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Cite this article: Loepelt J, Shaw RC, Burns KC. 2016 Can you teach an old parrot new tricks? Cognitive development in wild kaka (*Nestor meridionalis*). *Proc. R. Soc. B* **283**: 20153056.
<http://dx.doi.org/10.1098/rspb.2015.3056>

Received: 21 December 2015

Accepted: 9 May 2016

Subject Areas:

behaviour, cognition, ecology

Keywords:

innovation, problem-solving, age differences, exploration, parrot, *Nestor*

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2015.3056> or via <http://rspb.royalsocietypublishing.org>.

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

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Despite recent efforts to characterize innovative individuals within a species, we still know very little about the ontogeny of innovation ability. A number of studies have found that innovation rates are correlated with personality traits, such as neophilia and exploration. Juvenile birds are frequently more neophilic and explorative, yet few studies have found evidence of age-related differences in innovative problem-solving success. Here, we show consistently higher innovation efficiency in juveniles of a wild, omnivorous parrot species across a variety of tasks and contexts. We tested 104 kaka (*Nestor meridionalis*), ranging in age from four months to 13 years. Twenty-four individuals participated in all three of our problem-solving tasks, two of which involved a familiar feeder and one an entirely novel apparatus. Juveniles were the most efficient problem-solvers in all three tasks. By contrast, the adults' success was context dependent and limited to the novel apparatus, which did not require modification of a pre-learned behavioural response. This suggests greater behavioural flexibility in the juvenile birds, 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 throughout adulthood.

1. Introduction

Behavioural innovations can be observed as behaviour patterns not previously found in the population and frequently arise in response to a novel problem, or as a novel solution to an existing problem [1,2]. Innovative problem-solving abilities are of high adaptive value and increase individual survival chances in changing environments [3–5]. Foraging innovations, for example, enable an individual to both exploit new food sources and find alternative means of exploiting familiar food resources as conditions change [1,6,7]. Thus, more innovative 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 or fitter offspring [11,12].

Studies looking at within-species variation in the tendency to innovate frequently reveal 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], rapid social learning [18,19], or lower competitive ability [20,21], may also increase innovativeness. Studies on wild and captive hyaenas and birds recently suggested that the range of exploratory behaviours an individual exhibits, rather than temporal or spatial exploration measures, determines innovative problem-solving success [6,22–24]. Exploratory diversity may increase the chance of discovering a behaviour pattern suitable for a novel situation, the same way larger groups of animals may show higher innovation efficiency than smaller groups because they contain more diverse individuals [16,17].

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 in [6,10,25]) and those that have report varying results (see also [26]). In primates, there is evidence suggesting increased innovation in adults, potentially owing to their greater experience and foraging

Figure 1. (a) A kaka using the feeders at Zealandia. (b) The set-up in the block-removal task. (c) A kaka removing the block. (d) A kaka opening the lid in experiment 2. (e) A kaka succeeding in the string-pulling task. (Online version in colour.)

competence [27–29]. Whereas in passerines, two studies indicate higher innovative problem-solving abilities in juveniles [30,31]. This has been explained by the ‘necessity drives innovation’ hypothesis [32] arguing that juveniles are poorer competitors and so 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 any differences found reflect a general difference in problem-solving ability between juveniles and adults, or are task- or context dependent. In wild kea for example, research on 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], we investigated age-related differences in innovative problem-solving abilities in a large-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 problem-solving skills as they are generalist, extractive foragers [38], characteristics thought to be associated with increased problem-solving success [39,40]. Yet kaka are also neophobic [41–43], a trait that has been linked to the inhibition of problem-solving abilities [6,15]. Kaka are closely related to the mountain-dwelling and neophilic kea [33,44]. Both species are thought to live to about 20 years in the wild [45,46] and are endemic to New Zealand and the only species in the tribe Nestorini. While both social and physical cognition has been well studied in the kea [47–50], 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 four months to 13 years, allowing us to explore the development of innovation ability and related behavioural traits or prerequisites in this species.

2. Material and methods

(a) Subjects, study site, and general procedure

We tested free-ranging kaka at Zealandia, a 225 hectare large wildlife sanctuary surrounded by a pest-exclusion fence, in

Wellington, New Zealand. Since the founding of Zealandia and ensuing reintroduction of kaka into the region in 2002, the population has been monitored by banding nestlings with a unique colour combination of two narrow aluminium bands on one leg and one wider cohort steel band on the other (except for the 2013/2014 breeding season when kaka were banded with the cohort band only; see the electronic supplementary material for more information). From 2008 to 2013, nestlings also received an radio frequency identification (RFID) tag. The exact age was therefore known for all of the subjects in this study, and individual identification was possible. During our study, the kaka population was estimated at 350–400 individuals. This estimate included a number of unbanded birds from unmonitored nests. Unidentifiable individuals were excluded from data analysis. None of the kaka had previously participated in any cognitive study.

We conducted our experiments at two feeding stations. The stations each have two or three approximately 1.8 m high wooden platforms where kaka are offered supplementary food (parrot pellets) in stainless steel feeders (figure 1*a*). All subjects were familiar with these feeders and regularly used them. We installed RFID readers on the platforms to obtain additional information on the bird’s identity when band reading was impossible (electronic supplementary material, figure S1). Records from RFID readers installed near the feeding platforms suggest that prior to testing the youngest birds had been using the feeders for at least two weeks to three months. Between February and October 2014, we tested birds up to five days per week. Test sessions lasted 2 h and took place during times that kaka typically frequented feeders. All kaka that came to the test platform during a session and fulfilled trial criteria were included in the analyses (see ‘Data scoring’ for our trial criteria and details on trials with multiple subjects). Our experiments were (i) a block-removal task (BR; 47 sessions), (ii) a lid-opening task (LO; 40 sessions), and (iii) a string-pulling task (SP; 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. Twenty-seven of these kaka

were juveniles (less than 1 year old), 42 were subadults (1–4 years old), and 35 were adults (more than 4 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 $\pm$ s.e.: block removal: 8.8 ± 1 , lid opening: 14.6 ± 3.8 , string pulling: 20.4 ± 4.9 ; see electronic supplementary material, table S11 for individual data).

(b) Experiments

(i) Experiment 1: block removal

The kaka feeders (figure 1*a* and electronic supplementary material, figure S2), used at Zealandia, are $25 \times 22 \times 11$ cm galvanized 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 the test platform, which simultaneously decreased competition between subjects and kept the appearance of the experimental set-up 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 1*c*).

(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 set-up. This enabled us to evaluate the possibility that birds failed experiment 1 owing to neophobia. Although all kaka approached the block in their efforts to access the feeder, birds potentially 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. Owing 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 set-up 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, when 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 were not 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 were combined for analyses.

(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 an approximately 24 cm long dowel (1.6 cm in diameter) to a branch that was close to one of the feeding platforms and tied a 50 cm long, 3 mm thick light

green nylon string to the dowel. We threaded a loop of green 0.35 mm fishing line through each cashew nut as an attachment point for tying the nut to the string (electronic supplementary material, 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*).

(c) Data scoring

A trial started the moment a kaka approached the apparatus (landed on the test platform/branch or notably looked at the reward at the end of the string) and stayed for more than 15 s. A trial ended the moment the subject left the apparatus (left the test platform or moved more than 2 m from the string) for more than 15 s or once the problem was solved. We used trial duration as a proxy for how long an individual spent working on the problem. The task was solved successfully when the subject manipulated the apparatus in a way that allowed it to access the food reward.

For each kaka, we recorded the number of successful trials as well as the total number of trials that they completed in each experiment. We calculated two measures for task-solving speed: the number of trials and the total amount of trial time a kaka required to find a solution to the problem.

We measured individual persistence as the average 'time spent per trial' (in the case of solvers, this was 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 the case of solvers, this was 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, we coded the behaviour for each focal individual and noted that conspecifics were present on the test platform/branch during the trial. We did not include trials that were directly interfered with by another subject, whether by chasing away the focal subject or solving the task, in our performance analysis. However, we did include these trials in the analysis of exploratory strategies.

For each trial, we also scored whether the subject was naive, had previously been present (but had not participated) 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 electronic supplementary material, tables S1–S3.

(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) for the 104 individuals that participated in at least one task. We included task, age, individual persistence, and exploration diversity as well as the relevant interactions with task as fixed factors. For task, the reference category was set to block removal and for age, the reference category was set to adults. Subject was included as a random factor to control for repeated measures [51]. We subsequently dropped those terms from the model with the least explanatory power until the minimal model only contained variables that significantly predicted problem-solving success. Wald statistics and *p*-values for significant terms were obtained from the minimal model and for non-significant terms by individually including them in the minimal model.

Table 1. The number and percentage of kaka that were successful out of the total number of individuals tested in each of the three experiments.

age group	block removal			lid opening			string pulling		
	solvers	total	%	solvers	total	%	solvers	total	%
juveniles	9	21	42.86	6	11	54.55	8	8	100
subadults	3	34	8.82	6	28	21.43	8	15	53.33
adults	0	32	0.00	1	22	4.55	4	7	57.14
total	12	87	13.79	13	61	21.31	20	30	66.67

We then investigated whether the factors that were retained in the minimal model for the overall solving ability (Y/N) of all 104 subjects also affected task performance (measured as the proportion of successful trials) for the 24 individuals that participated in all three experiments. For this GLMM with a binomial error structure, the response variable was the number of successful trials out of the total number of trials.

To investigate the effect of age and task type on persistence and exploration diversity, we included these as fixed factors in GLMMs with a normal distribution and identity link (using robust estimation). We included data from all 104 kaka and specified subject as a random factor.

Using GLMMs we analysed how age, persistence, and exploratory diversity affected the number of trials (Poisson distribution with log link) and absolute amount of time (normal distribution with identity link) until a solution was found. To limit the number of potentially confounding variables, we analysed the first experiment only (12 solvers), when all subjects were still naive at the time of their initial success in the task. In the follow-up experiments, solvers differed not only in their amount of testing experience, but also in the level of social information they may have gathered by watching other individuals solve the problem. Model selection criteria were the same as described above.

To test whether competition at the apparatus affected 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 effects as well as subject ID as a random factor to control for repeated measures. To avoid pseudo-replication across experiments (a subject may have had several trials in more than one experiment), we analysed each task separately. Similarly, we tested for the effect of social information a subject had had the opportunity to gather by observing conspecifics interact with the apparatus (reference category set to 'naive'). Here, we excluded all trials that were conducted after the subject's initial success.

P-values below or equal to 0.05 were considered significant.

3. Results

(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 (four juveniles, 13 subadults, and seven adults). Of the 24 individuals, 18 solved at least one task and five solved all three (for the total number of subjects and solvers in each of the experiments, see table 1). Per trial, on average kaka spent 45.5 ± 2 s (mean $\pm$ s.e.) on the block-removal task, 38 ± 2.3 s on the lid-opening task, and 19.1 ± 1.5 s on the string-pulling task. Kaka exhibited an average of three different exploratory behaviours in each of the tasks (s.e._{BR} = 0.1, s.e._{LO} = 0.2, and

s.e._{SP} = 0.3) in their efforts to solve the problem. Furthermore, they found two different successful techniques in lid opening and eight different successful techniques in the string-pulling task (see electronic supplementary material, table S4).

For the 104 kaka that participated in at least one task, task type, age, and exploration diversity were the only significant predictors of an individual's ability to solve the task (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 electronic supplementary material for additional analysis on individual persistence and exploration diversity).

Examining the proportion of successful trials for the 24 kaka that completed all three tasks, we found main effects for task and age (GLMM: task: $F_{2,67} = 21.079$, $p = 7.9 \times 10^{-8}$; age group: $F_{2,67} = 16.826$, $p = 1.2 \times 10^{-6}$; $n_{BR} = n_{LO} = n_{SP} = 24$; see electronic supplementary material, table S5 for coefficient estimates). The string-pulling experiment had the highest success rate and block-removal the lowest, while juveniles performed better than subadults and adults (figure 2). No adults solved the block removal task and only one succeeded in lid opening. Subadults tended to perform better than adults in both of the feeder experiments; however, this difference disappeared in the string-pulling task and was non-significant overall (contrast estimate (subadults – adults) = 0.206 ± 0.119 , $p = 0.088$). Although more explorative kaka tended to have a higher proportion of successful trials, exploration diversity did not significantly influence the proportion of successful trials for the 24 individuals that participated in all three experiments ($F_{1,65} = 3.872$, $p = 0.053$; $n_{BR} = n_{LO} = 24$, $n_{SP} = 23$; electronic supplementary material, table S5).

(b) Individual variation in behavioural measures

Juvenile kaka were more persistent than subadult and adult kaka (GLMM: $F_{2,173} = 12.634$, $p = 7.6 \times 10^{-6}$; $n_{BR} = 87$, $n_{LO} = 61$, $n_{SP} = 28$) and showed greater exploratory diversity (GLMM: $F_{2,166} = 9.019$, $p = 1.9 \times 10^{-4}$; $n_{BR} = 87$, $n_{LO} = 61$, $n_{SP} = 27$). However, the difference in exploratory diversity was present only in the lid-opening and string-pulling 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 electronic supplementary material, tables S6 and S7.

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

Juveniles solved the block-removal task faster than subadults, both in terms of the number of trials (GLMM: $F_{1,10} = 65.790$, $p = 1 \times 10^{-5}$; $n = 12$ solvers) and the absolute amount

Table 2. GLMM analysis of the factors affecting whether an individual solved the task. Data were fitted to a binomial distribution with a logit link. We conducted the analysis on all 104 subjects ($n_{BR} = 87$, $n_{LO} = 61$, $n_{SP} = 27$) and included bird ID as a random factor (estimated variance component for bird ID in the minimal model = 2.7×10^{-9}). Please note, for three individuals it was not possible to extract the exploration diversity value and mean time spent per trial (until a solution was found) in the string-pulling task from the video record due to technical failure.

	<i>F</i>	d.f. 1	d.f. 2	<i>p</i> -values
full model				
exploration div.	22.487	1	169	4.5×10^{-6}
task	6.336	2	169	0.002
age group	6.379	2	169	0.002
time spent per trial	1.021	1	168	0.314
task $\times$ exploration div.	0.742	2	167	0.478
task $\times$ age group	0.328	4	165	0.859
task $\times$ time spent per trial	0.071	2	166	0.932
minimal model				
	coefficient estimate	s.e.		
exploration diversity	−9.110	1.921		
task: block removal	0			
task: lid opening	−0.187	0.567		
task: string pulling	−2.304	0.680		
age group: juveniles	−2.232	0.716		
age group: subadults	−0.368	0.639		
age group: adults	0

Figure 2. Mean proportion of successful trials $\pm$ s.e. for each experiment and age group for the 24 individuals that participated in all three tasks. (Online version in colour.)

of time required to find a solution (GLMM: $F_{1,10} = 16.797$, $p = 0.002$; $n = 12$ solvers). Juvenile kaka pulled the block out within their first four trials, whereas it took subadults at least 10 trials to do so (no adults solved this task). Speed in solving the block-removal task was not correlated with either persistence or exploration diversity (see electronic supplementary material, tables S8 and S9).

(d) Social effects

The presence of conspecifics on the test platform or branch did not affect the 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: $F_{1,575} = 0.520$, $p = 0.471$, $n = 577$ trials).

Watching another individual solve the problem did not increase the likelihood of an individual successfully completing a trial in the block-removal and lid-opening tasks (block removal: $F_{3,619} = 0.300$, $p = 0.826$, $n = 623$ trials; lid opening: $F_{3,480} = 2.119$, $p = 0.097$, $n = 484$ trials). However, trials in the string-pulling experiment that were conducted after the subject had directly observed another kaka succeed were more likely to be successful ($F_{2,94} = 5.577$, $p = 0.005$, $n = 97$ trials; see also electronic supplementary material, figure S4 and table S10).

4. Discussion

Juvenile kaka outperformed adult kaka in all three of our problem-solving tasks. This was expressed both in terms of more individuals solving the task and higher individual success rates in juveniles. This finding is consistent with results in passerines [30,31] and provides the first evidence for age-related differences in innovative problem-solving abilities in parrots and across different tasks. In addition, success rate in adults was context dependent, suggesting that decreased behavioural flexibility, rather than neophobia, inhibited the adults' innovation abilities in our tasks.

Whether an individual eventually solved the task also correlated positively with the diversity of exploratory behaviours displayed by the kaka, which is consistent with findings in hyaena [6] and other bird species [23] and confirms the importance of creative and flexible behaviour in generating innovations [52]. Even in experiment 1, where juveniles and adults did not differ in their proportion of exploratory behaviours, a more creative approach to the problem was chosen almost exclusively by the younger birds. For example, almost all adults tried to force

Figure 3. Mean $\pm$ s.e. (a) time spent per trial (individual persistence) and (b) proportion of exploratory behaviours for the different age groups as well as solvers and non-solvers. Data are shown for all individuals for whom these measures could be scored (n is given at the base of the bars). (Online version in colour.)

open the feeder by grabbing the lid with the beak from the front and lifting it up, but juveniles and subadults did so from various angles of 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 solution to the problem.

Interestingly, problem-solving success, persistence, and exploratory behaviours all appear to decrease gradually with age. Subadult individuals tended to perform better, show greater exploratory diversity, and be more persistent than adult birds in both feeder experiments. Furthermore, juveniles solved the block-removal problem faster 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 across experiments, possibly owing to differing levels of task difficulty, habituation to experimenter and test procedures, [26] or the visibility of the food reward. The performance difference between tasks was most prominent in adults: none were able to solve the block-removal task, only one succeeded in lid opening, yet over half the adults tested were successful in the string-pulling task. By contrast, the increasing success rate across tasks was far more gradual in juveniles and subadults. This suggests that the familiarity with the feeders may have inhibited the adults' success in the first two experiments. Potentially, adults failed to modify their learned behavioural response to the familiar problem (opening the feeder) to fit the new situation (blocked or missing tread plate). This may suggest that juveniles are more flexible in their behaviour, which is also supported by their higher scores in exploratory diversity and consistent with research suggesting that

behavioural plasticity decreases with age [53–56]. However, juveniles also had less reinforcement for the normally functioning feeders and hence less reinforcement history to overcome.

It is unlikely that the individual differences in problem-solving performance in our study were mainly caused by motivational or competitive differences as has been found previously [20,31,57,58]. Supplementary food is freely available to kaka at the wildlife sanctuary throughout the day. It is therefore unlikely that juveniles were under increased competitive stress as a consequence of their not yet fully developed foraging skills, thus the 'necessity drives innovation' hypothesis [31,32] may not apply here. It is also likely that all individuals landing on the platform and trying to access the feeders were indeed motivated for food. However, juveniles may have been more reliant on the feeders as a food source, whereas the adults, who are more experienced foragers, may have been more likely to abandon the task in favour of foraging for alternative food resources, which could have resulted in their high failure rates in the feeder experiments. Indeed, our analysis showed that adults were less persistent in all tasks than juveniles. However, the adults' increased success rate in the string-pulling task suggests that they were in fact motivated to work for the high-value food reward in the context of a novel feeding situation.

It is unlikely that neophobia greatly inhibited the adult's problem-solving success [13,15]. Although it is conceivable that neophobia caused the adults to avoid touching or moving the novel block in experiment 1, adults also failed the lid-opening task where no novel object was present. However, the adults had the greatest success in the string-pulling task, where the entire apparatus was novel. Furthermore, with the

exception of one bird, all adults attempted to use their beak to prise open the front of the feeder in the block-removal task and 18 out of 22 adults did so in the lid-opening task. Thus, adults interacted with feeders and tried to open them, which would have been unlikely to occur if neophobia prevented them from engaging with the problem (for additional analyses of the latency to approach the problem, which supports this hypothesis, see the electronic supplementary material).

Similar to other problem-solving studies on wild, social living animal populations [6,31,59] but in contrast to findings in captivity [60–62], we found little evidence that social learning contributed to immediate or eventual success in a task. Several individuals directly observed a conspecific pull out the block in experiment 1, yet none of them subsequently tried to move the block themselves. A similar pattern was found in experiment 2. It was only in the string-pulling task that observing a conspecific solve the problem increased the likelihood of an individual succeeding. Social learning may have been facilitated in this experiment because of the novelty of the task or the visibility of the food reward. Thus, social learning may have contributed to the adults' elevated success rate in experiment 3. Indeed, three of the four adult solvers had observed another kaka solve the problem at least once before their own success in the string-pulling task.

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

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

Data accessibility. The datasets supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. J.L. designed the study, carried out fieldwork and data analyses, and drafted the manuscript. R.C.S. and K.C.B. contributed to the study design, data analyses, and writing the manuscript.

Competing interests. We have no competing interests.

Funding. This research was supported by Victoria University of Wellington.

Acknowledgements. We thank Zealandia Wildlife Sanctuary staff, especially Raewyn Empson and Matu Booth for permission to conduct this research and providing records on RFID tags, age, and sex of the subjects. We further thank all the volunteers who assisted with testing, especially Judi Miller and Linton Miller.

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