times without 137 apparent purpose (SD, personal observation). Although this bird, and Pelecaniformes more 138 generally, is largely understudied in behavioural and cognitive sciences, we nevertheless 139 know that pelicans possess a large relative brain size (the Lefebvre's 'seventh group': 140 Lefebvre, Whittle, Lascaris, & Finkelstein, 1997) associated with slow life history including 141 late sexual and physical maturity, long incubation period, and longevity (Ricklefs, 2004). 142 Moreover, cognitive capacities, such as learning, flexibility, and innovation, are crucial to 143 learn important social aspects of foraging (Anderson, 1991; Danel et al., 2020) or to find new 144 feeding opportunities (de Ponte Machado & Hofmeyr, 2004). The great white pelican may thus represent a relevant biological model to evaluate the predictions of theories on the 145 146 evolution of tool use.

147 In this study, we aimed to assess the capacity of twelve great white pelicans to use tools in 148 two problem-solving tasks. Nest building involves specific behaviours in this species, ranging 149 from collecting, pouch storing, and disgorging materials on the ground (Brown & Urban, 150 1969; Elliott, 1992). We therefore built two devices that required a similar range of toolmanipulation behaviours (i.e. touch, pick up, drop), with a restricted need to orientate the 151 152 tools towards the apparatuses' relatively large apertures. During Tool-use task 1, we assessed 153 spontaneous foraging tool use. Subjects had to drop a tool inside an apparatus to get access to 154 an out-of-reach reward. As for the second experiment, Tool-use task 2, our goal was to 155 evaluate whether pelicans could use tools after being given experience with the functional 156 features of the apparatus ('platform-pushing group') or trial-and-error learning of tool-157 dropping behaviour ('stone-nudging group'). We administered a slightly modified replica of 158 the experimental design initially created by Bird & Emery (2009a) with rooks (Corvus 159 frugilegus), which also possess morphological constraints (Matsui et al., 2016), and further 160 employed using different methods with several other non-tool-using birds (e.g. Eurasian jays, 161 Garrulus glandarius: Cheke et al., 2011; great-tailed grackles, Quiscalus mexicanus: Logan, 162 2016; keas, Nestor notabilis: Auersperg, Gadjon, & Huber, 2010; Auersperg, von Bayern,

163 Gadjon, Huber, & Kacelnik, 2011; and Goffin cockatoos, Cacatua goffiniana: Laumer, Bugnyar, & Auersperg, 2016) and one habitually tool-using species (New Caledonian crow: 164 165 Auersperg et al., 2011; von Bayern, Heathvote, Rutz, & Kacelnik, 2009). As material 166 manipulation occurs in some specific contexts, and regarding aspects of this species' 167 cognition and behaviour, our first hypothesis predicts that pelicans will be able to use 168 spontaneously novel tools to reach an out-of-reach reward (Tool-use task 1). Our second 169 hypothesis also predicts that this species will use tools, and show increased motivation to 170 interact with the apparatus and the tools, after experience with the task is provided (Tool-use 171 task 2).

- 172 Methods
- 173 Subjects

174 Twelve captive great white pelicans were tested at the Bird Park in Villars-les-Dombes, 175 France. Five were males (Cra, Cro, Hyd, Jac, Jee), and seven were females (Asa, Bal, Coo, 176 Her, Jan, Jgo, Jyw). All subjects were adults and their age varied between 3 to 16 years. Pelicans belonged to the free-flight bird show and were brought down to 85-90% of their ad 177 178 libitum weight during the park's high season (from Mar-Nov), which was also the 179 experimental period. All birds were maintained within an outdoor enclosure of two 180 compartments (1st compartment: 17.97 x 5.88 x 2.26m, including an indoor room: 2.34 x 2.34 x 2.26m; 2nd compartment: 24.74 x 17.91 x 2.26m). Tests took place in the first compartment 181 182 each early morning from 8 a.m. to 1 p.m.

183 Statement about the STRANGEness of the test sample (based on the STRANGE 184 framework: Rutz & Webster, 2021; Webster & Rutz, 2020): all subjects initially selected lived in the same social group and contributed data (original sample). Thus, no pelican was 185 excluded due to specific "personality" types. Our sample may have been biased with at least 186 187 four of the seven STRANGE factors: first, most of our pelicans were hand-reared and 188 originated from the gene pool of the park avian collection ("Rearing history" and "Genetic 189 make-up"). Subjects' participation to the free-flight bird show also required some degree of 190 cooperation between birds and avian keepers. Second, subjects had prior experience with one 191 cognitive study ("Acclimation and habituation" and "Experience"): they had been previously 192 tested on a social-learning task conducted by Danel et al. (2020), who investigated their 193 capacity to acquire a novel behaviour by watching experienced conspecific demonstrators.

194 Apparatus

Tool-use task 1. The apparatus consisted of an inclined rectangular box with a transparent
 top that was opened at both ends. The reward was presented in the centre of the apparatus

197 inside an empty cardboard tissue box (24 x 12.5 x 7.5cm), which was held in position by a wooden protrusion (Figure 1). In the pre-test phase, the apparatus was shortened (40 x 38 x 198 199 12.5cm), so the pelican could push out the tissue box directly by inserting its beak into the apparatus's upper end. In the test phase, the apparatus was longer (85.7 x 38 x 12.5cm), so 200 201 that the tissue box containing the reward was out-of-reach. In order to retrieve the reward, the 202 subject had to pick up one of the tools provided on the ground (20 sticks: from 17.7 to 51cm 203 in length; 20 stones up to 11cm large, each stone weighted about 50g and was heavy enough 204 to collapse the tissue box), and to drop it into the box's upper end.

205

< Insert Figure 1 about here >

206 *Tool-use task 2.* The apparatus consisted of a long transparent square-formed tube (95 x 207 12 x 15cm) fixed on the centre of a board (1.5 x 59 x 40cm; Figure 2a & c). The out-of-208 reach reward was presented in the centre of a collapsible platform held up by magnets 15cm 209 above the ground. The subject had to pick up a tool on the ground (20 sticks: from 17.7 to 210 51cm long; 20 stones up to 9.5cm large) and to drop it into the mouth of the tube in order to collapse the platform and get the reward. In the experience phase, two apparatuses were 211 212 created: for the stone-nudging group, a rimmed square plank was mounted around the mouth of the tube (45.5 x 42.5 x 2.7cm), upon which a stone was placed (5cm in diameter; Figure 213 214 **2b1**). To reach the reward, the subject had to push – 'nudge' – the stone with its beak towards 215 the mouth of the tube so the tool would ultimately fall into it (Video 1, see Supplementary 216 Materials). For the platform-pushing group, the transparent square-formed tube was 217 considerably shortened (20 x 12 x 15cm; Figure 2b2). Here, the subjects had to learn about 218 the mechanism of the collapsing platform, by pushing it down directly with the beak (Video 219 1, see Supplementary Materials). The recording equipment consisted of a camera (Samsung 220 camera HMX-F90) and a tripod, which were removed from the aviary after each trial.

221

< Insert Figure 2 about here >

222 Procedure

223 *Tool-use task 1*.

Habituation phase. Subjects were familiarized with the recording equipment and the
unrewarded apparatus during two 30 min sessions (one session per day on two consecutive
days).

Pre-test phase. Pelicans were first trained to take the tissue box from the shortened
apparatus, by pushing it down with the beak. Once they had obtained the reward eight times
in a row, they were considered qualified to proceed to the test phase.

230 Test phase. Fifteen 12 min trials were administrated (usually two trials per day). On each test day, the experimenter entered the aviary and closed the door separating the first 231 232 compartment from the second compartment in order to set up the experiment. To prevent any 233 visual contact between the first compartment (the test bird) and the second compartment (the 234 rest of the group), the grid wall in between the two compartments was covered with an 235 opaque fabric. After having triggered the camera and baited the tissue box in the apparatus, 236 the experimenter allowed the subject to enter the first compartment. Participation was made 237 on a voluntary basis, so the order in which subjects participated changed randomly from day 238 to day.

239 *Tool-use task 2.*

240 Pre-test phase. Birds were presented with the apparatus and the tools (i.e. sticks and 241 stones) available on the ground during eight trials of 20 min each. This was carried out in 242 order to establish whether tool-use behaviour was already part of the species' behavioural 243 repertoire (i.e., any behaviour consisting of manipulating, displacing, and dropping one of the 244 tools provided into the mouth of the tube).

245 Experience phase. After the pre-test phase, pelicans were randomly assigned to two experimental groups. In the platform-pushing group, six subjects (Asa, Bal, Coo, Hyd, Jgo, 246 247 Jee) were trained to retrieve the reward by pushing the collapsing platform with the beak through the shortened tube. The training process was as follows: initially, the reward was 248 249 partly reachable on the platform, so while trying to take the reward the subjects caused the 250 platform to collapse unintentionally. Progressively, the reward was moved out-of-reach and 251 subjects were gradually shaped to push the platform with the beak. This phase was 252 considered completed when the subjects had retrieved the reward sixteen times in a row at 253 maximum (only birds from the platform-pushing group reached this criterion, see below).

254 The other six individuals in the stone-nudging group (Her, Cro, Jan, Jyw, Jac, Cra) were trained to nudge a stone into the apparatus from a rimmed square plate with a central hole. At 255 256 the beginning of the training process, one stone was placed right on the edge of the tube. 257 Thus, when the pelican interacted with the apparatus the stone accidentally fell down into the 258 tube. When the association between the stone falling and the release of the reward was 259 acquired, the stone was progressively moved to the plate's edge. Here again, subjects met 260 criterion when they obtained the reward (using the stone located at the border of the plate) 261 sixteen times in a row at maximum (only one bird from the stone-nudging group reached this 262 criterion, see below).

263

264

Test phase. After each group had met criterion in the training phase, subjects moved to the test phase. Here, the procedure was the same as the pre-test phase of *Tool-use task 2*.

265 Coding and data analysis

266 All tests were video recorded, and continuous second-by-second coding of the videos was 267 performed. For both tool-use tasks, we followed a specific coding scheme including 6 268 behaviours: 1 = perch on the apparatus, 2 = insert the beak in the apparatus, 3 = interaction269 with the apparatus (i.e. touching the apparatus with the beak), 4 =touch a tool, 5 =pick up a 270 tool, and 6 = insert a tool. Based on this coding scheme, the number of behaviours exhibited by each bird was counted by assigning a score of 1 when this behaviour lasted at least 1s 271 272 (e.g., when a subject interacted with the apparatus during 1 s, this behaviour was coded as 1; 273 conversely, if no interaction was counted - or behaviour from the coding scheme - this was 274 coded as 0). We assessed inter-observer reliability by using a sub-sample of the videos, 275 whereby 36 trials from Tool-use task 1 (180 trials in total) were independently scored by two 276 observers. Inter-observer reliability was high (percentage agreement: 99%, Cohen's kappa 277 coefficient: 0.95).

278

Model 1: Tool use task 1.

279 We used a Generalized Linear Mixed model (GLMM) with a negative binomial error 280 structure (overdispersion score with a Poisson error structure: 9.12). Time (i.e. time to 281 perform each behaviour) was set as dependant variable, Behaviour ("Insert beak in the 282 apparatus" and "Interaction with the apparatus"), Trial (1 vs 2 vs ...10), and Trial*Behaviour 283 as fixed factors, and Subject (i.e. subject's identity) as random effect. We limited our 284 investigation to the behaviours specified above, given the absence or rarity of other behaviours ("Insert a tool within the apparatus", "Pick up a tool", "Perch on the apparatus", 285 286 and "Touch a tool"; see Results).

287 *Model 2: Tool use task 2.*

288 To assess whether the individuals from the platform-pushing group changed their 289 behaviour after experience with the functional properties of the task, we ran a GLMM with a 290 negative binomial error structure (overdispersion score with a Poisson error structure: 80.74). 291 Time was set as dependant variable, Behaviour ("Insert beak in the apparatus", "Touch a 292 tool", and "Interaction with the apparatus") and *Phase* (pre-test phase vs test phase) as fixed 293 factors, and Subject as random effect. Here again, we limited our investigation to the 294 behaviours specified above, given the absence or rarity of other behaviours ("Insert a tool within the apparatus", "Pick up a tool", and "Perch on the apparatus"; see **Results**). 295

GLMM analyses were conducted using the packages *lme4* (Bates, Mächler, Bolker, & Walker, 2015) and *multcomp* (Hothorn, Bretz, & Westfall, 2008) in R software (R Core Team, 2019).

299 Ethics

300 This research conforms to the 'Guidelines for the use of animals in research' as published 301 in Animal Behaviour (1991, 41, 183-186) and the ARRIVE guidelines, and has been carried 302 out in accordance with the U.K. Animals (Scientific Procedures) Act, 1986 Amendment 303 Regulations (SI 2012/3039) and associated guidelines, EU Directive 2010/63/EU for animal 304 experiments, and the National Institutes of Health guide for the care and use of Laboratory 305 animals (NIH Publications No. 8023, revised 1978). The Bird Park's (Ain, France) scientific 306 board provided the authorization to perform environmental enrichments through strictly non-307 invasive behavioural experiments on captive pelicans.

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317 Results

318 Tool-use task 1

319 No subject was able to solve the task, namely to drop a tool within the apparatus to get 320 access to the food reward. Indeed, we did not report any behaviour consisting of "Pick up a 321 tool" or "Insert a tool within the apparatus". Overall, behaviours that involved "Insert the beak in the apparatus" and "Perch on the apparatus" were rare (respectively: mean = 31.91s, 322 323 SD = 48.20s; mean = 1.16s, SD = 2.72s). At least in one of their total test trials, seven birds 324 tried to obtain the reward by inserting their beak within the apparatus's aperture (Bal, Coo, 325 Jac, Jgo, Jan, Jee, Jyw), and three by perching on it (Coo, Jani, Jyw). Although most pelicans 326 rarely touched a tool (Bal, Coo, Hyd, Jac, Jan, Jee, Jgo, mean = 5.91s, SD = 7.46s), they 327 interacted with the apparatus (Asa, Bal, Coo, Cra, Hyd, Jac, Jgo, Jan, Jee, and Jyw, mean = 947.41s, SD = 1217.39s). The GLMM analysis revealed a significant effect of the factor 328 329 *Behaviour* (p < .001; estimated parameters are provided in **Table 1**) and the factor *Trial* (p < .001)

330 .001). The interaction *Trial*Behaviour* was also significant, suggesting that pelicans 331 increased their behavioural interactions towards the apparatus (p < .001) but decreased their 332 beak insertions within the apparatus across trials (p < .001). As shown in **Figure 3**, subjects' 333 behaviour was subject to a great inter-individual variability.

334

< Insert Figure 3 and Table 1 about here >

Tool-use task 2

336 *Pre-test phase: stone-nudging group and platform-pushing group.*

337 No subject was able to drop a tool within the device to collapse the platform supporting 338 the food reward. Here again, behaviours consisting of inserting the beak within the apparatus 339 were seldom at the group level (platform-pushing group: mean = 14.00s, SD = 16.18s; stone-340 nudging group: mean = 133.25s, SD = 183.51s). More specifically, in both groups, three 341 subjects tried to insert their beak within the apparatus (platform-pushing group: Bal, Coo, 342 Jee; stone-nudging group: Jac, Jan, Jyw), while no one attempted to perch on the device. 343 Most pelicans touched a tool and interacted with the apparatus in this phase (platform-344 pushing group: Bal, Coo, Hyd, Jee, Jgo, mean = 515.60s, SD = 524.43s for "Interaction with 345 the apparatus"; and Coo, Jgo, Jee, mean = 27.40s, SD = 37.81s for "Touch a tool"; stone-346 nudging group: Cra, Jac, Jan, Jyw, mean = 1939.5s, SD = 1556.22s for "Interaction with the 347 apparatus", and Jan, Jyw, Jac, mean = 9.25s, SD = 9.03s for "Touch a tool"). One subject 348 (Jee) from the platform-pushing group picked up a tool during its first trial without directing 349 it towards the apparatus, and no one inserted a tool in the device. No subject from the stone-350 nudging group picked up a tool on the ground or tried to insert it in the apparatus. As shown 351 in Figure 4, we also noted inter-individual differences.

352

< Insert Figure 4 about here >

353

Experience phase: stone-nudging group and platform-pushing group.

Although all subjects in the platform-pushing group rapidly learned to use the beak to push the platform in this phase, only one subject in the stone-nudging group successfully moved the stone into the aperture to get the reward (Jac; Video 1, see Supplementary Materials). Noteworthy, instead of trying to move the stones towards the hole, most subjects tended to throw the stone on the ground when the experimenter replaced them on the plate. Consequently, only the platform-pushing group was allowed to proceed to the test phase.

360 *Test phase: stone-nudging group and platform-pushing group.*

The only subject from the stone-nudging group that passed the criterion in the previous experience phase (Jac) did not pick up a tool on the ground to obtain the reward. Only two subjects (Bal, Jee) from the platform-pushing group tried to insert their beak in the apparatus, 364 and no perching behaviour was reported. The majority of birds from this group interacted with the apparatus and touched a tool (Asa, Bal, Coo, Hydra, Jgo, Jee, mean = 807.16s, SD = 365 366 1265.65s for "Interaction with the apparatus", and Asa, Bal, Jee, Jgo, mean = 61.50s, SD =84.59s for "Touch a tool"). According to the GLMM analysis, subjects made significantly 367 368 more behavioural interactions with the apparatus than the other behaviours (p < .001; "Insert 369 the beak within the apparatus": p = 0.15 and "Touch a tool": p = 0.06). However, there was 370 no significant effect of the factor *Phase* (p = 0.46) and *Phase*Behaviour* (p = 0.51). Thus, 371 behavioural interactions with the apparatus did not increase significantly after experience 372 with the functional properties of the task (pairwise post-hoc test comparisons are provided in 373 Table 2).

374

< Insert Table 2 about here >

375 Discussion

Overall, most pelicans were unable to spontaneously use the tools provided (Tool-use task 1), even after they had been gradually shaped to produce the stone-dropping behaviour (Tooluse task 2: stone-nudging group). Knowledge of the collapsing-platform mechanism of the apparatus had also no effect on the subjects' motivation or capacity to use tools (Tool-use task 2: platform-pushing group). Cognitive requirements of flexible tool use, notably the initial difficulty of perceiving objects as tools, are discussed as the main constraints for the emergence of tool-use skills in this species.

383 Before delving into explanations of the absence of tool-related competence in pelicans, 384 methodological biases must be ruled out so as to ensure that the reported experiments truly 385 reflected the subjects' failure to understand the task. For instance, although similar devices have been appropriate to ground foragers such as corvids (e.g. rooks: Kasprzykowski, 2003), 386 387 they may have created constraints regarding our species' physical abilities. Pelicans indeed frequent a quite different foraging niche, consisting of a wide variety of aquatic habitats 388 389 (Elliott, 1992). Nevertheless, object manipulation and transportation have been reported to 390 often occur on land in captive (SD, personal observation) as well as wild individuals (e.g. 391 Brown & Urban, 1969), and some free-ranging populations are efficient ground-foragers 392 (Mwema, de Ponte Machado, & Ryan, 2010; de Ponte Machado, 2004, see also Danel et al., 393 2020 for a social foraging task carried out on land). Furthermore, all subjects from the 394 platform-pushing group learned rapidly through associative learning/operant conditioning 395 how to obtain the reward when the platform could be reached directly with the beak. Whether 396 these subjects understood causality (that the platform collapsed if they applied a physical 397 force on it), however, remains unlikely.

398 Another possibility is that tool use may not easily arise when subjects lack first-hand manipulative experience with the objects (e.g. their mechanical properties, affordances, and 399 400 manoeuvrability: Fayet, Hansen, & Biro, 2020; Taylor et al., 2011). However, Tool-use task 401 2 was specifically designed to allow the subjects all necessary experience with the apparatus 402 and the tools and, even after proper training, all pelicans (except one subject: Jac, during the 403 experience phase) were unable to use tools. Finally, a lack of motivation does not appear to 404 explain the failure of pelicans in both tool-use tasks. Although we noted a decrease in 405 specific behaviours during Tool-use task 1 ("Insert the beak within the apparatus" and 406 "Touch a tool"), pelicans interacted with the apparatus significantly more across trials. 407 Similarly, there was no significant effect of experience during the test phase of Tool-use task 408 2 (platform-pushing group).

409 Noteworthy, one subject (Jac) was able to repeatedly drop stones within the apparatus to 410 release an out-of-reach reward during the experience phase of Tool-use task 2. This bird not 411 only pushed the stone towards the tube's aperture, but also had sufficient control over the tool by lifting it above the hole probably to create an additional force on the platform. During the 412 413 experience phase, Jac surprisingly dropped a thin stick that fell from a tree above the 414 apparatus's platform. This demonstrates that this subject could also use non-trained tool 415 items, similarly to other bird species tested in similar tasks (e.g. New Caledonian crows: von 416 Bayern, Heathcote, Rutz, & Kacelnik, 2009). However, when task properties slightly changed 417 in the subsequent test phase (when tools were located on the ground), this individual did not 418 repeat the action sequence required to solve the task. As this subject did not engage in any 419 attempts to touch the tool in this phase, its failure is unlikely due to motor difficulties in 420 grabbing tools directly on the ground. This subject's experience with objects and rearing 421 history were the same as the other tested pelicans. We suggest that more instances of *learned* 422 tool-use behaviour may appear in studies with a larger sample size.

Our sample, however, may have been affected by certain biases (i.e. captivity and rearing experience, Webster & Rutz, 2020). For instance, subjects' participation in the tasks may have been favoured by low neophobia due to previous experience with humans. Participation in a previous cognitive experiment may also have represented a bias (Webster & Rutz, 2020), although the foraging apparatus was dissimilar to the present ones and did not require the use of environmental objects (Danel et al., 2020).

We believe additional insights can be gained by looking at the behavioural pattern of individuals during the training phase of Tool-use task 2. Rather than trying to move the stones towards the hole, most subjects tended to throw the stones on the ground when the

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432 experimenter replaced them on the plate. This manipulation pattern of pelicans' behaviour when interacting with tools is reminiscent of a recent study that failed to induce tool-use 433 434 behaviour in wild-caught great tits (Johnsson & Brodin, 2019). Instead of directing tools 435 towards the apparatuses, most tits threw them away after grabbing and tossing them with the 436 beak. This suggests that both avian species failed at making any link between the tools and 437 the reward obtained. In other words, although some pelicans possess morphological (the 438 sensorimotor processes to hold a tool) and behavioural (object manipulation or 'object related 439 non-tool use': Hunt, Gray, & Taylor, 2013) predispositions required to use tools (Call, 2013; 440 Visalberghi, Sabbatini, Taylor, & Hunt, 2017), and are able to learn to use tools in a goal directed manner, they may lack the initial cognitive capacity to perceive the need for tools 441 442 (how objects work and can be used as tools: Hunt, Gray, & Taylor, 2013). Perceiving that a familiar object can be exploited as a tool might be cognitively demanding (Hunt, Gray, & 443 444 Taylor, 2013), even for species that use tools frequently in the wild (e.g. Sonso chimpanzee 445 community, Pan troglodytes schweinfurthii: Grund, Neumann, Zuberbühler, & Gruber, 2019; 446 Lamon, Neumann, Gier, Zuberbühler, & Gruber, 2018; New Caledonian crow: von Bayern, 447 Heathcote, Rutz, & Kacelnik, 2009).

448 Pelicans' behaviours contrast with those of some captive habitually non-tool-using species 449 that performed the stone-dropping behaviour required in the present study, such as Goffin 450 cockatoos (Laumer, Bugnyar, & Auersperg, 2016) and keas (Auersperg Gajdon, & Huber, 451 2010; Auersperg, von Bayern, Gajdon, Huber, & Kacelnik, 2011; see also tool-related studies 452 on other habitually non-tool-using species e.g. macaws, Ara ambiguous and Ara 453 glaucogularis: O'Neill, Picaud, Maehner, Gahr, & von Bayern, 2020; Goffin cockatoos: 454 Auersperg, Szabo, von Bavern, & Kacelnik, 2012; Eurasian jays, Garrulus glandarius: 455 Cheke, Bird, & Clayton, 2011; and vasa parrots, Coracopsis vasa: Lambert, Seed, & 456 Slocombe, 2015). Rooks, for instance, which have shown surprising tool-related capacities 457 among non-habitual avian tool users, were able to appreciate their functional properties (e.g. 458 using large stones over small ones) and to exploit successfully their experience with the tools 459 and the task (Bird & Emery, 2009a; Bird & Emery, 2009b). Moreover, some subjects seemed 460 capable of learning rapidly about their physical environment, inhibiting inefficient 461 behaviours, remembering information, focusing attention, and foreseeing the outcomes of their actions (e.g. Bird & Emery, 2009a; Bird & Emery, 2009b; Tebbich, Seed, Emery, & 462 463 Clayton, 2007). Each of these capacities has been proposed to be involved in flexible tool-use (Coolidge & Wynn, 2005; Kane & Engle, 2000, 2002). 464

465 As pelicans are able to solve novel foraging problems after observation of experienced conspecifics (Danel et al., 2020), future experiments may assess this species' capacity to use 466 467 tools through social learning (Bandini, Motes-Rodrigo, Steele, Rutz, & Tennie, 2020). Further tests may also investigate whether this ability develops early during ontogeny (e.g. at 468 469 juvenile stage: Tan, 2017), and/or when pelicans are given the opportunity to manipulate a various range of objects (e.g. anthropogenic objects). Additionally, in order to assess the 470 471 generalisability of our findings, this experiment should be carried out in wild populations 472 (Rutz & Webster, 2021; Webster & Rutz, 2020).

To conclude, our study demonstrates that captive great white pelicans were unable to solve 473 novel problems by using the provided tools (i.e. sticks and stones). However, our results must 474 475 be interpreted with caution. Indeed, at this stage, we cannot conclude that facultative tool-use 476 is cognitively demanding in pelicans (Hunt, Gray, & Taylor, 2013; Visalberghi, Sabbatini, 477 Taylor, & Hunt, 2017). We hope that our experiment encourages future investigations to 478 assess the cognitive demands of flexible tool-use in a taxonomically various range of non-479 habitually tool-using species, in order to test the validity of existing theories on the evolution 480 of tool use and cognition.

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- 482 **Declarations**
- 483 **Conflict of interest** the authors declare there is no conflict of interest.
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485 **References**

- Anderson, J. G. T. (1991). Foraging Behavior of the American White Pelican (*Pelecanus erythrorhyncos*) in Western Nevada. *Colonial Waterbirds*, 14, 166-172. doi:
 10.2307/1521506
- Auersperg, A. M. I., Gajdon, G. K., & Huber, L. (2010). Kea, *Nestor notabilis*, produce
 dynamic relationships between objects in a second-order tool use task. *Animal Behaviour*, 80, 783-789. doi: 10.1016/j.anbehav.2010.08.007
- Auersperg, A. M. I., Köck, C., Pledermann, A., O'Hara, M., & Huber, L. (2017). Safekeeping
 of tools in Goffin's cockatoos, *Cacatua goffiniana*. *Animal Behaviour*, *128*, 125-133.
 doi: 10.1016/j.anbehav.2017.04.010
- Auersperg, A. M., Szabo, B., Von Bayern, A. M., & Kacelnik, A. (2012). Spontaneous
 innovation in tool manufacture and use in a Goffin's cockatoo. *Current Biology*, *2*, 903904. doi: 10.1016/j.cub.2012.09.002
- Auersperg, A. M., Von Bayern, A. M., Gajdon, G. K., Huber, L., & Kacelnik, A. (2011).
 Flexibility in problem solving and tool use of kea and New Caledonian crows in a multi
 access box paradigm. *PLoS One*, *6*, e20231. doi: 10.1371/journal.pone.0020231
- Bandini, E., Motes-Rodrigo, A., Steele, M. P., Rutz, C., & Tennie, C. (2020). Examining the
 mechanisms underlying the acquisition of animal tool behaviour. *Biology Letters, 16*,
 20200122. doi: doi.org/10.1098/rsbl.2020.0122
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). "Fitting Linear Mixed-Effects
 Models Using lme4". *Journal of Statistical Software*, 67, 1-48. doi:
 10.18637/jss.v067.i01.
- Bird, C. D., & Emery, N. J. (2009a). Insightful problem solving and creative tool
 modification by captive non-tool-using rooks. *Proceedings of the National Academy of Sciences*, 106, 10370-10375. doi: 10.1073/pnas.0901008106
- 510 Bird, C. D., & Emery, N. J. (2009b). Rooks use stones to raise the water level to reach a
 511 floating worm. *Current Biology*, 19, 1410-1414. doi: 10.1016/j.cub.2009.07.033
- Biro, D., Haslam, M., Rutz, C. Tool use as adaptation (2013). *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 368, 20120408.* doi:
 10.1098/rstb.2012.0408
- 515 Bentley-Condit V. K., Smith, E. O. (2010). Animal tool use: current definitions and an
 516 updated comprehensive catalog. *Behaviour*, 147, 185-221.
 517 doi:10.1163/000579509X12512865686555

- 518 Boire, D., Nicolakakis, N., & Lefebvre, L. (2002). Tools and brains in birds. *Behaviour*, *139*,
 519 939-973. doi: 10.1163/156853902320387918
- Bowker, M. B., & Downs, C. T. (2008). Fluctuations in numbers of great white pelicans at
 Lake St Lucia in response to changing water-levels. *African Journal of Ecology, 46*,
 282-290. doi: 10.1111/j.1365-2028.2008.00967.x
- Bräuer, J., Hanus, D., Pika, S., Gray, R., & Uomini, N. (2020). Old and new approaches to
 animal cognition: there is not "one cognition". *Journal of Intelligence*, *8*, 28. doi:
 10.3390/jintelligence8030028
- 526 Brosnan, S. F. (2009). Animal behavior: the right tool for the job. *Current Biology*, *19*, 124527 125. doi: 10.1016/j.cub.2008.12.001
- Brown, L. H., & Urban, E. K. (1969). The breeding biology of the great white pelican *Pelecanus onocrotalus roseus* at Lake Shala, Ethiopia. *Ibis*, *111*, 199-237. doi:
 10.1111/j.1474-919X.1969.tb02527.x
- 531 Call, J. (2013). Three ingredients for becoming a creative tool user. In C. M. Sanz, J. Call, &
- 532 C. Boesch (Eds.), Tool use in animals: Cognition and ecology (pp. 3-20). doi: 10.1017/
 533 CBO9780511894800.002
- Camacho, C., & Potti, J. (2018). Non-foraging tool use in European Honey-buzzards: An
 experimental test. *PloS one, 13*, e0206843. doi: 10.1371/journal.pone.0206843
- Cheke, L. G., Bird, C. D., & Clayton, N. S. (2011). Tool-use and instrumental learning in the
 Eurasian jay (*Garrulus glandarius*). *Animal Cognition*, 14, 441-455. doi:
 10.1007/s10071-011-0379-4
- Coolidge, F. L., & Wynn, T. (2005). Working memory, its executive functions, and the
 emergence of modern thinking. *Cambridge Archaeological Journal*, 15, 5-26. doi:
 10.1017/S0959774305000016
- 542 Danel, S., Osiurak, F., & von Bayern, A. M. P. (2017). From the age of 5 humans decide
 543 economically, whereas crows exhibit individual preferences. *Scientific reports*, 7, 1-9.
 544 doi: 10.1038/s41598-017-16984-0
- 545 Danel, S., Troina, G., Dufour, V., Bailly-Bechet, M., von Bayern, A. M., & Osiurak, F.
 546 (2020). Social learning in great white pelicans (*Pelecanus onocrotalus*): A preliminary
 547 study. *Learning & Behavior*, 1-7. doi: 10.3758/s13420-019-00404-6
- 548 Davis Jr, W. E. (2015). Anhingas play with sticks and other plant debris. *Hot Birds*, *43*, 244.
- 549 https://www.birdobserver.org/Portals/0/PDF_open/bo43-4-web.pdf#page=36

- Deaner, R. O., Van Schaik, C. P., & Johnson, V. (2006). Do some taxa have better domaingeneral cognition than others? A meta-analysis of nonhuman primate studies. *Evolutionary Psychology*, 4, 149-196. doi: 10.1177/147470490600400114
- De Kort, S. R., & Clayton, N. S. (2006). An evolutionary perspective on caching by
 corvids. *Proceedings of the Royal Society B: Biological Sciences*, 273, 417-423. doi:
 10.1098/rspb.2005.3350
- Elliott, A. (1992). Pelecanidae. In Handbook of the Birds of the World Alive. Volume 1:
 Ostrich to Ducks (pp. 290-311). Lynx Edicions, Barcelona, Spain.
- Emery, N. J., & Clayton, N. S. (2009). Tool use and physical cognition in birds and
 mammals. *Current Opinion in Neurobiology*, 19, 27-33. doi:
 10.1016/j.conb.2009.02.003
- 561 Farrar, B. G. (2020). Evidence of tool use in a seabird? doi: 10.31234/osf.io/463hk
- Fayet, A. L., Hansen, E. S., & Biro, D. (2020). Evidence of tool use in a seabird. *Proceedings of the National Academy of Sciences*, 117, 1277-1279. doi: 10.1073/pnas.1918060117
- Grund, C., Neumann, C., Zuberbühler, K., & Gruber, T. (2019). Necessity creates
 opportunities for chimpanzee tool use. *Behavioral Ecology*, *30*, 1136-1144. doi:
 10.1093/beheco/arz062
- 567 Hansell, M. (2000). *Bird nests and construction behaviour*. Cambridge University Press. doi:
 568 10.1017/CBO9781139106788
- 569 Hansell, M. (2007). *Built by animals: the natural history of animal architecture*. Oxford,
 570 Oxford University Press.
- Hansell, M., & Ruxton, G. D. (2008). Setting tool use within the context of animal
 construction behaviour. *Trends in Ecology & Evolution*, 23, 73-78. doi:
 10.1016/j.tree.2007.10.006
- 574 Hatzilacou, D. (1996). Feeding ecology of the Great White Pelican (*Pelecanus onocrotalus*)
 575 nesting at lake Mikri Prespa (North Western Greece). *Colonial Waterbirds*, 19, 190576 206. doi: 10.2307/1521963
- Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric
 models. *Biometrical Journal: Journal of Mathematical Methods in Biosciences, 50*,
- 579 346-363. doi: 10.1002/bimj.200810425
- 580 Hunt, G. R. (1996). Manufacture and use of hook-tools by New Caledonian
 581 crows. *Nature*, 379, 249-251. doi: 10.1038/379249a0

- Hunt, G. R., Gray, R. D., Taylor, A. H. (2013). In *Tool use in animals: cognition and ecology*. Sanz, C. M., Call, J., & Boesch, C. (Eds.). (2013). Cambridge University
 Press.
- Johnsgard, P. A. (1993). Cormorants, Darters and Pelicans of the World. Smithsonian
 Institution Press, Washington and London.
- Johnsson, R. D., & Brodin, A. (2019). Wild-caught great tits *Parus major* fail to use tools in a
 laboratory experiment, despite facilitation. *Ethology*, *125*, 324-331. doi:
 10.1111/eth.12857
- Kacelnik, A. (2009). Tools for thought or thoughts for tools? *Proceedings of the National Academy of Sciences, 106*, 10071-10072. doi: 10.1073/pnas.0904735106
- Kacelnik, A., Chappell, J., Weir, A. A. S. & Kenward, B. (2006). Cognitive adaptations for
 tool-related behaviour in New Caledonian crows. In: Comparative Cognition:
 Experimental Explorations of Animal Intelligence (Ed. by E. A. Wasserman & T. R.
 Zentall), pp. 515e528. Oxford: Oxford University Press.
- Kane, M. J., & Engle, R. W. (2000). Working-memory capacity, proactive interference, and
 divided attention: Limits on long-term memory retrieval. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 26*, 336-358. doi: 10.1037/02787393.26.2.336
- Kane, M. J., & Engle, R. W. (2002). The role of prefrontal cortex in working-memory
 capacity, executive attention, and general fluid intelligence: An individual- differences
 perspective. *Psychonomic Bulletin and Review*, 9, 637-671. doi: 10.3758/BF03196323
- Kasprzykowski, Z. (2003). Habitat preferences of foraging Rooks *Corvus frugilegus* during
 the breeding period in the agricultural landscape of eastern Poland. *Acta Ornithologica*,
 38, 27-31. doi: 10.3161/068.038.0107
- Kenward, B., Weir, A. A., Rutz, C., & Kacelnik, A. (2005). Tool manufacture by naive
 juvenile crows. *Nature*, 433, 121-121. doi: 10.1038/433121a
- Kühl, H. S., Kalan, A. K., Arandjelovic, M., Aubert, F., D'Auvergne, L., Goedmakers, A., ...
 & Ton, E. (2016). Chimpanzee accumulative stone throwing. *Scientific Reports*, 6,
 22219. doi: 10.1038/srep22219
- Lambert, M. L., Seed, A. M., & Slocombe, K. E. (2015). A novel form of spontaneous tool
 use displayed by several captive greater vasa parrots (*Coracopsis vasa*). *Biology Letters*, 11, 20150861. doi: 10.1098/rsbl.2015.0861

- Lamon, N., Neumann, C., Gier, J., Zuberbühler, K., & Gruber, T. (2018). Wild chimpanzees
 select tool material based on efficiency and knowledge. *Proceedings of the Royal Society B*, 285, 20181715. doi: 10.1098/rspb.2018.1715
- Laumer, I. B., Bugnyar, T., & Auersperg, A. M. I. (2016). Flexible decision-making relative
 to reward quality and tool functionality in Goffin cockatoos (*Cacatua goffiniana*). *Scientific reports*, 6, 28380. doi: 10.1038/srep28380
- Lefebvre, L. (2013). Brains, innovations, tools and cultural transmission in birds, non-human
 primates, and fossil hominins. *Frontiers in Human Neuroscience*, *7*, 245. doi: 10.3389/
 fnhum.2013.00245
- Lefebvre, L., Nicolakakis, N., & Boire, D. (2002). Tools and brains in birds. *Behaviour, 139*,
 939-973. doi: 10.1163/15685390d2320387918
- Lefebvre, L., Whittle, P., Lascaris, E., & Finkelstein, A. (1997). Feeding innovations and
 forebrain size in birds. *Animal Behaviour*, *53*, 549-560. doi: 10.1006/anbe.1996.0330
- Logan, C. (2016). Behavioral flexibility and problem solving in an invasive bird. *PeerJ*, *4*,
 e1975. doi: 10.7717/peerj.1975
- Louchart, A., Tourment, N., & Carrier, J. (2011). The earliest known pelican reveals 30
 million years of evolutionary stasis in beak morphology. *Journal of Ornithology*, *152*,
 15-20. doi: 10.1007/s10336-010-0537-5
- Mann, J., & Patterson, E. M. (2013). Tool use by aquatic animals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368, 20120424. doi:
 10.1098/rstb.2012.0424
- Matsui, H., Hunt, G. R., Oberhofer, K., Ogihara, N., McGowan, K. J., Mithraratne, K., ... &
 Izawa, E. I. (2016). Adaptive bill morphology for enhanced tool manipulation in New
 Caledonian crows. *Scientific reports*, 6, 1-11. doi: 10.1038/srep22776
- Mc Grew, W.C. (1993). The intelligent use of tools: Twenty propositions. In Tools, language,
 and cognition in human evolution, edited by K.R. Gibson and T. Ingold. Cambridge:
 Cambridge University Press, 151-170.
- Megaze, A., & Bekele, A. (2013). Diet preference and activity patterns of great white
 pelicans (*Pelecanus onocrotalus*, *Linnaeus*, 1758) at Lake Hawassa, Ethiopia. *Ethiopian Journal of Biological Sciences*, 12, 211-222.
 https://www.ajol.info/index.php/ejbs/article/view/115570
- Meyers, R. A., & Myers, R. P. (2005). Mandibular bowing and mineralization in brown
 pelicans. *The Condor*, 107, 445-449. doi: 10.1093/condor/107.2.445

- Mwema, M. M., de Ponte Machado, M., & Ryan, P. G. (2010). Breeding seabirds at Dassen
 Island, South Africa: chances of surviving great white pelican predation. *Endangered Species Research*, 9, 125-131. doi: 10.3354/esr00243
- O'Neill, L., Picaud, A., Maehner, J., Gahr, M., & von Bayern, A. M. (2019). Two macaw
 species can learn to solve an optimised two-trap problem, but without functional causal
 understanding. *Behaviour*, *156*, 691-720. doi: 10.1163/1568539X-00003521
- Osiurak, F., & Reynaud, E. (in press). The elephant in the room: What matters cognitively in
 cumulative technological culture. *Behavioral and Brain Sciences*.
 doi: 10.1017/S0140525X19003236
- Peckham, G. W., & Peckham, E. G. (1898). On the instincts and habits of the solitary wasps.
 Wisconsin, Geological Natural History Survey 2. Madison: Wisconsin Geological
 Natural History Survey.
- de Ponte Machado, M. (2007). Is predation on seabirds a new foraging behaviour for great
 white pelicans? History, foraging strategies and prey defensive responses. *Final report*of the BCLME (Benguela Current Large Marine Ecosystem) project on top predators
 as biological indicators of ecosystem change in the BCLME, 131-142.
- de Ponte Machado, M., & Hofmeyr, J. (2004). Great White Pelicans Pelecanus onocrotalus: 663 birds? 664 waterbirds or farm Bird Numbers, 13, 11-13. (see http://www.adu.uct.ac.za/sites/default/files/image tool/images/352/students/de Ponte 665 666 Machado M 2010 PhD thesis.pdf)
- Povinelli, D. J. (2000). Folk Physics for Apes. The Chimpanzee's Theory of How the World
 Works, Oxford University Press. doi: 10.1097/01.nmd.0000106127.32329.d1
- Pruetz, J. D., & Bertolani, P. (2007). Savanna chimpanzees, *Pan troglodytes verus*, hunt with
 tools. *Current Biology*, *17*, 412-417. doi: 0.1016/j.cub.2006.12.042
- R Core Team (2019). R: A language and environment for statistical computing. R Foundation
 for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
- Redrobe, S. (2014). Pelecaniformes (pelicans, tropic birds, cormorants, frigate birds,
 anhingas, gannets). *Fowler's zoo and Wild Animal Medicine*, *8*, 96-99.
- Rico-Guevara, A., Sustaita, D., Gussekloo, S., Olsen, A., Bright, J., Corbin, C., & Dudley, R.
 (2019). Feeding in birds: Thriving in terrestrial, aquatic, and aerial niches. In *Feeding*
- 677 *in vertebrates* (pp. 643-693). Springer, Cham. doi: 10.1007/978-3-030-13739-7_17
- Ricklefs, R. E. (2004). The cognitive face of avian life histories: the 2003 Margaret Morse
 Nice Lecture. *The Wilson Bulletin*, *116*, 119-133. doi: 10.1676/04-054

- Rutz, C., & Webster, M. M. (2021). Ethology adopts the STRANGE framework for animal
 behaviour research, to improve reporting standards. *Ethology*, *127*, 99-101. doi:
 10.1111/eth.13118
- Shumaker, R. W., Walkup, K. R., & Beck, B. B. (2011). *Animal tool behavior: the use and manufacture of tools by animals*. Baltimore, Johns Hopkins University Press.
- Sibley, D. A. (2000). Pelecaniformes. In: The Sibley Guide to Birds. National Society,
 Chanticleer Audubon Press Inc.
- Tan, A. W. (2017). From play to proficiency: The ontogeny of stone-tool use in coastalforaging long-tailed macaques (*Macaca fascicularis*) from a comparative perceptionaction perspective. *Journal of comparative psychology*, *131*, 89-114. doi:
 10.1037/com0000068
- Taylor, A. H., Elliffe, D. M., Hunt, G. R., Emery, N. J., Clayton, N. S., & Gray, R. D. (2011).
 New Caledonian crows learn the functional properties of novel tool types. *PloS one*, *6*,
 e26887. doi: 10.1371/journal.pone.0026887
- Taylor, A. H., Hunt, G. R., Medina, F. S., & Gray, R. D. (2009). Do New Caledonian crows
 solve physical problems through causal reasoning? *Proceedings of the Royal Society B: Biological Sciences*, 276, 247-254. doi: 10.1098/rspb.2008.1107
- Tebbich, S., & Bshary, R. (2004). Cognitive abilities related to tool use in the woodpecker
 finch, *Cactospiza pallida. Animal Behaviour*, 67, 689-697. doi:
 10.1016/j.anbehav.2003.08.003
- Tebbich, S., Taborsky, M., Fessl, B., & Blomqvist, D. (2001). Do woodpecker finches
 acquire tool-use by social learning? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 268, 2189-2193. doi: 10.1098/rspb.2001.1738
- Tebbich, S., Seed, A. M., Emery, N. J., & Clayton, N. S. (2007). Non-tool-using rooks, *Corvus frugilegus*, solve the trap-tube problem. *Animal Cognition*, 10, 225-231. doi:
 10.1007/s10071-006-0061-4
- Teschke, I., Cartmill, E. A., Stankewitz, S., & Tebbich, S. (2011). Sometimes tool use is not
 the key: no evidence for cognitive adaptive specializations in tool-using woodpecker
 finches. *Animal Behaviour*, *82*, 945-956. doi: 10.1016/j.anbehav.2011.07.032
- Teschke, I., Wascher, C. A. F., Scriba, M. F., von Bayern, A. M. P., Huml, V., Siemers, B., &
 Tebbich, S. (2013). Did tool-use evolve with enhanced physical cognitive abilities? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368,
- TII I muosopmicai Transactions of the Royal Society D. Diological Sciences, 500,
- 712 20120418. doi: 10.1098/rstb.2012.0418

- Van Leeuwen, E. J., Cronin, K. A., & Haun, D. B. (2017). Tool use for corpse cleaning in
 chimpanzees. *Scientific Reports*, 7, 1-4. doi: 10.1038/srep44091
- Van Schaik, C. P., Deaner, R. O., & Merrill, M. Y. (1999). The conditions for tool use in
 primates: implications for the evolution of material culture. *Journal of Human Evolution*, *36*, 719-741. doi: 10.1006/jhev.1999.0304
- Visalberghi, E., Sabbatini, G., Taylor, A. H., & Hunt, G. R. (2017). Cognitive insights from
 tool use in nonhuman animals. In J. Call, G. M. Burghardt, I. M. Pepperberg, C. T.
 Snowdon, & T. Zentall (Eds.), APA handbooks in psychology®. APA handbook of
 comparative psychology: Perception, learning, and cognition (p. 673–701). American
 Psychological Association. doi: 10.1037/0000012-030
- von Bayern, A. M. P., Danel, S., Auersperg, A. M. I., Mioduszewska, B., & Kacelnik, A.
 (2018). Compound tool construction by New Caledonian crows. *Scientific Reports*, 8,
 1-8. doi: 10.1038/s41598-018-33458-z
- von Bayern, A. M., Heathcote, R. J., Rutz, C., & Kacelnik, A. (2009). The role of experience
 in problem solving and innovative tool use in crows. *Current Biology*, *19*, 1965-1968.
 doi: 10.1016/j.cub.2009.10.037
- Washburn, S. L. (1959). Speculations on the interrelations of the history of tools and
 biological evolution. *Human Biology*, *31*, 21-31.
- Webster, M. M., & Rutz, C. (2020). How STRANGE are your study animals? *Nature*, *582*,
 337-340. doi: 10.1038/d41586-020-01751-5
- 733 Willinston, S. W. (1892). Note on the habits of *Ammophila*. *Entomological News*, 3, 85-86.
- Wimpenny, J. H., Weir, A. A. S., Clayton, L., Rutz, C., & Kacelnik, A. (2009). Cognitive
 processes associated with sequential tool use in New Caledonian crows. *PLoS One, 4*,
 e6471. doi: 10.1371/journal.pone.0006471
- Wirtz, P., & Kacher, H. (1983). Pelecanus onocrotalus (Pelecanidae) Kooperativer
 Fischfang. Film E 2783. Publikationen Zu Wissenschaftlichen Filmen, 16, 3-6.
 http://hdl.handle.net/21.11116/0000-0001-E9F8-1

1

Variable	Estimate	SE	Z	Pr(z)
Behaviour - Insert beak in the apparatus (Intercept)	-1.94	0.72	-2.68	<.001
Behaviour - Interaction with the apparatus	4.08	0.31	12.79	<.001
Trial	0.02	0.01	4.13	<.001
Trial: Behaviour - Interaction with the apparatus	1.09	0.32	3.40	<.001

741	Table 2. Pairwise comparisons within Behaviour and between Phase x Behaviour of Model 2 - Tool-
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use task 2.

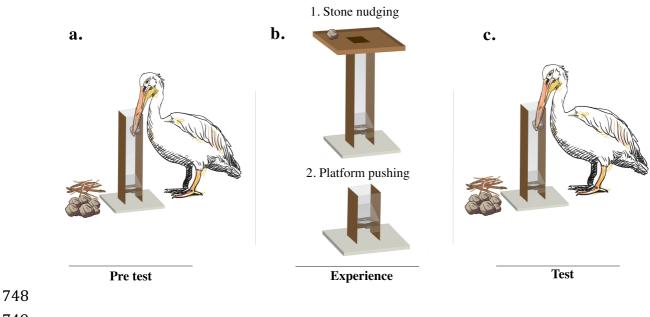
Contrast	Estimate	SE	Z	Pr(z)
Behaviour				
Insert beak - Interaction	-4.09	0.31	-12.7	<.001
Insert beak - Touch tool	1.10	0.32	3.40	<.001
Interaction - Touch tool	5.19	0.32	16.07	<.001
Phase x Behaviour				
Insert beak pre test - Insert beak test	-0.52	0.71	-0.73	0.97
Interaction pre test - Interaction test	0.05	0.57	0.10	0.84
Touch tool pre test - Touch tool test	0.13	0.67	0.20	0.49

743 Figures

Figure 1.

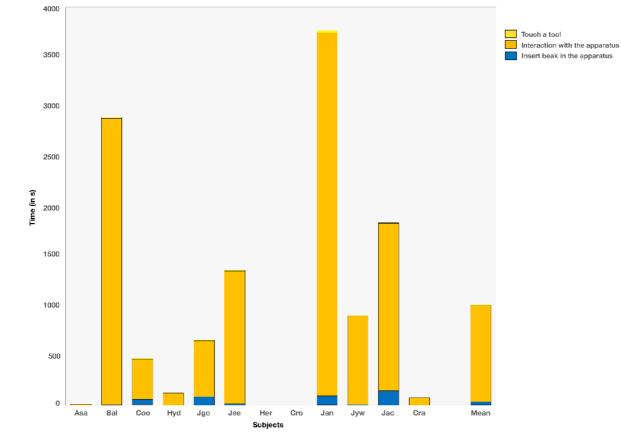


747 Figure 2.

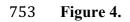


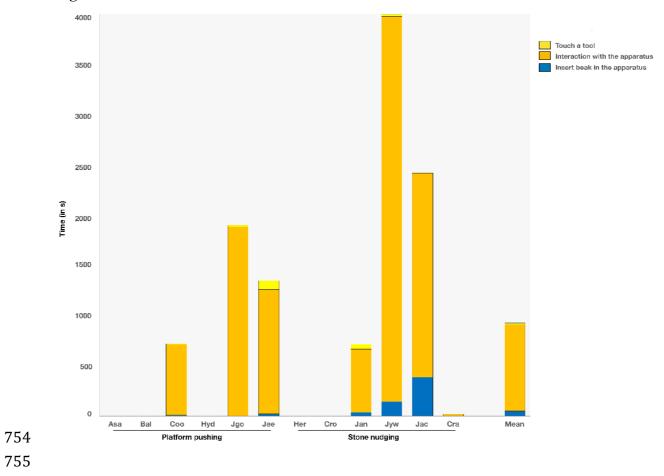
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Figure 3.









756 Figure captions

- **Figure 1.** Schematic representation of the apparatus used during Tool-use task 1.
- The reward, a fresh fish located inside a tissue box, was maintained horizontally inside the apparatus. To get the reward, the subject had to pick up a tool on the ground and to drop it
- into the upper end of the apparatus.
- **Figure 2.** Schematic representation of the apparatus used during Tool-use task 2.
- **a.** Subjects were first confronted in a pre-test phase to assess whether the subjects could spontaneously use tools (**Figure 2a**). The reward, a piece of fresh fish, was located on a
- 764 magnetised collapsing platform. To get the reward, the subject had to pick up a tool on the
- ground and to drop it into the top hole of the apparatus. **b.** After having checked that subjects
- did not use tools during the pre-test phase, subjects were divided into two groups and moved
- to the experience phase. The stone-nudging group was trained to nudge a stone into the apparatus from a rimmed square plate with a central hole, which was mounted around the
- tube's top (Figure 2b1). Subjects in the platform-pushing group were trained to reach the
 reward into a shortened tube by pushing the platform with their beak (Figure 2b2). c. The
- test phase followed the experience phase. The same procedure as the pre-test phase wasapplied (Figure 2c).
- **Figure 3.** Time spent (in s) in performing specified behaviours at the individual level and at
- the group level (Tool-use task 1).
- Figure 4. Time spent (in s) in performing specified behaviours at the individual level and at
- the group level (Tool-use task 2: pre-test). The two experimental groups are indicated (i.e.
- 777 platform pushing vs stone nudging).