Can you teach an old parrot new tricks? Cognitive development in wild kaka (*Nestor meridionalis*)

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11 ABSTRACT

12 Despite recent efforts to characterise innovative individuals within a species we still know very 13 little about the ontogeny of innovation ability. A number of studies have found that innovation 14 rates are correlated with personality traits such as neophilia and exploration. Juvenile birds are 15 frequently more neophilic and explorative, yet few studies have found evidence of age-related 16 differences in innovative problem-solving success. Here we show consistently higher 17 innovation efficiency in juveniles of a wild, omnivorous parrot species across a variety of tasks 18 and contexts. We tested 104 kaka (Nestor meridionalis), ranging in age from four months to 19 13 years. Twenty four individuals participated in all three of our problem-solving tasks, two of 20 which involved a familiar feeder and one an entirely novel apparatus. Juveniles were the most 21 efficient problem-solvers in all three tasks. By contrast, the adults' success was context-22 dependent and limited to the novel apparatus, which did not require modification of a pre-23 learned behavioural response. This suggests greater behavioural flexibility in the juvenile birds, 24 who also showed higher persistence and exploratory diversity than adults. These traits may enable young kaka to discover efficient foraging techniques, which are then maintained 25 26 throughout adulthood.

27 Keywords: Innovation, problem-solving, age differences, exploration, parrot, Nestor

28 1. INTRODUCTION

29 Behavioural innovations can be observed as behaviour patterns not previously found in the 30 population and frequently arise in response to a novel problem, or as a novel solution to an 31 existing problem [1,2]. Innovative problem-solving abilities are of high adaptive value and 32 increase individual survival chances in changing environments [3–5]. Foraging innovations, 33 for example, enable an individual both to exploit new food sources and find alternative means 34 of exploiting familiar food resources as conditions change [1,6,7]. Thus more innovative 35 individuals can be expected to be more successful foragers [8]. This in turn can have fitness consequences including longer lifespan, increased mating success [9,10] and producing more 36 37 or fitter offspring [11,12].

38 Studies looking at within species variation in the tendency to innovate frequently reveal 39 correlations with personality traits such as high exploration rates and low levels of neophobia [13–15]. Social factors such as larger group size [16,17], better social learning [18,19] or lower 40 41 competitive ability [20,21] may also increase innovativeness. Studies on wild and captive 42 hyenas and birds recently suggested that the range of exploratory behaviours an individual 43 exhibits, rather than temporal or spatial exploration measures, determines innovative problemsolving success [6,22-24]. Exploratory diversity may increase the chance of discovering a 44 45 behaviour pattern suitable for a novel situation the same way larger groups of animals may 46 show higher innovation efficiency than smaller groups because they contain more diverse individuals [16,17]. 47

While several studies suggest that juveniles tend to be more explorative and less neophobic [2,6,25], few have found a correlation between age and innovation ability (no effect of age reported by [6,10,25]) and those which did, report varying results (see also [26]). In primates there is evidence suggesting increased innovation in adults, potentially due to their greater 52 experience and foraging competence [27–29]. Whereas in passerines, two studies indicate 53 higher innovative problem-solving abilities in juveniles [30,31], which has been explained by 54 the 'necessity drives innovation' hypothesis [32] arguing that juveniles are poorer competitors 55 and hence more in need of innovative alternative solutions.

Furthermore, age-related differences in innovation tendency have rarely been studied across a variety of tasks. Thus it remains unclear whether those differences found can be attributed to a general difference in problem-solving ability between juveniles and adults, or are task- or context-dependent. In wild kea for example, a study investigating a naturally occurring foraging innovation revealed that the most successful individuals were the oldest [33]. However, when wild kea were confronted with a novel string-pulling task juvenile kea outperformed adults [34].

As foraging innovation frequency has been linked with larger-relative brain size [5,7,35,36], 63 64 we investigated age-related differences in innovative problem-solving abilities in a large-65 brained parrot species [37], the forest-dwelling kaka (Nestor meridionalis). Kaka are an especially interesting species for studying the effects of personality and ecology on innovative 66 67 problem-solving skills as they are generalist, extractive foragers [38], characteristics thought 68 to be associated with increased problem-solving success [39,40]. Yet kaka are also neophobic 69 [41–43], a trait that has been linked to the inhibition of problem-solving abilities [6,15]. Kaka 70 are closely related to the mountain-dwelling and neophilic kea [33,44]. Both species are 71 thought to live to about 20 years in the wild [45–48], are endemic to New Zealand and the only species in the tribe Nestorini. While both social and physical cognition has been well studied 72 73 in the kea [49–52], the kaka's cognitive abilities have not yet been investigated.

We presented free-ranging kaka with a series of three foraging problems in varying contexts
and measured individual differences in problem-solving performance, exploratory strategies

- and persistence. Individuals ranged in age from 4 months to 13 years, allowing us to explore
- 77 the development of innovation ability and related behavioural traits or prerequisites in this
- 78 species.

79 **2. METHODS**

80 (a) Subjects, study site and general procedure

81 Free-ranging kaka were tested at Zealandia, a 225 hectare large wildlife sanctuary surrounded by a pest-exclusion fence, in Wellington, New Zealand. Since the founding of Zealandia and 82 83 ensuing reintroduction of kaka into the region in 2002, the population has been monitored by 84 banding nestlings with a unique colour combination of two narrow aluminium bands on one 85 leg and one wider cohort steel band on the other (except for the 2013/2014 breeding season 86 when kaka were banded with the cohort band only – see supplement for more information). 87 From 2008 to 2013 nestlings also received an RFID tag. The exact age was therefore known 88 for all of the subjects in this study and individual identification was possible. The total kaka 89 population living in and around Zealandia was estimated at 350 to 400 individuals at the time 90 of testing. However, this included a number of unbanded birds who had hatched in natural 91 nests. Unbanded or unidentified individuals were excluded from data analysis. None of the 92 kaka had previously participated in any cognitive study.

93 We conducted our experiments at two feeding stations. The stations each have two or three 94 platforms where kaka are offered supplementary food (parrot pellets) in stainless steel feeders 95 (figure 1*a*). All subjects were familiar with these feeders and regularly used them. RFID readers 96 were installed on the platforms to obtain additional information on the bird's identity in cases 97 where band reading failed (figure S1). From similar RFID-tag readers, which were previously 98 installed at the testing stations, we can infer that the youngest kaka in this study had been using 99 the feeders for at least 2 weeks to 5 months prior to testing. Testing took place between 100 February and October 2014 on up to five days per week. We conducted two-hour testing 101 sessions during times that kaka typically frequented feeders. All kaka that came to the test 102 platform during a session and fulfilled our trial criteria were included in our analysis (for trial definitions and details on trials with multiple subjects see 'Data scoring'). Our experiments included (i) a block-removal task (47 sessions), (ii) a lid-opening task (40 sessions) and (iii) a string-pulling task (18 sessions). These experiments are described in detail below. For experiments i) and ii) we removed any feeders that were not required for the experiment. In the string-pulling task, we removed the feeders on the platform closest to the string and removed food from the other feeders.

Cashew nuts were used as the reward in all experiments. The block-removal and lid-opening apparatuses were always set up and reset out of the subject's view using a brown cloth as cover, but the baiting was then shown to the bird. In the string-pulling task, we directed the kaka's attention to the reward by tapping or holding it up. An assistant recorded all kaka present at the test location to control for potential social learning effects. We filmed all sessions to permit subsequent behaviour coding.

In total, 104 subjects participated in our study and they ranged in age from four months to 13 years. 27 of these kaka were juveniles (less than one year old), 42 were subadults (one to four years old) and 35 were adults (more than four years old; age classification according to Moorhouse and Greene [45]). Individuals received a total of 1 - 211 trials per task depending on the frequency of their visits to the feeding station (mean \pm SE: block-removal: 8.8 \pm 1, lidopening: 14.6 \pm 3.8, string-pulling: 20.4 \pm 4.9; see table S9 for exact numbers per subject).

121 **(b)** *Experiments*

122 (i) Experiment 1: Block-Removal

The kaka feeders (figures 1*a* and S2) used at Zealandia are $25 \times 22 \times 11$ cm galvanised steel boxes manufactured by Grandpa's Feeders (Windsong Enterprises). The food tray ($10 \times 19 \times$ 5 cm) is covered by a lid (11×22 cm) that is connected to an aluminium tread plate (13×30 cm). The tread plate functions as a push-down lever that opens the lid, enabling access to the food when the birds step on it. We positioned two feeders back to back on an approximately
1.70 m high wooden platform. Using two feeders simultaneously decreased competition
between subjects and kept the appearance of the experimental setup as close to the usual setting
as possible.

We used the familiar feeders to create a novel problem for the kaka by blocking the tread plate with a wooden block ($7 \times 12 \times 5$ cm, mahogany, untreated) placed underneath (figure 1*b*). The sides of the blocks featured zigzag-shaped grooves to facilitate grabbing hold of it. The block could be pulled or pushed out by the beak to re-establish the function of the tread plate (figure 125 1*c*).

136 (ii) Experiment 2: Lid-Opening

In our second experiment we used the same familiar feeders to create a novel foraging problem, without including a novel object in the experimental setup. This enabled us to evaluate the possibility that birds failed experiment 1 due to neophobia. Although all kaka approached the block in their efforts to access the feeder, potentially birds affected by neophobia may have avoided touching or interacting with the block in experiment 1.

In experiment 2 we removed the feeder tread plate and connecting rods so that the lid had to be flipped over to access the food. Due to the length of the lid, this was best achieved from the side of the box (figure 1*d*). To reduce the weight of the lid, hinges were moved 4.5 cm closer to the front and a $5.0 \times 2.0 \times 0.5$ cm piece of metal was attached to the end of the side bars.

We ran two versions of this experiment. We conducted the first 25 sessions with two feeders back to back on the platform to keep the experimental setup as similar to the usual situation and experiment 1 as possible. However, we removed the treadle on only one of the feeders as the lid flipped open would have obstructed the opening of the second feeder. The other feeder was empty during a session. The subsequent 15 sessions were conducted with only one feeder placed in the middle of the platform to ensure that the corner posts of the platform weren't obstructing the subjects. As there was no significant difference in performance (proportion of successful out of total number of trials) between the two versions (Mann-Whitney U test: U =208, $N_{V1} = 54$, $N_{V2} = 6$, p = 0.27), data was combined for the overall analysis.

155 (iii) Experiment 3: String-Pulling

An entirely novel problem was used for experiment 3. This tested the possibility that any differences in performance could be attributed to routinized behaviour (as may have been the case in experiments 1 and 2).

At each test location, we fitted a dowel of approximately 24 cm length and 1.6 cm in diameter to a branch in close proximity to one of the feeding platforms. To this we tied a 50 cm long, 3 mm thick light green nylon string. Green 0.35 mm fishing line was threaded through the cashew nuts and tied into a loop to provide a hanger for attaching the nuts to the string (figure S3). This facilitated rapid re-baiting of the string in the field. In this experiment pulling up the string enabled the kaka to reach the food reward (figure 1*e*).

165 (c) Data scoring

166 We extracted the start and end time of each trial from the video record to receive an approximate measure of the amount of time an individual spent working on the problem. A 167 168 trial started the moment a kaka approached the apparatus (landed on the test platform/branch 169 or noticeably looked at the reward at the end of the string) and stayed for more than 15 sec. A 170 trial ended the moment the subject left the apparatus (left the test platform or moved >2 m from 171 string) for more than 15 sec, or once the problem was solved. The task was solved successfully 172 when the subject manipulated the apparatus in a way that allowed it to access the food reward. 173 For each kaka we recorded the number of successful trials as well as the total number of trials 174 that they completed for each experiment. We measured speed in solving the task by counting the number of trials and calculating the total amount of trial time it took an individual to find asolution to the problem.

We measured individual persistence as the average 'time spent per trial' (in case of solvers up until a solution was found). Kaka exhibited a range of exploratory behaviours in their efforts to solve the problem. We calculated an individual's 'exploration diversity' as the proportion of the total number of distinct behaviours the subject showed over the course of testing (in case of solvers up until a solution was found) out of the total possible behaviours used by all kaka during each experiment.

In cases where multiple subjects were working on the problem at the same time, behaviour was coded for each focal individual and it was noted that conspecifics were present on the test platform/branch during the trial. We did not include trials that were directly interfered by another subject, whether by chasing away the focal subject or solving the task, in our performance analysis. We did include these trials in the analysis of exploratory strategies.

For each trial we also scored whether the subject was naïve, had previously been present at the test location during a session, had witnessed manipulations of the apparatus that indicated how the problem could be solved or had directly observed a conspecific solve the task and retrieve the reward. These four different levels of social information were used to determine whether social learning affected the likelihood to complete a trial successfully. For more details on data extraction see supplementary material, tables S1 to S3.

194 (d) Statistical Analysis

We used a generalized linear mixed model (GLMM) with a binomial distribution and logit link to explore possible predictors of whether an individual solved the task (Y/N). We tested variables task, age, individual persistence and exploration diversity as well as the relevant interactions with task. For task the reference category was set to block-removal, for age the

199 reference category was set to adults. Subject was included as a random factor to control for 200 repeated measures [53]. We subsequently dropped those terms from the model with the least 201 explanatory power until the minimal model only contained variables that significantly 202 predicted problem-solving success. Wald statistics and p values for significant terms were 203 obtained from the minimal model and for nonsignificant terms by individually including them 204 in the minimal model. We then used the minimal model as basis to investigate whether these 205 results held when restricting the analysis to the proportion of successful trials of those 24 206 individuals that participated in all three experiments. For this analysis we specified a repeated 207 measures structure and used the number of successful trials as response variable with the total 208 number of trials as denominator.

To inquire if persistence and exploration diversity were predicted by age, we used GLMMs with a normal distribution and identity link and used robust estimation. We specified subject as a random factor and tested for differences between tasks by including it as a fixed factor.

212 We used GLMMs to analyse how age, persistence and exploratory diversity affected the 213 number of trials (Poisson distribution with log link) and absolute amount of time (normal 214 distribution with identity link) until a solution was found. To limit the number of potentially 215 confounding variables, this analysis was done on the data of the first experiment only (12 216 solvers), when all subjects were still naïve at the time of their initial success in the task. In the 217 follow-up experiments solvers differed not only in their amount of testing experience but also 218 in the level of social information they may have gathered by watching other individuals solve 219 the problem. Model selection criteria were the same as described above.

To ensure that competition at the apparatus did not affect the outcome of a trial, we used GLMMs with success as the binary response variable (Y/N) with a logit link and presence of a conspecific on the test platform/branch (Y/N; reference category set to N) as fixed effect as well as subject ID as a random factor to control for repeated measures within each experiment.
To avoid pseudo-replication across experiments (a subject may have had several trials in more
than one experiment), we did the analysis for each task separately. Similarly, we tested for the
effect of social information a subject had had opportunity to gather by observing conspecifics
interact with the apparatus (reference category set to "naïve"). Here, we excluded all trials that
were conducted after the subject's initial success.

229 *P* values below or equal to 0.05 were considered significant.

3. RESULTS

231 (a) *Problem-solving performance*

In total we tested 104 kaka ranging in age from four months to 13 years, with 24 participating in all three tasks (4 juveniles, 13 subadults, 7 adults). Of those 24 individuals, 18 solved at least one of the tasks and five solved all three of them (for the total number of subjects and solvers in each of the experiments see table 1). Kaka spent on average 45.5 sec (SE = 2 sec) per trial in the block-removal task, 38 sec (SE = 2.3 sec) in the lid-opening task and 19.1 sec (SE = 1.5 sec) in the string-pulling task and exhibited an average of three different exploratory behaviours in each of the tasks (SE_{BR} = 0.1, SE_{LO} = 0.2, SE_{SP} = 0.3) in their efforts to solve the problem.

Task type, age and exploration diversity were the only significant predictors of a kaka's ability to find a solution to the problem (minimal model, table 2). All of the interactions with task type were non-significant, as was individual persistence measured as the average time spent per trial (table 2; see supplementary material for additional analysis on individual persistence).

Examining the proportion of successful trials for the 24 kaka that completed all three tasks, we found main effects for task and age (table 3; figure 2). Success rates increased with each of the experiments with the highest proportion of successful trials shown in the string-pulling task. Additionally, juveniles performed significantly better than subadults and adults (table 3). None of the adults were able to solve the block-removal task and only one succeeded in the lidopening. Subadults also tended to perform better than adults in both of the feeder experiments, however this difference disappeared in the string-pulling task and was overall non-significant (Contrast estimate (Subadults – Adults) = 0.206 ± 0.119 , p = 0.088).

Exploration diversity was not a significant determinant of the proportion of successful trials for the 24 individuals that participated in all three experiments, although more explorative kaka tended to show a higher proportion of successful trials (table 3).

254 (b) Individual variation in behavioural measures

Juvenile kaka were significantly more persistent than subadult and adult kaka (GLMM: $F_{2, 173}$ = 12.634, p = 7.6E-6; $N_{BR} = 87$, $N_{LO} = 61$, $N_{SP} = 28$) and also showed significantly greater exploratory diversity (GLMM: $F_{2, 166} = 9.019$, p = 1.9E-4; $N_{BR} = 87$, $N_{LO} = 61$, $N_{SP} = 27$). However, the difference in exploratory diversity was present only in the lid-opening and stringpulling tasks as indicated by the significant interaction of task and age group ($F_{4, 166} = 4.895$, p= 0.001; figure 3). For full model outputs see tables S4 and S5.

261 (c) Speed in solving the first task (block-removal)

Juveniles solved the block-removal task significantly faster than subadults with regards to both the number of trials (GLMM: $F_{1, 10} = 65.790$, p = 1E-5; N = 12 solvers) and the absolute amount of time to find a solution (GLMM: $F_{1, 10} = 16.797$, p = 0.002; N = 12 solvers). Juvenile kaka pulled the block out in their first to fourth trial whereas it took subadults at least 10 trials to be successful (no adults solved this task). Speed in solving the block-removal task was not correlated with either persistence or exploration diversity (tables S6 and S7).

268 (d) Social effects

The presence of conspecifics on the test platform or branch had no effect on the successful outcome of a trial in any of the experiments (GLMMs: block-removal: $F_{1, 759} = 0.092$, p =0.762, N = 761 trials; lid-opening: $F_{1, 880} = 2.764$, p = 0.097, N = 882 trials; string-pulling: $F_{1, 875} = 0.520$, p = 0.471, N = 577 trials).

Watching another individual solve the problem did not significantly increase the likelihood to complete a trial successfully in the block-removal and lid-opening tasks (block-removal: $F_{3, 619}$ = 0.300, p = 0.826, N = 623; lid-opening: $F_{3, 480} = 2.119$, p = 0.097, N = 484 trials). In the string-pulling experiment, however, trials that were conducted after the subject had directly observed another kaka succeed were significantly more successful than trials in which the subject had not previously witnessed a solution ($F_{2, 94} = 5.577$, p = 0.005, N = 97 trials; figure S4; table S8).

4. DISCUSSION

In all three of our problem-solving tasks juvenile kaka performed significantly better than adult kaka. This was not only expressed in a higher number of individuals solving the task but also in higher individual success rates in juveniles. This finding is consistent with results in passerines [30,31] but also provides the first evidence of age-related differences in innovative problem-solving abilities in parrots and across tasks. In addition, success rate in adults was context-dependent, suggesting that decreased behavioural flexibility, rather than neophobia, inhibited the adults' innovation abilities.

288 Eventual problem-solving success was also positively correlated with the diversity of 289 exploratory behaviours displayed by the kaka, which is consistent with findings in hyena [6] 290 and confirms the importance of creative and flexible behaviour for generating innovations [54]. 291 A more creative approach to the problem was chosen almost exclusively by the younger birds. 292 Almost all adults tried to force open the feeder in the usual way by grabbing the lid with the 293 beak from the front and lifting it up, but juveniles and subadults did so from various angles of 294 the box and exhibited alternative strategies such as trying to hold the lid open with one foot. Juveniles were also more persistent than adults, spending more time per trial trying to find a 295 296 solution to the problem.

Interestingly, the decrease in problem-solving success as well as persistence and exploratory behaviours with age appears to be gradual. Subadult individuals tended to perform better, show greater exploratory diversity and be more persistent than adult birds in both feeder experiments. Furthermore, juveniles were significantly faster in finding a solution to the block-removal problem than the subadult solvers with regards to both number of trials and absolute time.

In addition to the effect of age, success rates also increased with each experiment, possibly due
to differing levels of task difficulty, habituation to experimenter and test procedure [26] or the

304 visibility of the food reward. The performance difference between tasks is most prominent in 305 adults, however. None of the adults were able to solve the block-removal task and only one 306 adult succeeded in lid-opening, whereas over half the adults tested were successful in the string-307 pulling task (the increase in success rates in juveniles and subadults is gradual across tasks by 308 contrast). This suggests that the familiarity with the feeders may have inhibited the adults' 309 success in the first two experiments. It appears that adults fail to modify their learned 310 behavioural response to the familiar problem (opening the feeder) to fit the new situation 311 (blocked or missing tread plate). This in turn suggests that juveniles are more flexible in their 312 behaviour which is supported by their higher scores in exploratory diversity and consistent with research suggesting that behavioural plasticity decreases with age [55–59]. 313

314 It is unlikely that the individual differences in problem-solving performance in our study were 315 mainly caused by motivational or competitive differences as has been found previously 316 [20,31,60,61]. Supplementary food is available to the kaka at the wildlife sanctuary throughout 317 the day. It is therefore unlikely that juveniles were under increased competitive stress as a 318 consequence of their not yet fully developed foraging skills and the 'necessity drives 319 innovation' hypothesis [31,32] appears not to apply here. We may also assume that all 320 individuals coming onto the feeder platform trying to access the feeders were indeed motivated 321 for food . Because of their greater foraging experience, adults may have been more likely to 322 abandon the task in favour of foraging for alternative food resources, which could potentially 323 have resulted in their high failure rates in the feeder experiments. Indeed, our analysis showed 324 that adults were less persistent in all tasks than juveniles. However, the adults' increased 325 success rate in the string-pulling task shows that they were in fact motivated to work for the 326 high value food reward.

Neophobia also does not appear to be a possible main inhibitor of the adult's problem-solving
success [13,15]. Although potentially, neophobia may have caused the adults to avoid touching

329 or moving the novel block in experiment 1, adults similarly failed in the lid-opening task where 330 no novel object was present. They did, however, show their highest success rates in the string-331 pulling task where the entire apparatus was novel to them. Furthermore, all except one adult 332 lifted the lid of the feeder from the front in the block-removal task and 18 out of 22 adults did 333 so in the lid-opening. This shows that the adults did interact with the feeders and did try to open 334 them, which would not be expected if neophobia was keeping them from engaging with the 335 problem (for additional analyses of the latency to approach the problem, which supports this 336 hypothesis, see supplement).

337 Similarly to other problem-solving studies on wild, social living animal populations [6,31,62] 338 but in contrast to findings in captivity[63–65], we found little evidence for social learning on 339 immediate or eventual success. Even though several individuals had directly observed a conspecific pull out the block in experiment 1, none of them tried to move the block themselves. 340 341 A similar pattern was found in experiment 2. Only in the string-pulling did watching a 342 conspecific solve the problem increase the likelihood to succeed. Social learning may have 343 been facilitated in this experiment because of the novelty of the task, or the visibility of the 344 food reward. Social learning may therefore have additionally contributed to the increase in 345 success by the adults in experiment 3. Indeed, three of the four adult solvers had observed 346 another kaka solve the problem at least once before their own success in the string-pulling.

347 **5. CONCLUSION**

Our results suggest that, in kaka, juveniles have the highest potential for foraging innovations and display greater exploratory diversity and persistence. Furthermore, the adults' innovative problem-solving success appears to be context-dependent and limited to those situations that are entirely novel and for which no pre-learned behavioural response pattern is available. This suggests that adults are able to use newly available food sources but might fail to adapt to

353	changes in the environment that require the use of a familiar resource in a different way. The
354	juveniles' greater behavioural flexibility and explorative nature might help them to learn about
355	their environment and to shape their foraging skills. In this way juveniles might find the most
356	efficient behavioural response to common foraging situations, which is then maintained
357	throughout adulthood.

358 Ethics

The research presented here was approved by the Victoria University of Wellington Animal
Ethics Committee (Application no. 2013R20) and the Karori Sanctuary Trust.

361 Data accessibility

362 The datasets supporting this article have been uploaded as part of the supplementary material.

363 Authors' contributions

- 364 J.L. designed the study, carried out field work and data analyses, and drafted the manuscript.
- 365 R.S. and K.B. contributed to the study design, data analyses and writing the manuscript.

366 Competing interests

- 367 We have no competing interests.
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542 Figure and table captions

543 Figure 1. (a) A kaka using the feeders at Zealandia. (b) The setup in the block-removal task.

- 544 (c) A kaka removing the block. (d) A kaka opening the lid in experiment 2. (e) A kaka
- 545 succeeding in the string-pulling task.
- 546 Figure 2. Mean proportion of successful trials \pm SE for each experiment and age group based
- on the subset of individuals that participated in all three of the tasks.
- 548 Figure 3. Mean \pm SE (a) time spent per trial (individual persistence) and (b) proportion of
- 549 exploratory behaviours for the different age groups as well as solvers and nonsolvers for all
- 550 individuals for whom these measures could be scored (*N* is given at the base of the bars).
- Table 1. Successful out of total number of individuals tested in each of the three experimentsin absolute numbers and as percentage.
- 553 Table 2. GLMM analysis of the factors affecting whether an individual solved the task.
- 554 Table 3. GLMM analysis of the factors affecting the number of successful trials (based on the
- 555 minimal model of the analysis of whether an individual solved the task).