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## The effects of age on social and individual learning in jackdaws (*Corvus monedula*)

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**Abstract**

Within a social group, problems such as finding and processing food may be solved most effectively by watching or interacting with experienced group members. Not only can social characteristics of demonstrators influence social learning processes, but also the observers' identity and age may play a role. Here, social and individual learning of jackdaws (*Corvus monedula*) of different age groups was investigated in a semi-natural setting. Two observer groups, which had observed a conspecific demonstrator opening a two-action food box, and a non-observer group were examined as to how they opened the same box. Employing the most ecologically appropriate mechanism, jackdaws learned socially through enhancement. Although both groups approached the test apparatus, only the juveniles learned how to open the apparatus. This may have been driven by an enhanced need to acquire information during early life. As more observers became available, the juveniles could watch and scrounge from each other. Individuals preferentially watched others with access to information and conspecifics they could scrounge food from. Whereas high-ranking animals to relied on monopolising the apparatus following initial social learning, lower-ranking individuals accumulated additional social information by observing high-ranking individuals opening the apparatus. Although we found an effect of social learning in both adult and juvenile jackdaws, only juveniles solved the task. This suggest that they are either more explorative than adults or better social learners. Jackdaws represent an interesting model system for studying the dynamics of social learning.

**Keywords**

corvid, jackdaw, social learning, two-action task, individual learning, age effect

**Introduction**

In an environment where animals interact with each other on a daily basis, social information is frequently present and available to everyone who is able to perceive and process it ('inadvertent social information' (Danchin, Giraldeau, Valone, & Wagner, 2004)). It is likely that social animals are able to utilise the readily available social information in a group (i.e. 'information scrounging' (Giraldeau, Valone, & Templeton, 2002)) and those who are successful at using such information from others will experience

1  
2  
3 46 some advantage over other group members (Russon, 1997; Whiten & van Schaik, 2007). Such *socially*  
4  
5 47 *biased learning* often plays an important role when members of a group learn about novel or familiar foods  
6  
7 48 (Fragazy & Visalberghi, 2004). Identity and characteristics of the observer(s) and the observed  
8  
9 49 conspecific(s) can further shape the nature of the social interaction. For example, observers of a certain age  
10  
11 50 or dominance rank might be more prone to use social information than others (Biro et al., 2003; Langen,  
12  
13 51 1996), and particular individuals might be more influential demonstrators for some observers than others.  
14  
15 52 Thus, the nature of the relationship between demonstrator and observer can modulate the salience of social  
16  
17 53 information (*directed social learning* (Coussi-Korbel & Fragaszy, 1995)). Furthermore, individuals might  
18  
19 54 employ two different social learning strategies; ‘When’ strategies, such as ‘copy when uncertain’ and  
20  
21 55 ‘Who’ strategies, such as ‘copy the majority’ or ‘copy if better’ (Laland, 2004). The ‘Who’ strategies also  
22  
23 56 include copying affiliated, older or successful individuals, kin or good social learners (e.g. chimpanzees,  
24  
25 57 *Pan troglodytes* (Biro et al., 2003; Matsuzawa, 1994); magpie-jays, *Calocitta formosa* (Langen, 1996)).

26 58 Social learning experiments in the wild contribute greatly to understanding the ecological and  
27  
28 59 evolutionary pressures that might have shaped observed behaviours (Federspiel, Clayton, & Emery, 2009).  
29  
30 60 Nevertheless, mainly experiments in captivity have so far allowed experimenters to include control  
31  
32 61 conditions, i.e. to test naïve subjects that were not allowed to observe a demonstrator performing a certain  
33  
34 62 behaviour before being tested on that same behaviour, as well as manipulate influencing factors, such as  
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36 63 visibility and frequency of the demonstrations or food provision. One task utilising this method was  
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38 64 performed on chimpanzees (Whiten, Horner, & de Waal, 2005). It combined use of a two-action task  
39  
40 65 (Dawson & Foss, 1965) within a group setting to create a powerful set-up for testing social learning and  
41  
42 66 cultural processes. Two demonstrators were trained to use one of two alternative tool use techniques and  
43  
44 67 were then reintroduced to their respective group, where they opened a test apparatus by using one of the  
45  
46 68 two techniques in the presence of their conspecifics. A Control group was exposed to the apparatus without  
47  
48 69 a model present. Whereas individuals in the Control group failed to solve the task, the novel behaviours  
49  
50 70 seeded by the two demonstrators spread differentially in the two experimental groups with individuals  
51  
52 71 preferentially using the technique they had observed and that was prevalent within their own group. In a  
53  
54 72 follow-up study, it was found that ‘ghost conditions’, in which the apparatus was operated automatically  
55  
56 73 rather than by a chimpanzee demonstrator, were not sufficient for learning to occur in the chimpanzee

74 observers (Hopper et al., 2007). It therefore seemed that the social stimulus of a conspecific opening the  
75 apparatus was vital and that the studies provide support for traditions in chimpanzees.

76 In some corvids, social information also seems to play a role in the context of foraging. For  
77 example, when in close proximity to foraging family members, Florida scrub jays (*Aphelocoma*  
78 *coerulescens*) learned to forage at a novel food patch (Midford, Hailman, & Woolfenden, 2000); rooks  
79 (*Corvus frugilegus*) choose to land and forage where others are already foraging (Waite, 1981) and choose  
80 the same novel food as a social partner (Dally, Clayton, & Emery, 2008). Both hooded crows (*Corvus*  
81 *cornix*) and ravens (*Corvus corax*) pick up information about the location of food at roosts that act as  
82 'information centres' (Marzluff, Heinrich, & Marzluff, 1996; Sonerud, Smedshaug, & Bråthen, 2001); and  
83 in experimental studies, ravens that had observed others opening a food box approached and opened the  
84 box more readily than non-observers (Fritz & Kotrschal, 1999). Langen (1996) found evidence for social  
85 learning of a novel foraging skill in wild white-throated magpie-jays. Individuals had to open a door in  
86 order to gain access to food. Those who had been able to watch trained demonstrators were more likely to  
87 acquire the opening skill than those without models. Age and aggression levels affected the social learning  
88 process, in that younger birds were more likely to acquire the technique than older ones and the presence of  
89 aggressive animals led to others either refraining from or being encouraged to perform the demonstrated  
90 action.

91 The current study investigates social learning in jackdaws in a semi-naturalistic context. Jackdaws  
92 are highly social corvids that form stable pair-bonds for life (Roëll, 1978) by food-sharing, which is  
93 thought to be involved in the initial formation of bonds by juveniles (von Bayern, de Kort, Clayton, &  
94 Emery, 2007). They roost and forage in large groups, often together with rooks, feed on seeds and insects  
95 and, in contrast to most other corvids, do not cache food (de Kort & Clayton, 2006). Their socio-cognitive  
96 abilities seem to be highly developed and include a pronounced sensitivity to the attentional states of other  
97 jackdaws (Davidson, Butler, Fernández-Juricic, Thornton, & Clayton, 2014; von Bayern & Emery, 2009a)  
98 and even humans (von Bayern & Emery, 2009b). In studies of social learning in jackdaws, it was found that  
99 observers preferentially handled a box (out of two boxes) which the demonstrator had fed from (Schwab,  
100 Bugnyar, & Kotrschal, 2008), learned about the location of food by displacing others from food containers  
101 (Wechsler, 1988) and preferred an object that had been handled last by a human experimenter (Mikolasch,

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2  
3 102 Kotrschal, & Schloegl, 2012). Individuals that witnessed another jackdaw obtaining food were more  
4  
5 103 successful at opening a food box and foraging from it than non-observers (Federspiel and Emery,  
6  
7 104 unpublished data).

8  
9 105 For social animals, like jackdaws, a more natural method to test social learning is within a group  
10  
11 106 setting. Testing animals in a group in captivity creates a set-up which combines the benefits of a  
12  
13 107 ecologically valid scenario, whilst maintaining a high level of experimental control. Thus, in the current  
14  
15 108 study, a novel approach to social learning research in birds was used, presenting a two-action task (Dawson  
16  
17 109 & Foss, 1965) to birds in a group setting, using a similar procedure to the chimpanzee studies (Hopper et  
18  
19 110 al., 2007; Whiten et al., 2005). As such, both demonstration and test sessions were conducted within the  
20  
21 111 group. Two observer groups were tested after having observed a demonstrator opening an apparatus by  
22  
23 112 either ‘lifting’ or ‘pushing’. In order to investigate a potential difference in learning abilities between birds  
24  
25 113 of a different age (see e.g. Langen, 1996 or Biro et al., 2003 and (Whiten & Mesoudi, 2008) for a review on  
26  
27 114 experimental designs in social diffusion experiments), the bird groups consisted of either juveniles or adults  
28  
29 115 only.

30 116 Our objectives were to examine social learning processes in jackdaws in a controlled, but  
31  
32 117 ecologically valid setting and to test for differences in social learning between birds of different ages. We  
33  
34 118 expected jackdaws to socially learn to open the box because they are highly social, utilise social  
35  
36 119 information in finding food (Schwab et al., 2008; von Bayern & Emery, 2009b) and have demonstrated the  
37  
38 120 ability to socially learn in an experimental pilot study (Federspiel and Emery, unpublished data) and social  
39  
40 121 attention in other contexts (Davidson et al., 2014; Mikolasch et al., 2012; Mikolasch, Kotrschal, &  
41  
42 122 Schloegl, 2013; Schwab, Swoboda, Kotrschal, & Bugnyar, 2012; von Bayern et al., 2007; von Bayern &  
43  
44 123 Emery, 2009a, 2009b). We further anticipated effects of observer age on social learning as jackdaws, like  
45  
46 124 other large-brained birds, go through an extended juvenile period in which increased opportunities for  
47  
48 125 social learning occur (Emery, Seed, & von Bayern, 2007). Furthermore, we investigated whether ‘directed  
49  
50 126 social learning’ after Coussi-Korbel and Fragaszy (1995) and Laland’s (2004) ‘Who’ strategies apply to  
51  
52 127 jackdaws and thus whether the individuals’ characteristics other than age might further shape the social  
53  
54 128 learning process.

55 129

## 130 **Methods**

### 131 ***Subjects and Housing***

132 Three groups of jackdaws, housed in three different aviaries, participated in this experiment. Two  
133 were used as observer groups (Group 1 [n = 8 juveniles] & Group 2 [n = 7 adults]) and one used as a  
134 Control group (n = 12 adults; Table 1). The demonstrator (Dohli) was a female bird (hatched in 2006) who  
135 was housed together with the Control group (not during the experimental period). The bird was socially  
136 bonded with experimenter 2 (AMPvB), who nursed it back to health after a past injury. The close proximity  
137 to experimenter 2 in experiments was therefore rewarding to the demonstrator. All birds apart from !Khosha  
138 and Poldi were hand-raised and all were habituated to the presence of humans. For individual identification,  
139 the birds were banded with coloured leg rings. The 3 groups were housed in different parts of an outdoor  
140 aviary measuring 6 m x 5 m x 2.80 m (Group 1), 10 m x 9 m x 2.80 m (Group 2) and 15 m x 9m x 2.80 m  
141 (Control group) and kept according to the guidelines of the University of Cambridge.

142

143 INSERT TABLE 1 HERE

144

145 The three parts of the aviary could be separated visually by drawing opaque curtains between  
146 them. The aviary was equipped with nest boxes, branches, bushes, perches, poles, rocks and toys. Food was  
147 provided ad libitum after experimental sessions (cereals, cooked rice, curd, dried insects, dry cat food, eggs,  
148 various types of fruit, mealworms *Tenebrio molitor* and minced beef heart) and water was available at all  
149 times. During the experimental phase, mealworms were removed from the maintenance diet to ensure  
150 motivation during test sessions. Morio worms (*Zophobas morio*) were used as a reward during test sessions.

151

152

### 153 ***Apparatus and Experimental Set-Up***

154 All experimental sessions were conducted in the outdoor aviaries. The training of the demonstrator  
155 took place indoors out of view of the other jackdaws.

156 Each group was tested in compartments located in their respective parts of the housing aviary. All  
157 birds were well habituated to the presence of an experimenter in their aviaries. For demonstration sessions,

1  
2  
3 158 the demonstrator was released into a cage (96 cm x 50 cm x 65 cm) containing the test apparatus (Fig. 1) at  
4  
5 159 a location clearly visible to the whole group (the demonstrator had been trained to enter the cage  
6  
7 160 voluntarily through a little door (20 cm x 30 cm).  
8

9 161

10  
11 162 INSERT FIGURE 1 HERE  
12

13 163

14  
15 164 During demonstration sessions, two experimenters were present: experimenter 1 (IGF) sat  
16  
17 165 approximately 2 m from the cage, operating the video camera (Canon Digital Camcorder, Model MD101  
18  
19 166 Pal), a Dictaphone and the remote control with which the apparatus could be opened and closed;  
20  
21 167 experimenter 2 (AMPvB) stayed near the demonstrator in order to keep it relaxed and motivated and kept  
22  
23 168 her glance focussed on the ground, so as not to provide any cues to the observer birds. Motivation was  
24  
25 169 provided by mere presence of experimenter 2 based on a strong social bond between her and the  
26  
27 170 demonstrating individual (Dohli). For test sessions, the apparatus was placed at the same location in the  
28  
29 171 aviary, but without the cage, and only experimenter 1 was present.  
30

31 172 The test apparatus consisted of a wooden box (18 cm wide, 16 cm deep and 33 cm high; Fig. 2) with a  
32  
33 173 treadle (5.5 cm x 11 cm x 1.5 cm) mounted horizontally on the front of the apparatus (5cm from the floor  
34  
35 174 and 3 cm from the left side; see Fig. 2).  
36

37  
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39  
40  
41 176 INSERT FIGURE 2 HERE  
42

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44 177

45  
46 178 A yellow wooden ball (approximately 1 cm<sup>3</sup>) with a wire stuck through the centre was attached to the  
47  
48 179 centre of the treadle (6.5 cm from the edge). The ball could be lifted up 2.5 cm, or, with some force, pushed  
49  
50 180 halfway into the treadle (approximately 0.75 cm).  
51

52  
53 181 Next to the treadle, at the same height and 4 cm from the right side of the apparatus, a perch (11.5  
54  
55 182 cm long, 1.5 cm thick) was attached to the apparatus, which enabled the birds to sit while operating the ball  
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1  
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3 183 and potentially feed afterwards. A feeder opening (6 cm x 4.5 cm x 4 cm) was cut out of the centre of the  
4  
5 184 apparatus, at the jackdaws' eye-level. The opening to the apparatus was baited with Morio worms in full  
6  
7 185 view of the subjects and could be opened and closed by a wooden panel with a Plexiglas window. The  
8  
9 186 window's movements were operated by a remote control ('Digital Proportional Radio Control System  
10  
11 187 Zebra 2 AM'), which controlled a motor connected to the window on the inside of the apparatus.

12  
13  
14 188 For the habituation phase, two versions of the habituation apparatus that were slightly different to  
15  
16 189 the test apparatus were used, both of them lacking the treadle with the yellow wooden ball: a functional  
17  
18 190 'open-window' habituation apparatus with a loosely attached window which could easily be pushed  
19  
20 191 inwards and a non-functional 'closed-window' habituation apparatus, which allowed no access to the bait,  
21  
22 192 because the window was blocked.

23  
24 193 The birds could feed freely from the open-window habituation apparatus (version 1) by pushing  
25  
26 194 the window in with their head or beak. The window of the closed-window habituation apparatus (version 2)  
27  
28 195 was blocked and the jackdaws could therefore not feed from this apparatus. Both apparatuses were baited.  
29  
30 196 Only one version of the habituation apparatus was presented at a time. To make the distinction between the  
31  
32 197 two windows more obvious, black tape was stuck on both sides of the feeder opening of the closed-window  
33  
34 198 apparatus (see Fig. 2). The birds stopped approaching the closed-window apparatus after a few trials. The  
35  
36 199 next step was to introduce them to the test apparatus in the actual demonstration sessions. The test  
37  
38 200 apparatus looked like the closed-window version of the habituation apparatus, however, it differed slightly  
39  
40 201 as it had a treadle and ball attached to it. Having observed the demonstrations, the subjects should have  
41  
42 202 learned that the seemingly non-functional test apparatus could be operated by manipulating the newly  
43  
44 203 attached treadle with the ball in order to open the window and access the food reward.

45  
46 204

#### 47 205 ***Procedure***

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49  
50 206 The study was conducted from November 2008 to January 2009 at the avian cognition station  
51  
52 207 associated with the Max Planck Institute for Ornithology in Starnberg, Germany. To avoid different  
53  
54 208 influences of demonstrator identity (Fragazy & Visalberghi, 2004) and to ensure that all observers

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3 209 experienced similar demonstrations, the same bird (Dohli) acted as a demonstrator for both groups. The  
4  
5 210 study was divided into

- 6  
7 211 • a *demonstrator training phase*,
- 8  
9 212 • a *habituation phase* for observers (juveniles of Group 1 and adults of Group 2) and non-observers  
10  
11 213 (adults of the Control group),
- 12  
13 214 • a *demonstration phase* consisting of 24 for the juvenile observer group (lifting) and 21 30-min  
14  
15 215 sessions for the adult observer group (pushing), until each individual had observed at least 30  
16  
17 216 demonstrations,
- 18  
19 217 • and a *test phase* consisting of 30 min sessions for all three groups.

20  
21 218 The demonstrator was first trained to lift up the yellow ball and then demonstrated the action to  
22  
23 219 the juvenile group during their *Demonstration Phase*. During each demonstration session, 1 to 10  
24  
25 220 demonstration actions were given by the demonstrating subject, depending on their motivation. One such  
26  
27 221 action was counted as complete when the ball had been lifted up at least 2 cm (approximately twice the  
28  
29 222 length of the ball itself). The moment the demonstrator had completed the action, i.e. lifted the yellow ball  
30  
31 223 up at least 2 cm, the window opened and the group watched the demonstrator feeding from the opened  
32  
33 224 window. Once each individual of the juvenile observer group (lift) had observed at least 30 individual  
34  
35 225 demonstrations in total during 24 demonstration sessions, the group was tested in 20 test sessions – now  
36  
37 226 without the demonstrator present. Subsequently, the demonstrator was re-trained to push the ball down  
38  
39 227 instead of lifting it up. The adult observer group (push) was then provided with 21 demonstration sessions  
40  
41 228 until each individual had observed at least 30 demonstrations before proceeding to the *Test Phase*  
42  
43 229 consisting of 20 test sessions. Here, one demonstration was counted as complete when at least a third of the  
44  
45 230 ball had been pushed into the treadle (force was needed to achieve this, and the normal exploratory pecking  
46  
47 231 behaviour was not sufficient). At the moment this was achieved by the demonstrator, experimenter 1  
48  
49 232 opened the window with the remote control and the demonstrator bird retrieved and ate the reward. Finally,  
50  
51 233 the Control group was tested without a previous demonstration phase with demonstration sessions.

52 234

53 235 *Demonstrator Training Phase*

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1  
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3 236 Training of the demonstrator took place in visual isolation from the other jackdaws. After  
4  
5 237 habituation to the apparatus, the demonstrator was gradually shaped to open it, training it first to feed freely  
6  
7 238 from the apparatus, then to touch the wooden ball and finally to lift it upwards (technique 1). As soon as the  
8  
9 239 bird lifted up the ball, Experimenter 1 opened the window of the apparatus via the remote control. When  
10  
11 240 the demonstrator was comfortable with approaching and reliably opening the apparatus, they were trained  
12  
13 241 to eat from the apparatus inside the cage. Training was complete when the demonstrator responded  
14  
15 242 consistently by lifting up the ball without any preceding explorative actions and feeding from the apparatus  
16  
17 243 opening straight afterwards inside the cage. Subsequently, the demonstrator was trained to open the  
18  
19 244 apparatus via technique 2 (pushing downwards) in a similar manner, shaping their exploratory pecking  
20  
21 245 behaviour into a forceful vertical stabbing movement directed at the centre of the ball, which pushed the  
22  
23 246 ball into the treadle (determined by observing a thin line that was drawn around the centre of the ball). It  
24  
25 247 took the demonstrator 12 sessions of approximately 20 minutes to learn and apply opening technique 1 in a  
26  
27 248 consistent manner and 10 sessions of approximately 20 minutes to learn and exclusively use technique 2.

28 249

30 250 *Habituation Phase: Observer Groups and Control Group*

31  
32 251 Since jackdaws, like most corvids, are highly neophobic birds and the test apparatus included  
33  
34 252 novel, potentially intimidating parts (the treadle and yellow ball), all three groups had to be habituated to  
35  
36 253 the yellow wooden ball (detached from the apparatus), the video camera and tripod, the remote control, the  
37  
38 254 cage and the open- and closed-window version of the apparatus (see '*Apparatus and Experimental Set-*  
39  
40 255 *Up*'). This occurred prior to the demonstration sessions, in order to rule out neophobia as an explanation for  
41  
42 256 differences in the behaviour between the different experimental groups. These objects were placed into  
43  
44 257 each of the three parts of the aviary in a randomised order and left until the birds ceased to show neophobic  
45  
46 258 reactions towards them, had all touched the wooden ball and fed from the open-window apparatus.  
47  
48 259 Habituation lasted approximately 1 week.

49 260

51 261 *Demonstration Phase: Observer Groups*

52  
53 262 Once habituated to the apparatus, the observers were given demonstration sessions. Prior to the  
54  
55 263 demonstration sessions, the cage and the apparatus were positioned in the aviary (Fig. 1), and the test group

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2  
3 264 was visually isolated from the other groups by drawing the black curtains between compartments. At the  
4  
5 265 beginning of the demonstration sessions, the group and the demonstrator were shown a Morio worm, which  
6  
7 266 was then visibly placed into the feeder opening of the apparatus. Subsequently, the experimenter who had  
8  
9 267 performed the baiting closed the apparatus window and the demonstrator was released into the  
10  
11 268 demonstrator cage. Video and audio recording was begun as soon as the cage door was closed. The  
12  
13 269 observers could either watch the demonstrations from 'near' (on top of the cage or on the ground within 2  
14  
15 270 body lengths from the cage) or 'far' (on one of the wooden perches above the cage, at a distance of  
16  
17 271 approximately 2.70 m in the juvenile observer group and at 2.50 m in the adult observer group), depending  
18  
19 272 on the position of the given subject. A demonstration was only counted as 'observed', if the head of the  
20  
21 273 given jackdaw was oriented towards the demonstrator. The birds received approximately 20 blocks of 1-10  
22  
23 274 demonstrations per day, depending on the demonstrator's motivation. Demonstrations were continued until  
24  
25 275 each individual of juvenile observer group (lift) had observed at least 30 openings by lifting and  
26  
27 276 consecutive feeding events and subsequently, after re-training the demonstrator, each individual of the adult  
28  
29 277 observer group (push) had observed at least 30 openings by pushing and consecutive feeding events. In  
30  
31 278 order to avoid a neophobic response towards the test apparatus and to control for total exposure time, the  
32  
33 279 non-observers (Control group) were presented with the test apparatus inside the cage for approximately the  
34  
35 280 same time of exposure as the observer groups, but without the interactions of the demonstrator.

36 281

37 282 *Test Phase: Observer Groups and Control Group*

39 283 After the birds in the observer groups had each observed at least 30 demonstrations, they were  
40  
41 284 tested during 20 30 min sessions using the same set-up as during the *Demonstration Phase*, but with the test  
42  
43 285 apparatus freely accessible, i.e. without the demonstrator cage. The Control group was tested without  
44  
45 286 having seen any demonstrations (but with the same amount of prior exposure to the test apparatus).  
46  
47 287 Experimenter 1 baited and closed the apparatus in sight of the birds which were then able to approach the  
48  
49 288 apparatus (experimenter 2 was not present). In order to open the test apparatus, the birds now had to  
50  
51 289 perform one of two actions at the yellow ball: lifting it upwards (technique 1) or pushing it downwards  
52  
53 290 (technique 2). The experimenter opened the window of the apparatus when a bird had performed one of the  
54  
55 291 two correct actions at the yellow ball. The apparatus was re-baited straight after the given bird had

1  
2  
3 292 swallowed the worm. If the birds did not approach the apparatus for 5 min, the experimenter dummy re-  
4  
5 293 baited, i.e. pretended to re-bait the apparatus in sight of the birds in order to increase their motivation and  
6  
7 294 focus their attention again on the apparatus and the food. All sessions were videotaped for subsequent  
8  
9 295 analysis. If a bird had achieved at least 40 openings, it was excluded from any further sessions. This was  
10  
11 296 done to avoid monopolisation of the apparatus by a single or a few dominant birds.

12  
13 297

### 14 298 *Establishment of Dominance Hierarchy*

15  
16 299 The dominance hierarchy within each group was calculated by conducting daily 20 min  
17  
18 300 observation sessions over the course of 2 months, during which the frequency and direction of  
19  
20 301 displacements (i.e. an animal retreats after having been approached by another) between group members  
21  
22 302 was recorded. Data for the juvenile observer group was then arranged into matrices, and a dominance  
23  
24 303 hierarchy was established. Based on random permutations (10,000) of the displacement matrices, Landau's  
25  
26 304 linearity index ( $h$ ) was calculated using MatMan 1.0 (Noldus Information Technologies, Wageningen, The  
27  
28 305 Netherlands, 1998). A measure of 1 indicates a linear dominance hierarchy; a measure of 0 indicates a non-  
29  
30 306 linear hierarchy (Appleby, 1983; de Vries, Netto, & Hanegraaf, 1993; Hemelrijk, 1990). The directional  
31  
32 307 consistency index ( $dci$ ) shows the consistency of the hierarchy (1 = consistent, 0 = not consistent; for a  
33  
34 308 more detailed description of MatMan 1.0 see de Vries et al. 1993 or MatMan 1.0 manual). Hierarchy  
35  
36 309 calculations were possible for the juvenile group (Group 1) only, as the adult birds of Group 2 interacted  
37  
38 310 less frequently; thus not enough data was available for calculating a dominance hierarchy.

39  
40 311

### 41 312 *Data Analysis*

42  
43 313 In the *Demonstration Phase*, we noted which birds observed any given demonstration and whether  
44  
45 314 they observed it from 'near' or 'far' (see '*Demonstration Phase: Observer Groups*'). The test sessions were  
46  
47 315 scored using two methods, by defining 'states'; (times spans) and 'events' (individual behaviours). Two  
48  
49 316 sets of mutually exclusive states were included: set 1 for the presence/absence of a bird at the set-up; set 2  
50  
51 317 for defining where exactly the bird was in relation to the apparatus. Events were scored for behaviours at  
52  
53 318 the test apparatus (see ESM (1)).

1  
2  
3 319 Videotapes of the experimental sessions were coded using The Observer 5.0 behavioural analysis  
4  
5 320 program (Noldus Information Technology, Wageningen, The Netherlands), and data were analysed with  
6  
7 321 STATISTICA 7 (StatSoft Inc., 1984-2004) (see ESM (2)). Non-parametric statistics were used to analyse  
8  
9 322 the data. All tests were two-tailed, and  $\alpha$  was set at 0.05. Trends were reported for  $0.10 > \alpha > 0.05$ . Where  
10  
11 323 two or more post-hoc tests were performed, we additionally stated significant differences after Bonferroni  
12  
13 324 correction. States and events of the three groups were compared with Kruskal-Wallis ANOVAs and/or  
14  
15 325 Mann-Whitney U tests. Adjusted p-values were given for tests including data with two or more ties, i.e.  
16  
17 326 equal values in both groups (Siegel, 1956). We examined the influence of dominance hierarchy on the  
18  
19 327 behaviour of our subjects at the apparatus by performing Spearman rank correlations of the ranks with total  
20  
21 328 states and events (session 1-7; see ESM (3)). Furthermore, we examined whether the observers used the  
22  
23 329 same opening technique as the demonstrator. We further investigated influences of various factors on social  
24  
25 330 learning during the *Test Phase*, when new demonstrators became available as additional individuals started  
26  
27 331 to open the apparatus. In order to examine whether the number of times a bird, i.e. any focal individual that  
28  
29 332 might have observed a conspecific opening the apparatus during the *Test Phase*, opened the apparatus is  
30  
31 333 dependent on kinship (with the observed individual, i.e. the respective new demonstrator), the combination  
32  
33 334 of the observer's and demonstrator's sex, total number of scroungings by the observer, the relative  
34  
35 335 hierarchy (observer - demonstrator) and/or total number of openings performed by that demonstrator in the  
36  
37 336 *Test Phase*, we calculated a generalized linear mixed model (GLMM) with a Poisson distribution and a log-  
38  
39 337 link function. Relative hierarchy scores were derived from subtracting the demonstrator's rank from the  
40  
41 338 observer's. Therefore, positive scores indicated that in a given dyad, the observer was higher in rank than  
42  
43 339 the demonstrator, whereas negative scores stood for observers lower in rank than demonstrators. We started  
44  
45 340 with the full model comprising the listed fixed factors in Table 3. We included 'dyad' (i.e. all 56 possible  
46  
47 341 dyads of the juveniles observer group) and 'participated trials' (i.e. the number of trials in which both  
48  
49 342 members of each given dyad were present, where 'trial' is defined as the time span starting with the  
50  
51 343 experimenter replenishing the apparatus and ending with an individual removing the reward) as random  
52  
53 344 factors in order to account for the differences between individuals, their various possible dyadic  
54  
55 345 combinations and the different number of trials each observer participated in. To derive the final model, we  
56  
57 346 determined the relative AICc (Akaike information criteria with a correction for finite sample sizes) by  
58  
59  
60

1  
2  
3 347 calculating the difference between each model's AICc and the model with the lowest AICc (Burnham &  
4  
5 348 Anderson, 2010). Additionally, we calculated Akaike weights ( $\omega_j$ ) representing posterior probabilities of  
6  
7 349 the model used to calculate evidence ratios (Burnham & Anderson, 2010). Fixed factors are presented in  
8  
9 350 the final model irrespective of their statistical significance. Figures were assembled using Adobe Illustrator  
10  
11 351 (Adobe Systems Incorporated; Figures 1-2) or Graph Pad Prism (GraphPad Software, Inc.; Figures 3-6).

12  
13 352

## 14 353 **Results**

### 15 354 ***Experiment***

#### 16 355 *Time Spent at the Apparatus*

17  
18  
19  
20 356 Groups differed in the time they spent at the apparatus (Kruskal-Wallis ANOVA,  $H = 21.605$ ,  $N =$   
21  
22 357  $26$ ,  $P < 0.001$ ; Fig. 3). Both observer groups spent more time at the apparatus than the Control group  
23  
24 358 (Mann-Whitney U tests, juvenile group:  $Z = 3.361$ ,  $N_1 = 8$ ,  $N_2 = 8$ ,  $P = 0.001$ ; adult group:  $Z = 3.554$ ,  $N_1 =$   
25  
26 359  $10$ ,  $N_2 = 8$ ,  $P < 0.001$ ). Of the Control group, only one individual ever got within 2 body lengths of the  
27  
28 360 apparatus: Zulu stayed close to the apparatus in session 20 for 6.3 s. Individuals of the juvenile observer  
29  
30 361 group (lift) spent more time at the apparatus than members of the adult observer group (push; Mann-  
31  
32 362 Whitney U test,  $Z = 3.199$ ,  $N_1 = 8$ ,  $N_2 = 10$ ,  $P = 0.001$ ; Fig. 3). These results would also pass the sequential  
33  
34 363 Bonferroni correction with  $p < 0.017$ .

35  
36 364

37  
38 365 INSERT FIGURE 3 HERE

39  
40 366

#### 41 367 *Time Spent at Relevant Parts of the Apparatus*

42  
43 368 Groups spent different amounts of time at the parts of the apparatus from which an opening could  
44  
45 369 be performed (treadle or perch; Kruskal-Wallis ANOVA,  $H = 15.600$ ,  $N = 26$ ,  $P = 0.014$ ). The juvenile  
46  
47 370 observer group spent more time on those parts of the apparatus than the adult observer group (Mann-  
48  
49 371 Whitney U tests: overall time:  $Z = 3.110$ ,  $N_1 = 8$ ,  $N_2 = 10$ ,  $P = 0.002$ ). As the individuals of the Control  
50  
51 372 group were almost never present and never touched or looked at the apparatus, their data was excluded  
52  
53 373 from all further analyses.

54  
55 374

1  
2  
3 375 *Latency to Approach and Touch the Apparatus*

4  
5 376 The juvenile observer group was faster at getting within 2 body lengths of the apparatus than the  
6  
7 377 adult group (Mann-Whitney U tests,  $Z = -2.843$ ,  $N_1 = 8$ ,  $N_2 = 10$ ,  $P = 0.004$ ; Fig. 4).

8  
9 378

10  
11 379 INSERT FIGURE 4 HERE

12  
13 380

14  
15 381 The juvenile observer group was also the fastest to first touch the apparatus, either by  
16  
17 382 manipulating it, opening it or sitting on it (Mann-Whitney U tests,  $Z = -3.199$ ,  $N_1 = 8$ ,  $N_2 = 10$ ,  $P = 0.001$ ;  
18  
19 383 Fig. 5), and first look at the apparatus closely (Mann-Whitney U tests,  $Z = -2.754$ ,  $N_1 = 8$ ,  $N_2 = 10$ ,  $P =$   
20  
21 384 0.006).

22  
23 385

24  
25 386 INSERT FIGURE 5 HERE

26  
27 387

28  
29 388 Subjects of the juvenile observer group (Group 1) sat on the perch or the treadle sooner than adults  
30  
31 389 of Group 2 (Mann-Whitney U tests:  $Z = -3.288$ ,  $N_1 = 8$ ,  $N_2 = 10$ ,  $P = 0.001$ ).

32  
33 390

34  
35 391 *Total Number of Actions at the Apparatus: Looks, Manipulations and Openings*

36  
37 392 The juvenile observer group looked at and manipulated the apparatus more often than the adult  
38  
39 393 observer group (Mann-Whitney U tests,  $N_1 = 8$ ,  $N_2 = 10$ : looks:  $Z = 3.288$ ,  $P = 0.001$ ; manipulations of  
40  
41 394 apparatus:  $Z = 3.288$ ,  $P = 0.001$ ), and also manipulated the yellow wooden ball more often ( $Z = 3.110$ ,  $P =$   
42  
43 395 0.002). When we took into account the amount of time the animals were present and looked at the  
44  
45 396 frequencies of performed actions (i.e. number of actions per time present), we found that the above results  
46  
47 397 held for manipulations at the apparatus and the wooden ball, with the juvenile observers performing more  
48  
49 398 of both types of manipulations per time (Mann-Whitney U tests,  $N_1 = 8$ ,  $N_2 = 10$ : apparatus:  $Z = 2.044$ ,  $P =$   
50  
51 399 0.041; ball:  $Z = 3.110$ ,  $P = 0.002$ ). Members of the adult observer group never attempted any openings by  
52  
53 400 lifting or pushing and thus never achieved any actual openings. Overall, the juvenile observers performed  
54  
55 401 256 openings (range per bird = 0-67, median = 32.00, 95% confidence intervals = -17.80/+72.17), only one  
56  
57 402 of which was a push opening. The first opening was a lift opening that was performed by the highest-



1  
2  
3 403 ranking bird Mapuche in the first test session, after 12 min and 31 sec and after 12 performed  
4  
5 404 manipulations at the apparatus and 1 ball manipulation. The only push opening was performed by the mid-  
6  
7 405 ranking Heinrich during the 13<sup>th</sup> session, after having been present at the set-up for a total of 381 min and  
8  
9 406 40 sec. Before the opening, he had performed 26 manipulations at the apparatus, with 59 of them at the  
10  
11 407 ball, and observed 22 openings by five different birds, all of which had been lift openings. Apart from  
12  
13 408 Mapuche and Heinrich, 4 other birds achieved openings. They first opened the apparatus in the 1<sup>st</sup> (Kaya),  
14  
15 409 2<sup>nd</sup> (Maya), 3<sup>rd</sup> (Cheyenne) and 7<sup>th</sup> (Balu) test session, respectively. When individuals had performed 40  
16  
17 410 openings, they were excluded at the end of the session during which they had reached that number. This  
18  
19 411 was done in order to give other individuals the opportunity to also approach the apparatus thereafter.

412

#### 413 *Dominance Hierarchy of the Juvenile Observer Group*

414 Analysis of a total of 154 displacements revealed a stable, linear dominance hierarchy ( $h = 0.964$ ,  
415  $dci = 0.935$ ,  $P < 0.001$ ). With Mapuche being the highest in dominance rank, the order was as follows:  
416 Mapuche > Balu > Cheyenne > Kaya > Heinrich > Maya > Sioux > Apache.

417

#### 418 *Factors influencing social learning opportunities within the juvenile observer group*

419 The longer the animals spent within 2 body lengths of the apparatus, the more time they spent on  
420 the treadle or the perch (Spearman rank correlations,  $N = 8$ :  $R = 0.7881$ ,  $P = 0.004$ ) and the more they  
421 manipulated the apparatus ( $R = 0.810$ ,  $P = 0.015$ ) and the ball ( $R = 0.605$ ,  $P = 0.002$ ). The birds that were  
422 present at the apparatus most frequently were typically higher-ranking animals, occupying the treadle and  
423 the perch at the apparatus (Spearman rank correlation,  $R = -0.786$ ,  $N = 8$ ,  $P = 0.021$ ; Fig. 6).

424

425 INSERT FIGURE 6 HERE

426

427 Furthermore, higher-ranking animals manipulated the apparatus and the ball more frequently  
428 (Spearman rank correlations,  $N = 8$ : total numbers of manipulations: apparatus:  $R = -0.857$ ,  $P = 0.007$ ; ball:  
429  $R = -0.738$ ,  $P = 0.037$ ; frequencies of manipulating the ball, i.e. manipulations per time present:  $R = -0.905$ ,  
430  $P = 0.002$ ) and watched more openings being performed by others ( $R = -0.714$ ,  $P = 0.047$ ). Individuals

1  
2  
3 431 differed in terms of their performance over time: Two of the birds (Balu, Maya) improved their  
4  
5 432 performance over time (Spearman rank correlations: fraction of successful manipulations, i.e. those leading  
6  
7 433 to an opening, of the wooden ball & no. of sessions participated in before (potential) exclusion), one  
8  
9 434 worsened (Kaya), for 3 we found no effect (Cheyenne, Heinrich, Mapuche), and 2 never opened the  
10  
11 435 apparatus (Apache, Sioux) (Table 2).

12 436

13  
14 437 INSERT TABLE 2 HERE15  
16 438

17  
18 439 The frequency of an individual (observer) observing another individual (demonstrator) opening the  
19  
20 440 apparatus is best explained by the total number of scroungings by the observer from the demonstrator,  
21  
22 441 relative hierarchy, and total number of openings performed by the demonstrator in the *Test Phase* (Table  
23  
24 442 3). Thus, observers who performed many scroungings also watched the apparatus being opened more often  
25  
26 443 than others. The higher the relative hierarchy, i.e. the difference of rank between the observer and  
27  
28 444 demonstrator, the lower the number of openings that were watched. Thus, whereas lower ranking  
29  
30 445 individuals tended to watch higher ranking ones, higher ranking ones do not seem to watch lower ranking  
31  
32 446 conspecifics. Demonstrators that performed a high number of successful openings were watched more  
33  
34 447 often than others (Table 4).

35  
36 44837  
38  
39 449 INSERT TABLE 3 HERE40  
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42 45043  
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45 451 INSERT TABLE 4 HERE46  
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48 45249  
50  
51 453 **Discussion**

52  
53  
54 454 In sum, social learning, most likely local or stimulus enhancement, seemed to initially draw the jackdaws to  
55  
56 455 the apparatus. Juveniles were more explorative than adults and thus subsequently learned to open the  
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58  
59  
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1  
2  
3 456 apparatus via individual learning. Dominant juveniles monopolised the apparatus, which further influenced  
4  
5 457 social and/or individual learning opportunities within that group.

6  
7 458 We found that both observer groups spent more time at the test apparatus than the non-observers  
8  
9 459 (Control group), but only individuals in the juvenile group learned to successfully manipulate and thus  
10  
11 460 open the apparatus. The juvenile observers also spent more time near the relevant parts of the apparatus  
12  
13 461 than the adult observers. In contrast, the non-observers hardly ever approached the apparatus. The fact that  
14  
15 462 the only difference between observers and non-observers was that the former experienced a social stimulus  
16  
17 463 i.e. observed the demonstrator opening and feeding from the apparatus, suggests that there was a social  
18  
19 464 learning effect, drawing the attention of the observers to the apparatus.

20 465 Observing conspecifics near the apparatus may also have helped to overcome the jackdaws'  
21  
22 466 neophobia, because observers may have learned that it is safe to approach. However, the fact that all three  
23  
24 467 groups, hence also the non-observers, had previously fed from the open-window apparatus, and were  
25  
26 468 habituated to treadle and the ball (see *Habituation Phase*), renders neophobia as an explanation for the  
27  
28 469 difference in approach behaviour between observers and non-observers unlikely. Whereas both observer  
29  
30 470 groups readily approached the apparatus from trial 1, only the juvenile observer group (lift) opened the  
31  
32 471 apparatus. We can see three possible explanations for why only the juveniles succeeded. First of all, lifting  
33  
34 472 may be easier than pushing. Due to the lack of a baseline given that the non-observers did not interact with  
35  
36 473 the apparatus, it is difficult to say if lifting the ball was simply the more natural (or simpler) behaviour of  
37  
38 474 the two, observers had acquired the opening technique by observing the demonstrator during the  
39  
40 475 *Demonstration Phase* or learned the technique via individual or social learning during the *Test Phase*.  
41  
42 476 However, we believe that lifting was not the more natural or simpler, but rather the more complex  
43  
44 477 behaviour out of the two. When exploring objects, jackdaws usually peck at them, whereas lifting seems to  
45  
46 478 be a much less prevalent behaviour (von Bayern, personal observation). In order to exclude this explanation  
47  
48 479 entirely, future studies should compare individuals of the same age groups in both social learning  
49  
50 480 conditions and in the control. Due to the restricted number of available groups this was not possible in the  
51  
52 481 current study.

53 482 Second, juveniles may be generally more explorative and thus more prone to individual learning  
54  
55 483 compared to adults. They were faster at approaching and touching the apparatus from the first presentation,  
56  
57  
58  
59  
60

1  
2  
3 484 and closely looked at and manipulated it more frequently than the adult observer group. The juvenile  
4  
5 485 observers were in their first summer of life and almost 5 years younger than the individuals of the adult  
6  
7 486 observer group. Jackdaws, like most corvids, exhibit slow development and prolonged parental care and  
8  
9 487 thus, growing up in such a protected environment may enable them to ‘afford’ engaging in more individual  
10  
11 488 learning opportunities. Throughout their first summer, they typically go through an explorative phase, still  
12  
13 489 protected by their parents, until they suddenly become neophobic in autumn (Katzir, 1981). Age therefore  
14  
15 490 seems to play an important role in jackdaws’ individual learning, with juveniles being more explorative and  
16  
17 491 hence more likely to discover the solution by individual learning, or individual learning combined with  
18  
19 492 social learning as discussed below.

20 493 Third, juveniles may be generally better at social learning or more receptive to social cues than  
21  
22 494 adults. It is thus also possible that a social stimulus is more salient for juveniles than for adults, because  
23  
24 495 they need to acquire skills for later in life during this crucial developmental window. During their  
25  
26 496 cognitive development they may thus be particularly receptive to (social) learning opportunities. Similar  
27  
28 497 observations have been made in other species. When Caracara Chimango raptors (*Milvago chimango*) were  
29  
30 498 presented with a food box after having observed a conspecific opening it, juvenile observers were more  
31  
32 499 successful and faster than adults at approaching and opening the box to gain a food reward (Biondi, Bó, &  
33  
34 500 Vassallo, 2010a; Biondi, García, Bó, & Vassallo, 2010b). A similar effect was found in a natural corvid  
35  
36 501 group of magpie-jays, where a novel foraging skill was more likely to be acquired by younger birds than  
37  
38 502 older ones (Langen, 1996).

39 503 Within the juvenile group, we looked at whether social learning was influenced by the  
40  
41 504 relationship between demonstrators and observers, as this can have an effect on whether social learning is  
42  
43 505 employed. This kind of influence was observed for the factor age in house mice (*Mus domesticus* (Choleris,  
44  
45 506 Guo, Liu, Mainardi, & Valsecchi, 1997)) and Norway rats (*Rattus norvegicus* (Galef & Whiskin, 2004)),  
46  
47 507 kinship in ringdoves (*Streptopelia risoria* (Hatch & Lefebvre, 1997)), social status and foraging success in  
48  
49 508 laying hens (*Gallus gallus domesticus* (Nicol & Pope, 1999)), familiarity in guppies (*Poecilia reticulata*  
50  
51 509 (Swaney, Kendal, Capon, Brown, & Laland, 2001)), sex and feeding activity in zebra finches (*Taenopygia*  
52  
53 510 *guttata* (Katz & Lachlan, 2003)), and affiliation in chimpanzees (Bonnie & de Waal, 2006). In jackdaws, a  
54  
55 511 recent study showed that the birds preferred to learn from non-affiliated individuals (Schwab et al., 2008).

1  
2  
3 512 However, the demonstrator used in the current study was not affiliated with any of the subjects since it was  
4  
5 513 outside of the experimental phase housed in another group (the Control group). Therefore such ‘uneven  
6  
7 514 social dynamics’, i.e. socio-positive relationships between the demonstrator and the observers with varying  
8  
9 515 intensity (Coussi-Korbel & Fragaszy, 1995), based on affiliation, did not play a role in the current study  
10  
11 516 during the *Demonstration Phase*. Nevertheless, during the *Test Phase*, influencing factors which played a  
12  
13 517 role during the acquisition of the novel opening technique were the opportunity to scrounge food, and thus  
14  
15 518 the (new) demonstrators’ proximity to the conspecifics, and demonstrator identity in terms of the difference  
16  
17 519 in dominance status between observer and demonstrator and how knowledgeable a given demonstrator was  
18  
19 520 (i.e. if and how often they had already opened the apparatus themselves). In most social learning  
20  
21 521 experiments (and also in the initial *Demonstration Phase* of the current study), the observers were tested for  
22  
23 522 social learning after *passive* observation of a conspecific performing a certain action. However, in the  
24  
25 523 subsequent test phase of the presented study, the animals were not only able to operate the wooden ball on  
26  
27 524 the apparatus themselves, but also to approach the new demonstrators, i.e. those animals that had already  
28  
29 525 acquired the novel behaviour during the *Test Phase*. They could stay in close proximity whilst those  
30  
31 526 demonstrators were opening the apparatus by lifting up the wooden ball. This proximity and opportunity to  
32  
33 527 interact with or even scrounge from the new demonstrators at the apparatus had an influence on number of  
34  
35 528 times demonstrators were observed and thus potentially also on the type and amount of social information  
36  
37 529 that was gained (Coussi-Korbel & Fragaszy, 1995). We found that the high-ranking juveniles of the  
38  
39 530 juvenile observer group spent more time at the apparatus than the low-ranking ones and monopolised the  
40  
41 531 parts from which an opening could be performed, i.e. the treadle and the perch. They also manipulated the  
42  
43 532 ball more frequently than the lower-ranking individuals. Thus, holding a high rank in the group’s hierarchy  
44  
45 533 creates the opportunity to monopolise not just food, but also social and individual learning opportunities.  
46  
47 534 When it comes to utilising social learning opportunities, however, it seems that the lower-ranking  
48  
49 535 individuals observed the higher-ranking ones opening the apparatus more often than vice versa and thus  
50  
51 536 had a higher chance to socially learn through observation rather than by trial and error. This may indicate  
52  
53 537 that whereas high-ranking jackdaws try to rely on monopolisation of the apparatus and thus the reward,  
54  
55 538 lower-ranking birds try to make use of the additional social information (after the *Demonstration Phase*).  
56  
57 539 Secondly, some of the *near* observers (who observed actions from the top of the cage or from the ground,

1  
2  
3 540 within 2 body lengths from the cage; see *Data Analysis*) were able to scrounge, i.e. benefit from the  
4  
5 541 conspecifics' actions. They could take the reward before the actor on some of the trials, which seemed to  
6  
7 542 have facilitated social learning, as scrounging promoted making use of social learning opportunities.  
8  
9 543 Moreover, jackdaws preferentially watched 'knowledgeable' individuals, i.e. individuals with access to  
10  
11 544 information, opening the apparatus (see 'Who' strategies (Laland, 2004)) and ones they could scrounge  
12  
13 545 food from, as was the case for common marmosets (Caldwell & Whiten, 2003), Florida scrub jays (Midford  
14  
15 546 et al., 2000) and meerkats (Thornton, 2008); however, see (Giraldeau & Lefebvre, 1987) for contrary  
16  
17 547 results). As suggested above, juveniles may be more likely to employ social learning in general. However,  
18  
19 548 there might have been another effect of age at work. In line with Laland's (2004) 'Who strategy', the age of  
20  
21 549 the demonstrator relative to those of the observers may matter. A preference to learn from older individuals  
22  
23 550 would explain why only our juvenile observers may have learned the task. The demonstrator was older than  
24  
25 551 the juvenile observers and the same age or younger than individuals of the adult observer group. A similar  
26  
27 552 observation was reported during an investigation of 'intra-community transmission of tool use' by  
28  
29 553 chimpanzees at a field site (Biro et al., 2003). The authors found that individuals preferentially paid close  
30  
31 554 attention to nut-cracking performed by conspecifics of the same age group or older and were more likely to  
32  
33 555 explore the nuts than older individuals. Future studies should further investigate this question.

34 556 If we accept/assume that initial social learning played a role in the success of the juvenile observer  
35  
36 557 group, three different underlying mechanisms may explain their behaviour. First of all, simple forms of  
37  
38 558 social learning might have been employed, such as social facilitation (the observer's behaviour is  
39  
40 559 influenced by the mere presence of a conspecific that has an influence on the observer's motivation  
41  
42 560 (Zajonc, 1965)), contagious behaviour (unlearned, species-specific behaviour is 'released' upon the sight of  
43  
44 561 others engaged in that behaviour (Thorpe, 1956)), or response facilitation, a term that has been used to  
45  
46 562 describe an alternative mechanism to imitation in two-action tasks (the presence of a conspecific  
47  
48 563 performing an act, which might result in obtaining a reward, increases the probability of an observing  
49  
50 564 individual performing the same action (Byrne, 1994)). We consider mere social facilitation as the  
51  
52 565 mechanism guiding the lifting behaviour unlikely as the birds were never tested immediately after a  
53  
54 566 demonstration session: demonstration sessions and test sessions were separated in time, which rendered  
55  
56 567 facilitation effects unlikely. Although it is not known how long a facilitation effect could last for and how  
57  
58  
59  
60

1  
2  
3 568 long the interval between demonstration and tests sessions would have to be in order to rule out facilitation  
4  
5 569 (Hoppitt, Blackburn, & Laland, 2007), we believe conducting test sessions on the day after demonstration  
6  
7 570 sessions would have introduced a salient delay.

8  
9 571 Second, an alternative explanation for our finding is individual trial-and-error learning following  
10  
11 572 an initial effect of stimulus (or local) enhancement by the demonstrator. A similar sequence of events led to  
12  
13 573 the milk bottle-opening of three different parids, where the authors concluded that trial-and-error learning  
14  
15 574 proceeded by stimulus enhancement led to the subsequent spread of the behaviour throughout Great Britain  
16  
17 575 (Fisher & Hinde, 1949; Hinde & Fisher, 1951).

18  
19 576 Finally, more complex forms of social learning might account for our findings, such as imitation  
20  
21 577 or emulation (a more ‘sophisticated’ version of stimulus or local enhancement, where the outcome or goal  
22  
23 578 of an action is copied, but not the exact actions needed to reach said goal or outcome (Tomasello, 1996);  
24  
25 579 but see also (Whiten & Ham, 1992)). In imitation, animals learn something about the action sequence that  
26  
27 580 they observe and typically copy that action in a relatively exact way (Federspiel et al., 2009; Whiten,  
28  
29 581 Horner, Litchfield, & Marshall-Pescini, 2004; Zentall, 2004). Yet, how exact an action has to be copied for  
30  
31 582 that action to qualify as imitation has not been defined. It appears that certain species are capable of  
32  
33 583 copying actions to a very detailed level; for example, in common marmosets (*Callithrix jacchus*) very  
34  
35 584 precise imitative behaviour was revealed using frame-to-frame analysis (Voelkl & Huber, 2007). Social  
36  
37 585 learning tasks that make use of an action sequence bypass that problem by adding an additional level of  
38  
39 586 complexity to the behaviour that has to be copied: not only the actions, but also the order in which the  
40  
41 587 actions are performed have to be copied in order for the behaviour to qualify as imitation (Whiten, 1998).  
42  
43 588 With jackdaws, using a sequence task would not have been practicable, as they seem to exhibit short  
44  
45 589 attention spans (Scheid, Range, & Bugnyar, 2007) and therefore most likely would not have observed the  
46  
47 590 whole sequence performed by the demonstrator; we thus opted for the two-action task paradigm. A further  
48  
49 591 distinction between ‘true imitation’, in which some sort of intention sharing between the demonstrators and  
50  
51 592 the observers is involved (found in great apes (Byrne & Tomasello, 1995); or common marmosets  
52  
53 593 (Bugnyar & Huber, 1997; Voelkl & Huber, 2000)), and ‘mimicry’ or ‘blind imitation’ (e.g. in pigeons,  
54  
55 594 *Columba livia* (McGregor, Saggerson, Pearce, & Heyes, 2006)) makes pinpointing the mechanism even  
56  
57 595 more difficult. Nevertheless, for the current study, the level of intention or understanding involved in  
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2  
3 596 opening the apparatus could only have played a minor role. We expected that when imitating, the animals  
4  
5 597 would apply the same technique as the animal they had observed from the first test trial on and  
6  
7 598 subsequently use that technique (almost) exclusively (if successful). In case of emulation by contrast, the  
8  
9 599 jackdaws would have been expected to reach the same goal or outcome from the beginning, but potentially  
10  
11 600 with *a few* intermediate steps, as in emulation only the outcome or goal is clear to the individuals, not the  
12  
13 601 exact action needed to reach that end-state. However, the successful jackdaws performed up to 90  
14  
15 602 manipulations at the apparatus and the yellow ball before they first opened the apparatus and also continued  
16  
17 603 to manipulate the apparatus and ball after having performed the first opening. Thus, not every manipulation  
18  
19 604 led to a successful opening. Since the observers did not appear to have understood how to open the  
20  
21 605 apparatus from the first trial, it is likely that they had only learned about the location of the ‘trigger’ from  
22  
23 606 the demonstrator via local or stimulus enhancement. Even though ‘performance emulation’, where a naïve  
24  
25 607 individual learns from observation of a knowledgeable individual ‘that a behaviour can be performed and  
26  
27 608 relies on subsequent trial-and-error learning to reproduce that behaviour’ (Galef, 2013), constitutes a  
28  
29 609 further alternative; at this stage, enhancement seems to be the most parsimonious explanation for the  
30  
31 610 observed behaviour. Furthermore, this also makes sense in relation to the jackdaws’ ecology. First, their  
32  
33 611 diet does not include hard-to-access types of food, and they therefore only need to learn about the location  
34  
35 612 of food, but not how to process it by extractive foraging. Therefore, enhancement seems to be the adequate  
36  
37 613 and sufficient mechanism for their requirements (Federspiel et al., 2009). Second, although individual  
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39 614 learning is thought to be more costly than social learning, as it is more time- and energy-consuming (Boyd  
40  
41 615 & Richerson, 1985), especially for young individuals, it seems ecologically sensible to combine a less  
42  
43 616 energetically expensive mechanism with individual learning. The primary advantage of individual learning  
44  
45 617 is the level of detail gained, which seems especially important in the early stages of life. The costs  
46  
47 618 associated with individual learning might then - compared to later in life - also still be affordable in energy  
48  
49 619 terms, as the juveniles enjoy the protection of the group and can afford to spend energy on learning for later  
50  
51 620 in life.

51 621           Due to the set-up and availability of birds, we were only able to test one juvenile and one adult  
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53 622 observer group. We acknowledge that it would have been ideal to test both adults and juveniles with both  
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55 623 opening techniques. Future studies should further investigate the influence of age differences in individual



1  
2  
3 624 and social learning in jackdaws as well as the influence of potentially different levels of difficulty at  
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5 625 employing one of the two described opening techniques by comparing birds of the same age in both social  
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7 626 learning conditions and the control condition. With the current study, we conclude that jackdaws learn  
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9 627 socially by employing local or stimulus enhancement, the ecologically most adequate and sufficient  
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11 628 mechanism for a species that does not rely on extractive foraging. Probably driven by the need to acquire  
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13 629 information and learn about the environment at an early stage of life, juvenile jackdaws appear to be both  
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15 630 better social learners and more explorative than adults, and therefore were more prone to acquiring  
16  
17 631 information through both social and individual learning. As such, juvenile jackdaws can afford costly  
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19 632 individual learning in the safe environment of their group. Within a group of social learners, social factors  
20  
21 633 determine who gains the most opportunities to learn socially. Whereas high-ranking animals rely on  
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23 634 monopolisation of the food source following initial social learning, lower-ranking individuals seem to make  
24  
25 635 up for the lack of access to the apparatus by having more social learning opportunities than high-ranking  
26  
27 636 individuals observing the latter. Scrounging further facilitates social learning, as is true for other species  
28  
29 637 (Caldwell & Whiten, 2003; Midford et al., 2000; Thornton, 2008), and the application of 'Who' strategies  
30  
31 638 (Laland, 2004) shapes who is a preferred demonstrator within a social group of jackdaws. Our findings of  
32  
33 639 relative dominance rank and other factors influencing social learning in jackdaws show that these colonial  
34  
35 640 breeding corvids are an interesting model system for studying the dynamics of social learning.

36 641

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49 648

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## 807 TABLES

808 **Table 1** Details for Group 1 (juveniles), Group 2 (adults) and the Control group.

809

Group 1 (aviary: 6 m x 5 m)			Group 2 (aviary: 10 m x 9 m)			Control Group (aviary: 15 m x 9 m)		
Subject	Sex	Hatched	Subject	Sex	Hatched	Subject	Sex	Hatched
Apache	f	2008	Csoka	F	2004	Cheeky	F	2003
Balu	m	2008	Jacky	F	2007	Choucas	M	2003
Cheyenne	m	2008	Karacho	F	2003	Jackomo	F	2003
Heinrich	f	2008	!Khosa	M	2006	Krakehl	F	2003
Kaja	f	2008	Poldi	M	2007	Krawall	M	2003
Maya	f	2008	Spinni	M	2005	Mono	F	2003
Mapuche	m	2008	Tschok	M	2004	Mokka	M	2003
Sioux	f	2008				Radja	M	2003
						Rani	F	2003
						Xenia	F	2003
						Zulu	F	2003
						<i>Dohli</i>	<i>F</i>	<i>2006</i>

810

811

812 **Table 2** Results of Spearman rank correlations of the fraction of successful manipulations of the wooden  
 813 ball (i.e. successful manipulations that led to an opening per overall number of manipulations) and the  
 814 number of sessions the individual had participated in (juvenile observer group) .

815

Individual	<i>N</i>	<i>R</i>	<i>P</i>
Balu	15	0.760	0.001***
Maya	9	0.732	0.025*
Kaya	6	-0.812	0.050*



Cheyenne	7	0.473	n.s.
Heinrich	8	0.082	n.s.
Mapuche	9	-0.583	n.s.

816

817 **Table 3** Stepwise backward model selection to explain openings watched by the observer (a focal  
 818 individual) executed by the demonstrator (an observed individual) as function of kinship, sex combination,  
 819 scroungings by the observer, relative hierarchy, and total openings of the demonstrator.

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Variable	Random Factors	Fixed Factors	F	df1	df2	P	AICc	$\Delta$ AICc	$\omega$
observed openings	dyad, participated trials	kin + sexes + scroungings + hierarchy + total openings by observed individual	3.58	7	48	0.004	276.02	3.71	0.08
		kin + scroungings + hierarchy + total openings by observed individual	6.37	4	51	$\leq 0.001$	272.96	0.64	0.39
		<b>scroungings + hierarchy + total openings by observed individual</b>	<b>8.54</b>	<b>3</b>	<b>52</b>	<b><math>\leq 0.001</math></b>	<b>272.32</b>	<b>0</b>	<b>0.53</b>

821 Rankings based on AICc are presented. The model with the lowest Akaike weight ( $\omega$ ) indicates that its  
 822 fixed factors explain response variable's variance best. The final model is highlighted in bold.

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824 **Table 4** F and t statistics for the final GLMM.

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Variable	Factor	F	df1	df2	beta	SE	t	p
observed openings	model	8.54	3	52	-4.02	1.192	-3.372	$\leq 0,001$
	scroungings	5.98	1	52	0.28	0.116	2.446	0.018

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hierarchy	3.07	1	52	-0.18	0.102	-1.754	0.085
openings by observed individual	7.124	1	52	0.06	0.021	2.669	0.01

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For Review Only

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3 827 **FIGURE LEGENDS**  
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6 828 **Fig. 1** The set-up for the *Demonstration Phase*, with the demonstrator at the test apparatus inside the cage  
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8 829 and observers watching from a branch above.  
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11 830 **Fig. 2** The test apparatus with the treadle and the wooden ball in the front on the left and the perch on the  
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13 831 right. Arrows indicate potential movement directions of the ball (lifting or pushing).  
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16 832 **Fig. 3** Box and whisker plots for the total time spent at the apparatus by members of all 3 groups. Boxes  
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18 833 show the interquartile range; the line in the centre of the boxes stands for the median value. Whiskers  
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20 834 indicate the largest and smallest value.  
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23 835 **Fig. 4** Box and whisker plots for the latency to approach the apparatus in the juvenile and adult observer  
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25 836 group (the Control group is not included, as only one individual of that group ever approached the  
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27 837 apparatus).  
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29 838 **Fig. 5** Box and whisker plots for the latency to touch the apparatus in the two observer groups.  
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33 839 **Fig. 6** Scatter plot for the time the animals in the successful juvenile observer group spent at the perch and  
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35 840 treadle depending on the hierarchy (1 = highest-ranking animal).  
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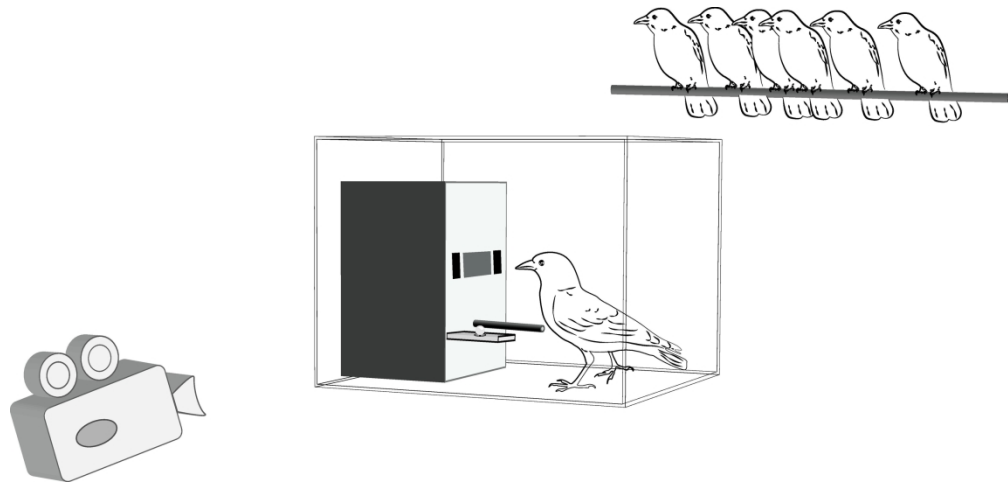


Fig. 1 The set-up for the Demonstration Phase, with the demonstrator at the test apparatus inside the cage and observers watching from a branch above.

230x109mm (300 x 300 DPI)

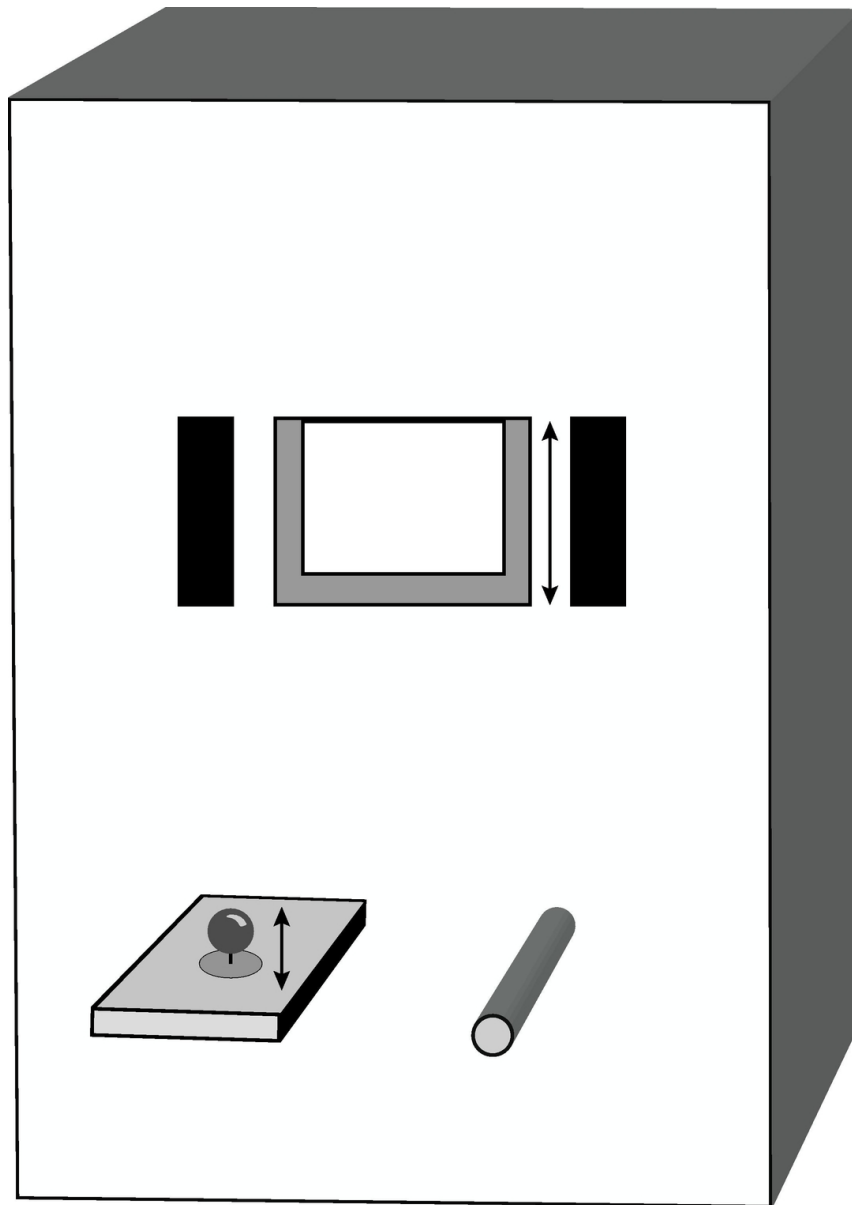


Fig. 2 The test apparatus with the treadle and the wooden ball in the front on the left and the perch on the right. Arrows indicate potential movement directions of the ball (lifting or pushing).

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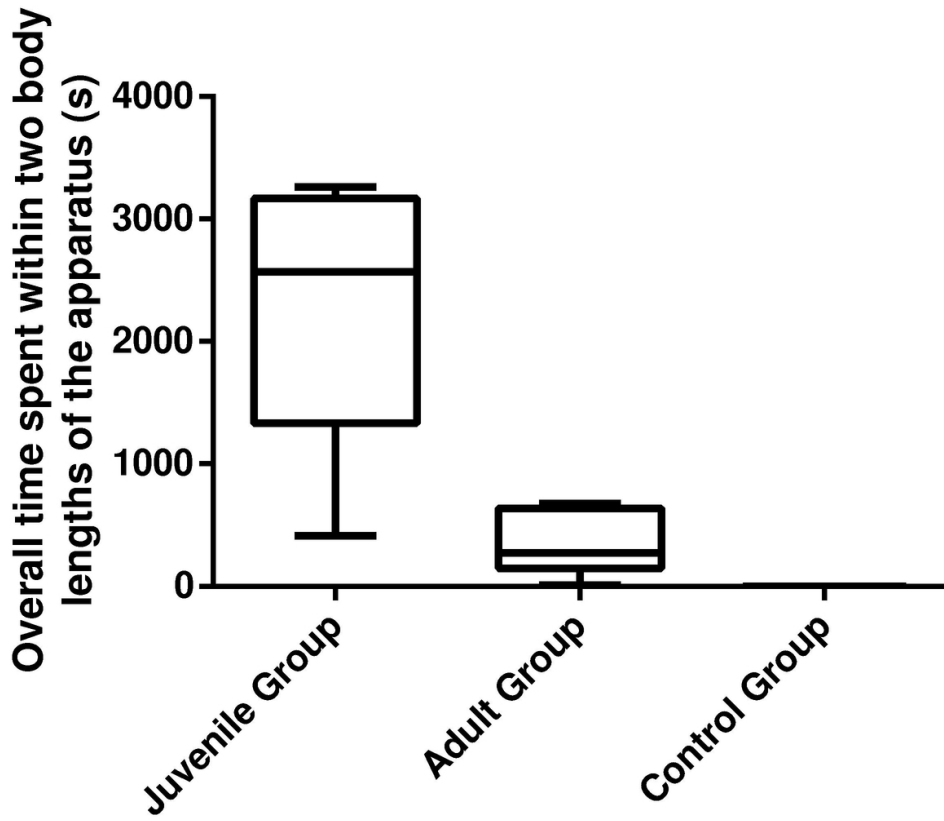


Fig. 3 Box and whisker plots for the total time spent at the apparatus by members of all 3 groups. Boxes show the interquartile range; the line in the centre of the boxes stands for the median value. Whiskers indicate the largest and smallest value.

103x92mm (300 x 300 DPI)

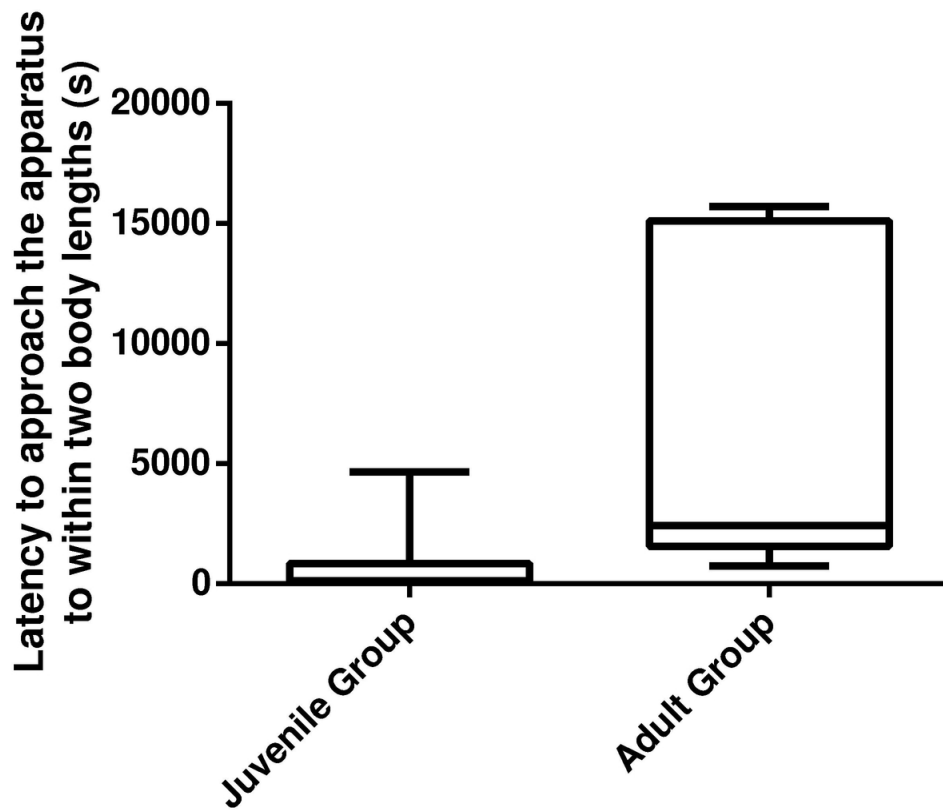


Fig. 4 Box and whisker plots for the latency to approach the apparatus in the juvenile and adult observer group (the Control group is not included, as only one individual of that group ever approached the apparatus).

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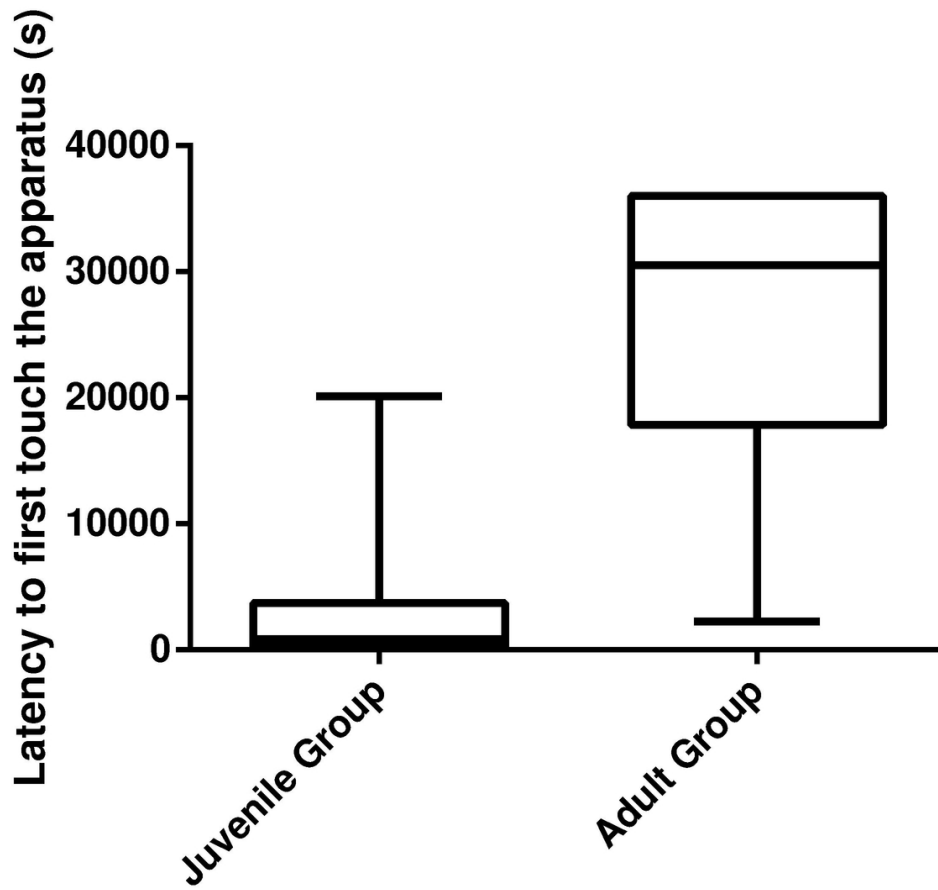


Fig. 5 Box and whisker plots for the latency to touch the apparatus in the two observer groups.

100x97mm (300 x 300 DPI)



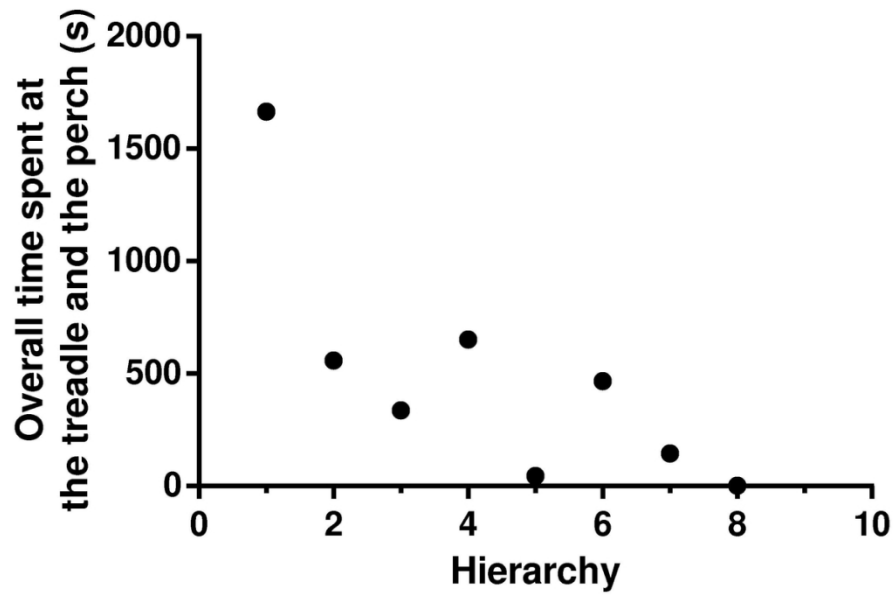


Fig. 6 Scatter plot for the time the animals in the successful juvenile observer group spent at the perch and treadle depending on the hierarchy (1 = highest-ranking animal).

112x73mm (300 x 300 DPI)