



## ABSTRACT

11

12 The use of information provided by others to tackle life's challenges is widespread, but should  
13 not be employed indiscriminately if it is to be adaptive. Evidence is accumulating that animals  
14 are indeed selective and adopt 'social learning strategies'. However, studies have generally  
15 focused on fish, bird and primate species. Here we extend research on social learning strategies  
16 to a taxonomic group that has been neglected until now: otters (subfamily Lutrinae). We  
17 collected social association data on captive groups of two gregarious species: smooth-coated  
18 otters (*Lutrogale perspicillata*), known to hunt fish cooperatively in the wild, and Asian short-  
19 clawed otters (*Aonyx cinereus*), which feed individually on prey requiring extractive foraging  
20 behaviours. We then presented otter groups with a series of novel foraging tasks, and inferred  
21 social transmission of task solutions with Network-Based Diffusion Analysis. We show that  
22 smooth-coated otters can socially learn how to exploit novel food sources and may adopt a  
23 'copy when young' strategy. We found no evidence for social learning in the Asian short-  
24 clawed otters. Otters are thus a promising model system for comparative research into social  
25 learning strategies, while conservation reintroduction programs may benefit from facilitating  
26 the social transmission of survival skills in these vulnerable species.

27

28 Keywords: group living, network-based diffusion analysis, otters, problem-solving, social  
29 learning, social networks

## INTRODUCTION

30

31 Animals can use personally-acquired information (e.g. through trial-and-error learning) or  
32 information provided by others to guide their daily decisions. The latter, termed ‘social  
33 information’, can affect for example what, where or when animals eat, whom they mate with  
34 and how they respond to predators [1]. Research on social learning has come a long way since  
35 the phenomenon was first described by Aristotle in the fourth century B.C. [1]. Theory predicts  
36 that indiscriminate social information use is unlikely to be adaptive [2]. In recent years, various  
37 studies have focussed on the possibility that animals may adopt ‘social learning strategies’  
38 [3,4], such as when to copy the behaviour of others rather than learning a-socially (‘when’  
39 strategies), and whose behaviour to copy (‘who’ strategies).

40 ‘Who’ strategies that involve copying kin may be adaptive [2,5]. The rationale for the  
41 ‘copy kin’ strategy is that social learning may be most useful when observers and  
42 demonstrators share the same environment, and individuals sharing local environments are  
43 often related. In addition, demonstrators may have more to gain from providing accurate  
44 information to kin than to non-kin [3]. However, empirical evidence for the ‘copy kin’ social  
45 learning strategy is mixed: while some species only copy the food choices from those  
46 genetically related and/or familiar to them (e.g. Mongolian gerbils [6]), others are more likely  
47 to copy the food choices of unfamiliar individuals (e.g. Norway rats [7,8]).

48 Copying older individuals is another ‘who’ strategy that one would expect to be  
49 favoured, as old age signals survival success. Evidence for this social learning strategy comes  
50 from guppies for example, where small (and thus younger) females will copy the mate choices  
51 of older, larger, females, while the latter are not influenced by the mate choices of younger  
52 demonstrators [9]. More recent evidence comes from, for example, nine-spined sticklebacks  
53 [10], chimpanzees [11,12], meerkats [13], blue tits [14] and zebra finches [15]. Weanling  
54 Norway rats are also more likely to copy the food choices of adults rather than juveniles [16].

55 In other cases, however, young Norway rats were found to be equally likely to learn from both  
56 young and old demonstrators [17].

57 With regards to ‘when’ strategies, theory suggests that social learning should be used  
58 in novel situations when pre-existing or established behaviour is unproductive, and asocial  
59 learning may be costly [2,18,19]. For example, callitrichid monkeys used social learning  
60 strategies only to solve the most difficult novel extractive foraging tasks [20]. Similar patterns  
61 might be observed when individuals follow a ‘copy when uncertain’ strategy, where they copy  
62 others in unfamiliar or changing conditions where the best action to take, or the solution to the  
63 novel challenge encountered, is unknown to them. The ‘copy when uncertain’ strategy is  
64 predicted by theory [18], and there is evidence for its use in various animals (e.g. [21,22]). For  
65 similar reasons, we might expect younger individuals to be more reliant on social learning (i.e.  
66 a ‘copy when young’ strategy), since they have less experience of the world, and so are likely  
67 to be generally more ‘uncertain’ in an informational sense. Young meerkats for example were  
68 more likely than adults to copy the location where conspecifics were interacting with a novel  
69 foraging apparatus [23], and younger female guppies copied the mate choices of older females,  
70 but not *vice versa* [9]

71 Previous empirical studies thus suggest that the particular ‘who’ and ‘when’ social  
72 learning strategies used depend on various factors. These determinants and resulting social  
73 learning strategies may differ between species, depending on, for example, opportunities for  
74 social interaction, the extent to which behaviour needs to be adjusted to changing spatial and/or  
75 temporal environments, and how risky or costly it is to obtain personal information [24].  
76 However, the great majority of such research has focussed on a limited number of primate [25],  
77 fish [26], bird [24] and insect species [27]. Here we extend research on social learning strategies  
78 to a taxonomic group that has been entirely neglected until now, but in which various social  
79 learning strategies are expected to be manifested: otters.

80           Otters show a great diversity of social systems among the 13 species, with some being  
81 fiercely territorial and others living in large family groups [28]. Otters also exhibit a wide range  
82 of foraging behaviours as they handle many different food types. The diet of smooth-coated  
83 otters, for example, consists almost entirely of fish, which they catch using coordinated hunting  
84 strategies [28]. Asian short-clawed otters, on the other hand, eat mainly crabs, and use their  
85 long, clawless fingers to feel around in silt and crevices for shellfish and other invertebrates.  
86 The otters then crush the shells using their teeth [28]. Given the variety of dietary and foraging  
87 specializations observed in different otter populations [29], it seems plausible that they may be  
88 socially transmitted between individuals [30].

89           Smooth-coated otters and Asian short-clawed otters also differ in their social group  
90 structure and their reliance on social foraging in nature: wild smooth-coated otters typically  
91 live in social groups of four to five individuals, consisting of an adult female and her offspring  
92 from several litters, where the older offspring help to raise new litters. These family groups  
93 hunt cooperatively and show group defence against predators [28]. In contrast, Asian short-  
94 clawed otters live in large social groups of up to 15 individuals, consisting of one female and  
95 her offspring [28]. They have been studied less in the wild than the smooth-coated otters, and  
96 their social behaviours are not particularly well documented. It is thought that they generally  
97 forage individually for crabs and shellfish, but coordinate predator defence within their groups  
98 [28].

99           Surprisingly, it is not known whether these, or any other species of otter, can learn  
100 socially. Due to their vulnerable conservation status [31,32], a better understanding of otter  
101 social learning tendencies could have valuable implications for future reintroduction programs,  
102 as has been seen in reintroduction cases of, for example, hatchery-reared fish [33] and prairie  
103 dogs [34]. Training of anti-predator behaviour and foraging skills for example may be more  
104 efficient and effective when involving conspecific demonstrators [33,34]. Furthermore,

105 research into otters' social learning strategies in terms of whom and when they copy could  
106 inform which type of demonstrator (e.g. young/old, male/female) to use and under which  
107 circumstances (e.g. when unfamiliar prey requires complex manipulation to exploit).

108 We presented novel extractive foraging tasks to captive groups of smooth-coated otters  
109 (*Lutrogale perspicillata*) and Asian short-clawed otters (*Aonyx cinereus*). We used Network-  
110 Based Diffusion Analysis (NBDA: [35,36]) to infer that individuals socially learned the task  
111 solutions from each other if the diffusion (spread) of the task solutions through the otter groups  
112 followed the groups' previously-determined social association networks. Given that both  
113 smooth-coated and Asian short-clawed otters live in stable family groups and are thought to  
114 rely on each other for foraging and/or anti-predator defence, we predicted that both species  
115 would be capable of socially learning the solution to novel extractive foraging tasks. We also  
116 assessed whether the otters used a) the 'copy when asocial learning is costly' strategy, by  
117 testing whether individuals' reliance on social learning increased with the difficulty of the  
118 novel foraging task presented, and b) the 'copy when young' (and thus uncertain) strategy, by  
119 testing whether offspring were more likely to learn socially than their parents.

120

## 121 **METHODS**

### 122 Study populations

123 We studied one group of smooth-coated otters (N=7 individuals) and three groups of Asian  
124 short-clawed otters (N=5, 6, and 6 individuals) at zoos and wildlife parks in the United  
125 Kingdom (see Table S1 in Supplementary Material for otter group compositions).

126

### 127 Association data

128 To calculate the social network for each group, we collected five consecutive days of  
129 association data. We distinguished individuals using differences in body size and shape and

130 facial marks. We used spatial proximity as an indicator of social association [37]: if otters were  
131 within one body length of each other (a metric suggested in [37]), they were classified as  
132 associating. We collected the data for three separate periods of one hour on each of the five  
133 days, during which we recorded every five minutes which otters were associating. We used  
134 these data to create an association network for each otter group. Each otter dyad's 'association  
135 index' was computed as the simple ratio of the total number of five-minute samples that the  
136 two otters were observed within one body length of each other, divided by the total number of  
137 five-minute samples those individuals were observed apart plus the samples in which they were  
138 associating (the 'Simple Ratio Index'; [38]). We use the coefficient of variation of the  
139 associations in each network to provide a measure of social differentiation [39]. Although the  
140 five-minute social association samples in the same observation hour were not independent of  
141 each other, the number of sampling periods to quantify the social association network does not  
142 enter into the Network-Based Diffusion Analysis that tests for social learning (see Data  
143 Analysis section below). There is therefore no issue of observation period 'pseudo-replication'  
144 somehow biasing the network-based results. Furthermore, any noise in the social network data  
145 reduces the power to detect social learning using Network-Based Diffusion Analysis and thus  
146 results in a more conservative estimate of the importance of social learning rather than a false  
147 positive [40].

148

#### 149 Diffusion experiments

150 Next we introduced new information to each otter group, in the form of novel extractive  
151 foraging tasks baited with desirable food rewards (e.g. pieces of fish; see Fig. 1 and Fig. 2).  
152 Several identical replicas of each task type (usually two or three task apparatuses more than  
153 the number of otters in each group) were placed into the enclosure at the start of each diffusion  
154 experiment, so that each otter could have a chance to solve the task, and the otters could easily

155 observe each other solving the tasks (see Supplementary Material Videos 1-3). Each task type  
156 was presented on a separate occasion to each group of otters, resulting in six ‘diffusions’ of the  
157 solutions to six different task types in the group of seven smooth-coated otters (Fig. 1), and  
158 four ‘diffusions’ of the solutions to four different task types in each of the three groups of Asian  
159 short-clawed otters (Fig. 2). We predicted that the otters would have more trouble solving the  
160 task types that, from our personal experience opening the tasks, required more complex  
161 extractive foraging techniques (e.g. Fig. 1 tasks 5-6; Fig. 2 tasks 3-4), and would thus be more  
162 inclined to copy each others’ solutions to those task types.

163

164 One task type was presented per day in between the otters’ regular feedings by the wildlife  
165 centres, ca. 2 hours after the normal food was last provided. The task apparatuses were left  
166 inside the enclosure until either they had all been solved (i.e. the food reward removed), or  
167 none of the otters had interacted with the task apparatuses for three hours. If the latter occurred,  
168 the same task type was presented again the following day. A ‘solve’ was recorded every time  
169 an otter managed to retrieve the food reward from a task apparatus. If another member of the  
170 group stole the reward, the otter that originally opened the task apparatus was recorded as  
171 solving the task. The order in which the otters solved each task type was recorded. It was not  
172 possible for the single experimenter (ZL) observing the otters from outside the enclosure to  
173 accurately record the exact time at which each individual solved each task, as otters would pick  
174 up the task apparatuses and take them to different parts of the enclosure. However, we were  
175 able to record in discrete time the minute in which each otter solved each task type. The raw  
176 data have been uploaded as part of the Supplementary Material.

177

178 Data Analysis

179 Network-Based Diffusion Analysis (NBDA) infers that individuals acquire novel behaviours  
180 socially if the order (Order of Acquisition Diffusion Analysis: OADA) or time sequence (Time  
181 of Acquisition Diffusion Analysis: TADA) in which the individuals start showing the novel  
182 behaviour follows their social association network [36]. In other words: if individual A  
183 associates often with individual B but rarely with individual C, we would infer social  
184 transmission if individual A started performing a novel behaviour following B's, but not C's,  
185 demonstration of that behaviour.

186         We initially used the OADA variant of NBDA to determine whether the order in which  
187 subjects solved the tasks was correlated with the pattern of their social associations. OADA  
188 makes fewer assumptions than the TADA variant of NBDA [36], and here we did not have  
189 exact times of acquisition, so we initially used OADA. However, the social networks for Asian  
190 short-clawed otters were highly homogeneous (see Results), meaning OADA was unable to  
191 estimate the effect of social transmission with precision. We therefore also used a discrete  
192 TADA [35,36] to estimate the effects of social transmission for this species, with time divided  
193 into one-minute periods (see Supplementary Material). This also allowed us to test the relative  
194 difficulty of each task for the Asian short-clawed otters.

195         In both OADA and (discrete) TADA, inference of social transmission results from  
196 comparing models that include social transmission to models with only asocial learning. Each  
197 model also contained age category (i.e. parent (coded as '1') /offspring (coded as '0')) and sex  
198 (female coded as '1', male as '0') as predictor variables. To assess whether otters differed in  
199 their reliance on social learning among tasks (e.g. they may have increased reliance on social  
200 learning with increasing task difficulty), we compared model fits assuming social transmission  
201 rates were the same vs. different for all tasks. We also fitted both additive and multiplicative  
202 versions of each social transmission model [36]. The additive model assumes that differences

203 between ages or sexes apply only to asocial learning, whereas the multiplicative model assumes  
204 that differences apply to both social transmission and asocial learning.

205 We used a model-averaging approach with Akaike's Information Criterion, corrected  
206 for small sample size (AICc), to select the best model [41]. For each variable considered, we  
207 give its total Akaike weight (as a %) and model-averaged estimate. We also provide  
208 unconditional 95% confidence intervals using Burnham and Anderson's method for adjusting  
209 profile likelihood confidence intervals for model selection uncertainty [41]. We use Akaike  
210 weights to quantify the relative support for the different models of social transmission and the  
211 asocial learning model. To give a more intuitive measure of the strength of social transmission,  
212 we derive estimates of the proportion of task solutions that occurred by social transmission  
213 [42].

214

## 215 **RESULTS**

216

### 217 Smooth-coated otters

218 The network structure (Fig. 3a) shows that although virtually all members of the group  
219 associated with each other (i.e. almost all network nodes are connected), individuals differed  
220 greatly in how much they associated with each other (i.e. different line thicknesses between  
221 nodes in Fig. 3a; social differentiation coefficient = 0.53).

222

223 Most smooth-coated otters solved all task types (Supplementary Material Table S2, Video 1).

224 The otters in this group appear to have solved the tasks by copying each other rather than  
225 through individual trial-and-error learning: there was 6.5x more support for the best of the  
226 social transmission models (Akaike weight: 79.4%) than for the asocial learning model (Akaike  
227 weight: 12.3%; Table 1), indicating that the solutions to the novel foraging tasks spread through

228 the otter group following the association network. The rate of social transmission per unit  
229 network connection, relative to the baseline rate of asocial learning, was estimated to be 45.2  
230 (95% C.I. = [0.44,  $\infty$ ]). This corresponds to the otters (except for the first solver or ‘innovator’  
231 in the group) using social information in 96.0% (95% C.I. = [27.5, 100]) of all task solves (see  
232 Table 2).

233

234 The smooth-coated otters do not seem to have adopted a ‘copy when asocial learning is  
235 costly’ strategy: the solving data were best described by models that specified an equal social  
236 transmission rate across tasks (Table 1), instead of a varying rate that might have indicated  
237 increased reliance on social transmission for more complex tasks. However, an ad hoc visual  
238 examination revealed that the spread of task solutions through the otter group seemed to  
239 follow the association network more closely in task types 1-4 than 5-6 (Fig. 4; Supplementary  
240 Material Video 1 shows a task 5 trial). When inspecting the sequence in which otters solved  
241 task types 1-4, the next individual to learn to solve a task tended to be a young otter that was  
242 one of the most strongly associated in the social network with ‘informed’ group mates, i.e.  
243 those that had already solved the task. In task types 5-6 this pattern was no longer apparent  
244 (Fig. 4). Furthermore, fitting a model *without* social transmission to the solving-order data for  
245 tasks 5 and 6 improved Akaike’s Information Criterion (corrected for small sample size) by  
246 4.41, suggesting that smooth-coated otters may have learned individually rather than socially  
247 how to solve task types 5 and 6.

248

249 The social transmission model with most support was multiplicative rather than additive (11.3x  
250 more support; see Table 1). This means that any sex/age differences in solving the tasks  
251 affected both asocial and social learning rates, rather than just asocial learning. There was little  
252 support for smooth-coated otter males differing from females in task-solving speed (total

253 Akaike weight = 24.9%; Table 3), with females being an estimated 1.02x (95% C.I. = [0.63,  
254 1.65]) faster to solve tasks than males. However, there was strong support for a difference  
255 between offspring and parents (total Akaike weight = 100.0%; Table 3), with offspring being  
256 an estimated 6.10x (95% C.I. = [1.11, 33.53]) faster to solve the tasks than the parents. The  
257 parents only solved 1 out of 6 tasks (father) and 3 out of 6 tasks (mother), compared to the  
258 offspring solving an average of 5.8 tasks. Given the stronger support for the multiplicative  
259 model (see Table 1), this indicates that young otters learned faster how to solve tasks both  
260 socially and asocially as compared to their parents.

261

#### 262 Asian short-clawed otters

263 The network diagrams are much more homogeneous for the three groups of Asian short-clawed  
264 otters than for the smooth-coated otters (Fig. 3b, c, d vs. a; social differentiation coefficients =  
265 0.16, 0.17, 0.32 vs. 0.53) suggesting that Asian short-clawed otters did not differ as much as  
266 the smooth-coated otters in how frequently individuals associated with each other. Fewer than  
267 half of the otters solved task 4 (Fig. 2; Supplementary Material Table S3, Video 3), suggesting  
268 that this was indeed the most complex task. NBDA (TADA) confirmed that tasks 3 and 4 were  
269 more difficult (slower) to solve than tasks 1 and 2 (expected time to solve relative to task 1:  
270 task 2= 2.45x faster; task 3= 0.33x slower; task 4= 0.42x slower).

271

272 The individuals in the three Asian short-clawed otter groups appear to have learned the  
273 solutions to the four novel foraging task types individually rather than socially: there was  
274 almost 3x more support for the asocial learning model (Akaike weight: 59.4%) than for the  
275 best-fitting social transmission model (Akaike weight: 20.1%; Table 1). The rate of social  
276 transmission per unit network connection, relative to the baseline rate of asocial learning, was  
277 estimated at 0 (95% C.I. = [0, 0.17]), corresponding to 0% (95% C.I. = [0, 17.3%]) of task

278 solutions occurring due to otters (excluding the innovator) socially learning from each other  
279 (Table 2). There was also no support for a ‘copy when asocial learning is costly’ strategy, as  
280 the task solving data were best described by models that specified a social transmission rate  
281 that was equal across all tasks (see Table 1). Together, these results suggest that Asian short-  
282 clawed otters are unlikely to have relied on social information to solve the novel foraging tasks.

283

284 In contrast to the smooth-coated otters, Asian short-clawed otter parents and offspring did not  
285 appear to differ in their task solving speeds (total Akaike weight = 27.1%), with offspring being  
286 an estimated 0.95x (95% C.I. = [0.56, 1.62]) slower than parents (Table 3). However, there was  
287 strong support for a difference between sexes (total Akaike weight = 92.8%), with females  
288 being an estimated 2.26x (95% C.I. = [1.12, 4.54]) faster to solve the tasks than males (Table  
289 3).

290

### 291 Species comparison

292 There was strong evidence for social transmission in smooth-coated otters, but not in Asian  
293 short-clawed otters (Tables 1-2). Across all tasks presented to each species, Asian short-clawed  
294 otters were estimated to use social information in a maximum of 17.3% of all task solves,  
295 compared to a minimum estimate of 27.5% in smooth-coated otters (see Table 2), suggesting  
296 that smooth-coated otters were more reliant on social transmission than Asian short-clawed  
297 otters. However, since some of the tasks presented to each species were different, we re-ran  
298 analyses using only the tasks presented to both. When including only the three tasks that  
299 required the same actions to be solved (smooth-coated otters: tasks 1, 3, 4 (Fig. 1) and Asian  
300 short-clawed otters: tasks 1, 2, 3 (Fig. 2)), the Network-Based Diffusion Analysis estimated  
301 that smooth-coated otters (except for the innovators) used social transmission in 100% (95%  
302 C.I. = [45.8, 100]) of task solves compared to 0% (95% C.I.= [0, 20.7]) for Asian short-clawed

303 otters. When the screw-top task was also excluded from the analysis (since a clear container  
304 was used for the Asian short-clawed otters (Fig. 2: task 3) and an opaque container for the  
305 smooth-coated otters (Fig. 1: task 4)), smooth-coated otters were estimated to use social  
306 transmission in 100% (95% C.I. = [15.3, 100]) of task solves compared to 20.4% (95% C.I.=  
307 [0, 59.5]) for Asian short-clawed otters. In all cases, the estimated effect of social transmission  
308 was thus much stronger for smooth-coated otters. However, in the latter most stringent  
309 comparison of the two species' performance on only two of the tasks, the 95% confidence  
310 intervals overlap. Therefore, overall our results strongly suggest that social transmission was  
311 less likely to be an important factor in the spread of task solutions in Asian short-clawed otters  
312 than in smooth-coated otters, but replication in a larger number of otter groups of both species  
313 presented with a larger battery of identical tasks is needed to confirm this finding.

314

315 Although males and females differed in task solving rates only in Asian short-clawed otters,  
316 there is only weak support for a meaningful species difference: the sex difference in solving  
317 rates was estimated to be 2.22x stronger in Asian short-clawed otters as compared to smooth-  
318 coated otters, but with a 95% confidence interval including 1: [0.71, 6.95] (Table 3). This  
319 indicates that we cannot exclude the possibility that the two species showed the same sex  
320 difference in solving rates. However, there was reasonable evidence that the relative age  
321 difference in task solving rates, with young otters solving significantly faster than their parents,  
322 was stronger in smooth-coated otters than in Asian short-clawed otters (7.48x; 95% C.I. = [1.38  
323 – 40.64]; Table 3). A caveat here is that the offspring in the smooth-coated otter group were 1-  
324 2 years old, while the offspring in the Asian short-clawed otter groups were 4-10 years old.  
325 Whether younger Asian short-clawed otter offspring would have outperformed their parents as  
326 observed in the smooth-coated otters thus remains to be investigated.

327

## DISCUSSION

328  
329 Social learning has been studied in many species, but never in otters, even though many otter  
330 species are likely to be capable of social learning given their gregarious nature, and knowledge  
331 of their social learning strategies may help inform reintroduction programs to support these  
332 vulnerable species. The aim of our study was threefold: to address whether otters would a)  
333 socially learn the solutions to novel extractive foraging tasks; b) exhibit a ‘copy when asocial  
334 learning is costly’ strategy, and c) show evidence of a ‘copy when young’ social learning  
335 strategy. We tested two species of otter that live in family groups but differ in life history traits  
336 as well as diet. Given their gregarious nature, we predicted that both species may show  
337 evidence of social learning. However, we made no predictions concerning species differences  
338 or the adoption of particular social learning strategies, given the exploratory nature of this study  
339 and the fact that no one has studied social learning in otters before.

340 We show for the first time that smooth-coated otters can learn from each other how to  
341 solve novel foraging tasks, while we found no support for this in the Asian short-clawed otters.  
342 These results are based on only a few captive groups. As so little is known about these species  
343 in the wild, it is unclear how differences between captive groups and those in nature in factors  
344 such as demographic composition and individuals’ experiences may affect the animals’  
345 behaviour and reliance on social learning. Our findings regarding otter species and age  
346 differences in social learning tendencies should thus be interpreted with caution and would  
347 benefit from replication on a larger captive sample and validation in wild populations.  
348 Nonetheless, our results offer a first insight into the social learning abilities of the genus  
349 Lutrinae. Furthermore, our results make ecological sense if we consider what *is* known about  
350 the natural foraging habits of these species: smooth-coated otters show coordinated group-  
351 hunting strategies such as creek-wide aligned swimming patterns to catch fish [28,43].  
352 However, their natural prey does not necessitate extensive extractive foraging behaviour to

353 consume. In our experimental setting, it thus makes sense that the smooth-coated otters would  
354 be naturally inclined to watch each other for foraging information, especially as they are  
355 unlikely to have adapted to deal with complex extractive foraging tasks. In contrast, the Asian  
356 short-clawed otters are not known to forage in groups, and their natural diet consists mainly of  
357 prey (i.e. shellfish, crabs) that require extractive foraging techniques, but not group-hunting  
358 strategies, to consume [28]. They may therefore have less of a natural tendency to turn to each  
359 other when facing novel food puzzles that are somewhat similar to the prey they encounter in  
360 the wild. However, virtually no information is available on the development of extractive  
361 foraging behaviours in Asian short-clawed otters and the extent to which these are (socially)  
362 learned in the wild. Field studies have provided extensive evidence for juveniles' reliance on  
363 social learning to acquire extractive foraging behaviours in other mammal species, including  
364 black rats [44], meerkats [13], and chimpanzees [12]. We cannot exclude the possibility that  
365 Asian short-clawed offspring younger ( $\leq 2$  years old) than those that were available to us (4-  
366 10 years old) might have relied on social information to solve our food puzzles. We have just  
367 acquired access to breeding populations of Asian short-clawed otters and additional  
368 populations of smooth-coated otters and hope to determine in the near future a) to what extent  
369 newborn pups use social information across development to acquire their extractive foraging  
370 skills, and b) whether we can replicate or reject our preliminary finding of a species difference  
371 in reliance on social learning between smooth-coated and Asian short-clawed otters.

372         With regards to our second research question, we did not find any evidence that either  
373 otter species adopted the 'copy when asocial learning is costly' strategy, which we would have  
374 inferred had we found increased reliance on social learning with increasing task difficulty. In  
375 the smooth-coated otters, the order in which we presented the tasks was confounded with task  
376 difficulty (since we did not initially intend to address this question at the time of experimental  
377 design), such that the last two tasks to be presented also appeared to be the most difficult ones.

378 Post-hoc analyses actually showed that the order in which the otters solved the tasks followed  
379 the social network more closely for the first four tasks than for the latter two, and for the latter  
380 two a model including only asocial learning (i.e. without social transmission) provided a better  
381 fit to the data. On the face of it, this is contrary to the predictions of a ‘copy when asocial  
382 learning is costly’ strategy. However, the result may instead be due to the otters having gained  
383 sufficient experience with the previous four tasks that by the end of the experimental period  
384 they no longer relied on each other to solve them. To address these concerns, we counter-  
385 balanced the task order across the groups of Asian short-clawed otters, but again found no  
386 support for social transmission in this species, even for the most difficult task that fewer than  
387 half of the otters managed to solve. Based on these results we therefore draw the tentative  
388 conclusion that these two otter species may not adopt a ‘copy when asocial learning is costly’  
389 strategy, although replication in several additional groups of both smooth-coated and Asian  
390 short-clawed otters with a randomized task presentation order is necessary to corroborate this  
391 conclusion. Even then, our results may be consistent with the strategic use of social learning in  
392 smooth-coated otters. Theoretical analyses [45] suggest that a ‘critical social learner’ strategy  
393 is often adaptive, whereby individuals try to copy others first and rely on trial-and-error  
394 learning only in situations where copying fails to yield satisfactory results (but see [46,47]).  
395 Further work might aim to investigate whether this strategy operates in otters.

396 Finally, our results suggest the possibility that smooth-coated otters adopt a ‘copy when  
397 young’ strategy: virtually all offspring solved all six tasks and did so over six times faster than  
398 their parents who solved half (mother) or only one (father) of the tasks. We found no such  
399 patterns in the Asian short-clawed otters. Again, further work is needed to be certain that this  
400 is a general difference between the species across a larger number of groups, as we cannot  
401 exclude the possibility that the adults and young in the single smooth-coated otter group we  
402 studied happened to differ in unrelated factors (e.g. motivation, fear of novelty, reinforcement

403 to explore/play with novel objects in the environment) that could have generated an apparent  
404 age difference in reliance on social learning. Nonetheless, this apparent species difference in  
405 social learning strategies makes sense if we consider species differences in life history traits:  
406 smooth-coated otters take almost double the time to reach sexual maturity and reproduce (when  
407 ca. 4 years old) as compared to the Asian short-clawed ones (when ca. 2 years old; [28]). This  
408 extended juvenile period in the family group in smooth-coated otters is likely correlated with  
409 an extended period for (socially) acquiring essential skills for survival. Asian short-clawed  
410 otters on the other hand reach sexual maturity, and presumably independence from the family  
411 group, much faster, which may explain their apparent overall lower tendency to learn socially,  
412 as well as a lack of evidence for the ‘copy when young’ strategy. However, as noted above, it  
413 is important to consider again here that the youngest Asian short-clawed otter tested was  
414 already four years old, and the oldest offspring was ten. A valid criticism of our interpretation  
415 is that none of our test subjects in this species qualified as ‘young’ in the first place. We can  
416 thus conclude that, while smooth-coated otters do seem to adopt a ‘copy when young’ strategy,  
417 further studies on younger Asian short-clawed otters and additional smooth-coated otter groups  
418 are necessary if we are to make a fair species comparison. Furthermore, Asian short-clawed  
419 otters are known to have group-coordinated anti-predator behaviour [28]. It may well be that  
420 this species would show evidence for social transmission in tasks that tested the transmission  
421 of anti-predator behaviour against a novel stimulus [48–50] rather than foraging behaviour.

422 Our findings that smooth-coated otters are capable of learning from each other how to  
423 exploit novel food sources, and that there may be species differences in otters’ reliance on  
424 social transmission, may have important conservation implications. Many otter species are  
425 listed as Near threatened, Vulnerable or Endangered by the International Union for  
426 Conservation of Nature (IUCN). Conservation organisations facilitating reintroduction  
427 programmes could benefit from using social transmission as a way of training captive-bred

428 otters to cope with life in the wild. Previous research suggests that animals trained on important  
429 life skills (e.g. anti-predator behaviour) through social learning have a higher survival rate once  
430 reintroduced into the wild [34]. Additional information on the captive animals' social networks  
431 and social learning strategies may facilitate these efforts by pointing to the best individuals to  
432 seed with the information for it to be transmitted. For example, young smooth-coated otters'  
433 training before release into the wild may benefit from sibling demonstrators performing  
434 survival skills, as we found that the novel foraging task solutions spread most efficiently  
435 between peers ('horizontal transmission') rather than from parents to offspring ('vertical  
436 transmission'). Furthermore, in some species, such as possibly the smooth-coated otter, older  
437 individuals may not be able to acquire new foraging skills as easily as younger otters, perhaps  
438 making them unsuitable for reintroduction programs as their ability to adapt to their new  
439 environment and hence their survival chances may be limited. Finally, we found no direct  
440 evidence for the otters' reliance on social learning to depend on (assumed) foraging task  
441 complexity. However, future studies could present various types of appropriate live prey not  
442 normally provided in captivity (e.g. live fish, urchins, molluscs etc.) to assess social learning  
443 tendencies in such more ecologically-relevant contexts.

444 In conclusion, this first exploration of social learning in otters shows that this taxon  
445 merits further study, not only because the wide range of life history traits represented across  
446 the various species can provide further insights into the evolution of social learning strategies,  
447 but also because conservation efforts may be facilitated by an increased understanding of these  
448 species' ability to adapt to change through social transmission.

449

#### 450 **Animal and Research Ethics**

451 This research was approved by the Anglia Ruskin University Life Sciences Departmental  
452 Research Ethics Panel, as well as the Colchester Zoo, the New Forest Wildlife Park and the

453 Paradise Wildlife Park. This research followed the ASAB Guidelines for the Use of Animals  
454 in Research [51].

455

#### 456 **Data Accessibility**

457 The data and R code are available as Supplementary Materials, and data and Supplementary

458 Videos are available from the Dryad Digital Repository:

459 <http://dx.doi.org/10.5061/dryad.ct3s3>

460

#### 461 **Authors' contributions**

462 ZL, WH and NJB designed the study. ZL conducted the experiments. WH performed the

463 statistical analyses. NJB, WH and ZL wrote the manuscript and NJB revised the manuscript

464 with input from WH. All authors gave final approval for publication.

465

#### 466 **Competing interests**

467 The authors declare no competing interests.

468

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476

477

478

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616

617 **FIGURE CAPTIONS**

618 **Figure 1.** The novel extractive foraging tasks presented to the smooth-coated otters.

619 1) A simple plastic box (55x175x130mm); 2) a plastic box with clips on the lid  
620 (45x135x135mm); this box was used as both tasks 2 and 3, once with four clips closed (task 2)  
621 and then with two clips closed and two clips removed (task 3); 4) a round plastic jar with screw-  
622 top lid (180x90mm diameter); 5) a round plastic tub with a pull-off lid (70x170mm diameter),  
623 and 6) a square plastic jar with screw-top lid (180x85x85mm). Each task was baited with half  
624 a fish and covered with its respective lid. The tasks are numbered in assumed order of difficulty  
625 with 1 being the easiest and 6 being the hardest.

626

627 **Figure 2.** The novel extractive foraging tasks presented to the Asian short-clawed otters. These  
628 differ from those presented to the smooth-coated otters (Fig. 1), as in this second iteration of  
629 the experiment on the second study species we wanted to create a more explicit range of task  
630 difficulties. Tasks were also slightly smaller to accommodate the smaller size of this otter  
631 species. 1) A simple plastic box (40x100x100mm); 2) a plastic box with two clips  
632 (45x100x85mm); 3) a plastic tub with a screw-top lid (130x75mm diameter), and 4) a frozen  
633 reward on a bamboo cane that had to be moved up and to the right to fit through the hole. The  
634 numbering of the tasks is in intended order of difficulty, with 1 being the easiest, and 4 being  
635 the most difficult. These tasks were baited with peanuts and one fish head per task at the New  
636 Forest Wildlife Park, and peanuts and mealworms mixed with either half a mouse or day-old  
637 chick legs at Paradise Wildlife Park. Task 4 required a different type of reward due to its design,  
638 so this was a block of ice with shrimp or mealworms frozen inside.

639

640 **Figure 3.** Association networks for the four otter groups. a) smooth-coated otters; b-d) Asian  
641 short-clawed otters. The line thicknesses are scaled according to the strength of association

642 between each dyad of otters. Black nodes represent males, grey nodes represent females;  
643 square nodes represent parents, circular nodes represent offspring. The numbers on the nodes  
644 represent the number of times each otter was the first individual to solve a task (i.e. the  
645 innovator).

646

647 **Figure 4.** The order of solving in the smooth-coated otters for each of the six tasks. The total  
648 association of each naïve individual with informed individuals is plotted against the sequence  
649 of solving (task solving event = 1 is when the first individual solved, etc.). Offspring are plotted  
650 as circles, parents as triangles. The individual that solved the task at each part of the sequence  
651 is plotted in red and joined with red lines. The dashed blue line shows the path we would expect  
652 the red line to take if there were no social transmission (but allowing that juveniles are faster  
653 to solve). If there is social transmission through the network the red line should be above the  
654 blue line. The solvers are labelled as Mum/Dad for parents and as Sis (sister)/ Bro (brother)  
655 with ID number for offspring. In a)-d): tasks 1-4, the individual to solve the task next tends to  
656 be an offspring with a relatively high level of association to informed otters relative to others  
657 for that solve, and the red line is clearly above the dashed blue line. In e)-f): tasks 5-6, this  
658 pattern is no longer apparent.

659

660

661

662 **TABLES**

663 **Table 1.** A comparison of the support (based on Akaike weight) for different social learning  
 664 models and the asocial learning model.

Model form	Rate of social transmission		
	same/different across tasks	Smooth-coated otters	Asian short-clawed otters
Asocial		12.3%	<b>59.4%</b>
Social transmission:			
Additive model	Same	7.0%	20.1%
	Different	0.8%	1.5%
Multiplicative model	Same	<b>79.4%</b>	19.6%
	Different	0.6%	0.5%

665 Shaded cells indicate the models with most support.

666

667 **Table 2.** Estimates of the effect of social transmission in each species.

Species	Social transmission rate per unit network connection (s)	% of events by social transmission (excluding innovation)
Smooth-coated otters	45.2 (0.44 - $\infty$ )*	96.0% (27.5% - 100%)
Asian short-clawed otters	dTADA: 0 (0 - 0.17)\$	dTADA: 0% (0 - 17.3%)

668 \* Note that it is common for OADA to fail to put an upper limit on the strength of social transmission  
 669 when the order of learning follows the network closely. This simply means it is plausible that all  
 670 individuals learned by social transmission, except the innovator.

671 <sup>§</sup>Order of acquisition diffusion analysis (OADA) was unable to precisely estimate the effect of social  
 672 transmission in Asian short-clawed otters, so we also ran a discrete time of acquisition diffusion analysis  
 673 (dTADA) for this species (see Main Text and Supplementary Material Table S4).

674

675 **Table 3.** Support (total Akaike weight) and estimates for the effects of sex and age.

Effect	Smooth-coated otters		Asian short-clawed otters		Ratio
	Support	*MAE (95% CI)	Support	*MAE (95% CI)	
Sex (female / male)	24.9%	1.02x (0.63 - 1.65)	92.8%	2.26x (1.12 - 4.54)	ASC/SC = 2.22x (0.71 - 6.95)
Offspring / parents	100.0%	6.10x (1.11 - 33.53)	27.1%	0.95x (0.56 - 1.62)	SC/ASC = 7.48x (1.38 - 40.64)

676 Cells shaded in grey indicate evidence for a sex/age effect on social transmission.

677 \*MAE = Model-Averaged Estimate averaged across the best supported set of models for that species  
 678 (i.e. the cell with highest support in Table 1), with back-transformed Wald 95% confidence intervals  
 679 based on unconditional standard errors. The ratios of effects are taken from a combined OADA model  
 680 for both species, including social transmission, sex and age, all of which were allowed to differ between  
 681 species.