

Current Biology

Innovative problem solving by wild falcons

Highlights

- Avian technical intelligence studies are mostly limited to corvids and parrots
- We introduce striated caracaras as a new avian model for technical cognition
- We use an 8-task comparative paradigm to assess problem solving in the wild
- Striated caracaras show rapid, flexible innovation on par with tool-using parrots

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In brief

Harrington et al. present wild striated caracaras with eight concurrent problem-solving tasks adapted from an innovation paradigm designed for comparative purposes. Striated caracaras show rapid, flexible innovation on par with tool-using parrots, highlighting this species as a promising new model for studies of avian cognition in natural settings.



Report

Innovative problem solving by wild falcons

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SUMMARY

Innovation (i.e., a new solution to a familiar problem, or applying an existing behavior to a novel problem^{1,2}) plays a fundamental role in species' ecology and evolution. It can be a useful measure for cross-group comparisons of behavioral and cognitive flexibility and a proxy for general intelligence.^{3–5} Among birds, experimental studies of innovation (and cognition more generally) are largely from captive corvids and parrots,^{6–12} though we lack serious models for avian technical intelligence outside these taxa. Striated caracaras (*Phalcoboenus australis*) are *Falconiformes*, sister clade to parrots and passerines,^{13–15} and those endemic to the Falkland Islands (Malvinas) show curiosity and neophilia similar to notoriously neophilic kea parrots^{16,17} and face similar socio-ecological pressures to corvids and parrots.^{18,19} We tested wild striated caracaras as a new avian model for technical cognition and innovation using a field-applicable 8-task comparative paradigm (adapted from Rössler et al.²⁰ and Auersperg et al.²¹). The setup allowed us to assess behavior, rate, and flexibility of problem solving over repeated exposure in a natural setting. Like other generalist species with low neophobia,^{21,22} we predicted caracaras to demonstrate a haptic approach to solving tasks, flexibly switching to new, unsolved problems and improving their performance over time. Striated caracaras performed comparably to tool-using parrots,²⁰ nearly reaching ceiling levels of innovation in few trials, repeatedly and flexibly solving tasks, and rapidly learning. We attribute our findings to the birds' ecology, including geographic restriction, resource unpredictability, and opportunistic generalism,^{23–25} and encourage future work investigating their cognitive abilities in the wild.

RESULTS AND DISCUSSION

Caracaras repeatedly innovated new solutions when concurrently faced with a subset of eight extractive foraging tasks (Figure 1) selected from a task battery presented previously to Goffin's cockatoos (*Tanimbar corella*), another opportunist generalist island endemic species.²⁰ We analyzed 51 trials (trial length $\bar{x} \pm \sigma$: 13.2 $\pm$ 5.4 min, range: 3.5–27.8 min) comprising 15 caracaras who participated in a maximum of five trials across 17 days (Table 1). Innovation rates during caracaras' first trial were as rapid as one solution per 1.6 min (i.e., 0.6 solutions per min, 0.3 $\pm$ 0.15 solutions per min, Figure 2).

Performance rate continued to improve across trials, despite temporary interruptions due to working within a natural setting (see STAR Methods; effect of trial: $\beta = 0.170$, SE = 0.06, $t_{(9,86)} = 3.05$, $p = 0.013$; effect of interruptions: $\beta = -0.031$, SE = 0.04, $t_{(16,68)} = -0.75$, $p = 0.46$; Figure 2). As a group, performance rate more than doubled from the first to fifth trials (0.3 $\pm$ 0.15 to 0.8 $\pm$ 0.6 solutions per min). In addition to performing faster, as trials progressed, caracaras also found an increasing proportion of solutions (trial 1–5: 0.64, 0.74, 0.82, 0.88, 0.92; effect of trial: $\beta = 0.681$, SE = 0.19, $\chi^2_{(1)} = 11.39$, $p = 0.0007$; effect of interruptions: $\beta = 0.174$, SE = 0.23, $\chi^2_{(1)} = 0.55$, $p = 0.46$). Both adult participants approached the box and performed on par

with younger birds, suggesting neophilia may not be restricted to young age as in some other species (see Greenberg²⁶ for review). On average, trial durations and solution latencies decreased in later trials (trial 1 duration: 904 $\pm$ 414 s, trial 5: 678 $\pm$ 352 s; trial 1 solution latency: 39.5 $\pm$ 43.4 s, trial 5: 12.9 $\pm$ 23.3 s).

Caracaras showed inter- and intra-individual differences in solution sequence across trials (Figures 3 and S1). Previous studies suggest that inter-individual variation may be characteristic of other neophilic, explorative species,^{20,21,27,28} whereas more neophobic species with less haptic exploration techniques tend to pursue more ecologically valid and obvious solutions (i.e., less inter-individual differences).^{21,22}

Latencies to absolute first solution tended to be shortest for the seesaw, swish, and plank (65 $\pm$ 60 s, 70 $\pm$ 41, and 75 $\pm$ 55, respectively) and longest for the tear and twig tasks (137 $\pm$ 84 s and 175 $\pm$ 118, respectively; Figure 3). For tasks with longer absolute solution latencies, many individuals employed a strategy of peering at the tasks from multiple angles, including bending at a panel to look from below at a protrusion or jumping atop the box to peer from above. When comparing the caracaras' success at each task with Goffin's cockatoos, we found a positive correlation between species for the proportion of trials in which a task was solved, but only when we exclude the wire



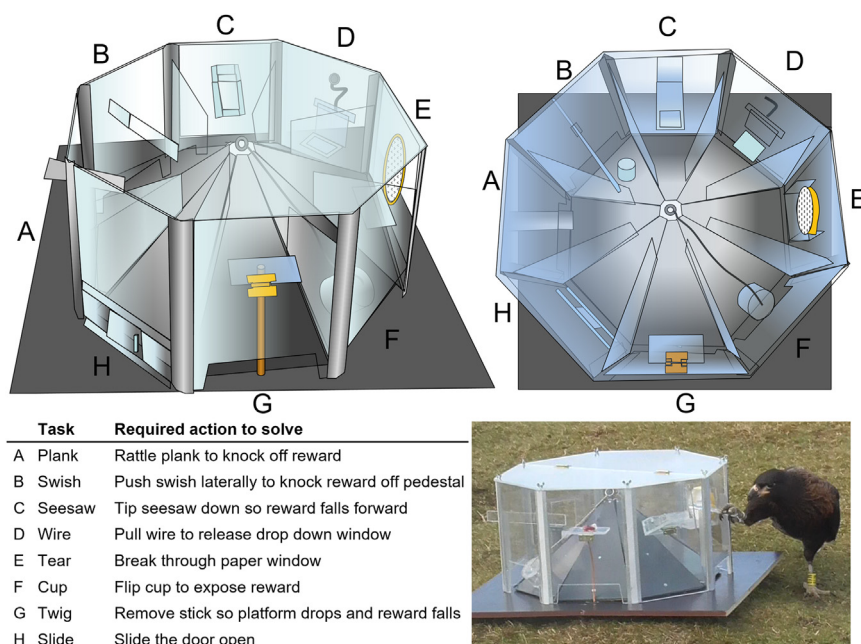


Figure 1. Eight-task innovation box and movements required to solve each task panel

Octagonal transparent Perspex innovation box with a transparent lid, eight removable transparent Perspex task panels (17 × 24 cm), and an opaque wooden base, custom-built by Markus Fitzka (Messerli Research Institute, University of Veterinary Medicine, Vienna). Bottom left: movement required to solve each task panel. Bottom right: a juvenile striated caracara uses a foot to solve the plank task.

See also [Figures S2, S3](#), and [Table S1](#).

task, which the caracaras solved in proportionally more trials (Spearman's $\rho = 0.83$, $p = 0.02$; Rössler et al.²⁰). The caracaras' high success with the wire task could be due to the frequent pulling and tearing motions that caracaras exhibit when feeding.¹⁸

Caracaras more quickly approached and contacted the box as trials progressed. Contact latency decreased from 108 ± 124 s in trial 1 to 16 ± 12 s in trial 5 (effect of trial: $\beta = -0.477$, $SE = 0.12$, $t_{(15,94)} = -3.84$, $p = 0.001$). In later trials, some caracaras immediately started running from outside the arena toward the box once it became available, with one hatch-year (H17, [Table 1](#)) solving all tasks within 5 min 14 s (including post-solution exploration time). Temporarily captive wild-caught chimango caracaras (*Milvago chimango*), the only other species within the caracara subfamily to receive attention in cognitive studies,^{27,29} also show decreased approach latencies and increased problem-solving success across trials when faced with a 4-task problem-solving box.^{27,28,30} However, chimangos first had a habituation phase, during which they could gather information prior to their initial problem-solving trial^{28,29}, whereas the striated caracaras did not. This lack of neophobia in the striated caracaras may be due to the environmental context in which the striated caracaras evolved (i.e., almost risk-free habitat).³¹

Qualitatively, caracaras' contact strategies appeared to be governed by morphological capabilities and maintained across individuals. Notably, caracaras used their foot in a raking or kicking (i.e., a quick, sharp punch) motion, and used their beak to peck, bite, and pull. At a group level, most tasks were initially solved with either the beak or the foot, whereas in later trials, some tasks became exclusively solved with the beak (i.e., twig and wire) or the foot (i.e., plank and seesaw; [Figure S2](#)). Additionally, we found that as tasks were haptically explored less prior to being solved, they were also being solved faster in subsequent trials (Spearman's $\rho = 0.90$, $p = 0.005$). It is possible that—as

with other birds that frequently manipulate items with their feet (e.g., barn owls *Tyto alba*,³² see also Gutiérrez-Ibáñez et al.³³)—caracaras may have specialized sensory receptors in their foot pads that aid in haptic exploration.

Individuals continued to spend time with tasks and interact with task protrusions after having retrieved the reward (post-solution duration within one body

length of tasks: 283 ± 144 s, 0–580 s; for post-solution contact frequencies see [Figure S3](#)). Tasks that were contacted more post-solution were solved faster in subsequent trials relative to less explored panels (Spearman's $\rho = -0.83$, $p = 0.015$). Moreover, at the individual level, increased exploration led to increased solution speeds in subsequent trials, though this effect loses significance when including the effect of trial (effect of contact frequency: $\beta = -0.583$, $SE = 0.244$, $t_{(6,76)} = -2.39$, $p = 0.0496$; with trial included: $\beta = -0.321$, $SE = 0.273$, $t_{(5,32)} = -1.17$, $p = 0.29$). When analyzing the panels separately, we found this effect differed depending on the task. In general, increased exploration led to faster solution times for all task panels except for the twig (see [Table S1](#) for model results). Continued interactions with tasks after the reward was taken may reflect exploration or play tendencies modulated by stimulus complexity (e.g., size and number of distinct elements), which affects exploratory response in many species.^{34–37} The behavior was most pronounced on tasks with protrusions: Caracaras repeatedly kicked the unbaited swish, plank, and seesaw features, and prolongedly bit and pulled the wire feature, sometimes with force to the point of jumping with it in their beak. Tactile exploration can increase information gain, which for opportunist extractive foragers could be especially important in revealing novel and hidden food sources or increasing task efficiency during future confrontations.^{38–40} Task features may have also induced a playful circular reaction,^{41,42} in which the interaction itself had a rewarding effect, e.g., by producing sound or movement, which encouraged repeated interaction. Furthermore, innovative problem solving shares important overlaps with curiosity, a topic that is gaining renewed interest in comparative cognition⁴³ due to its links with learning, attention, memory, and decision making. Species that are likely to exhibit more frequent and persistent interest in novel items or structures they encounter may be more likely to glean

Table 1. Individuals' success (total solutions found out of eight tasks) per trial grouped by age

Age	ID	Trial				
		1	2	3	4	5
HY	A17	5 [†]	7	–	–	–
	E18*	3	8	7	7	5
	G18*	3	–	–	–	–
	H17*	8	8	7	6	8
JUV	E17	6	6	8	6	–
	K15	5	3	–	–	–
	M15	1	8	6	8	7
	M17	0	7	6	8	6
	M18*	4	8	–	–	–
	P16	6 [†]	8	8	7	6 [†]
	V14	3	8	7	–	–
SA	C16	5	4	8	8	8
	V19	6	–	–	–	–
AD	P19	1	–	–	–	–
	X37	3	6	4	8	5
	Min	0	3	4	6	5
	Max	8	8	8	8	8
	Mean	4	7	7	7	6
	N	15	12	9	8	7

Trial duration spanned 3.5 to 27.8 min (mean $\pm$ SD: 13.2 $\pm$ 5.4 min). Asterisks denote males (inferred by pretrial weight). Daggers represent trials when only 7 of 8 solutions were possible (e.g., experimenter or transport error). En dashes denote no trial. Sample size with mean and range of solutions included at the bottom of the table. HY, hatch-year; JUV, juvenile; SA, sub-adult; AD, adult.

information that may be used later or discover new opportunities or solutions to problems.^{44,45}

Overall, the caracaras performed in line with tool-using Goffin's cockatoos on the same tasks. Although the Goffin's were

presented with a greater number of tasks, the caracaras achieved an innovation rate of 0.3 ± 0.2 solutions per min, while the Goffin's innovated 0.5 ± 0.3 solutions per min. Notably, nearly all caracaras solved all tasks, including more difficult tasks such as the wire or tear tasks, which less than 50% of Goffin's solved over repeated trials. Similar to the Goffin's, caracaras were also slower to solve tasks in which rewards were visually separated from the tasks' functional mechanisms, and instead tended to direct their initial interactions on these panels toward the food.²⁰

The caracaras' eagerness to participate in the tasks, coupled with their speed and flexibility in innovation, highlight them as a promising and relevant new model for examining avian technical intelligence in the wild. Caracaras achieved rapid success and showed signs of learning through improved performance and speed as trials progressed (Figure 2). These results support the feasibility of further research into the contexts of curiosity, exploration, and play in a falcon species. We emphasize the rare opportunity to expand comparative research to include a readily participatory wild falcon to investigate the processes underpinning innovative problem solving.⁴⁶

There is a growing body of evidence that falcons in general represent an important taxon for broadening our understanding of the diversity and evolution of avian cognition^{27–29}; however, they remain surprisingly understudied. We encourage future research with striated caracaras and more broadly within the caracara subfamily to examine: (1) What features and task functional mechanisms are most attractive, (2) how does interest in novel, unbaited structures differ from goal-directed exploration of baited apparatuses, (3) how do caracaras structure their play and object exploration, and (4) how does interest in novel structures vary within the population (e.g., inter-individual differences, age and sex effects, and effects of social dynamics). We also have the possibility to track their neophilic, exploratory, and problem-solving behaviors over time, as well as to evaluate the fitness-related value of these behaviors for those individuals who enter the breeding population.

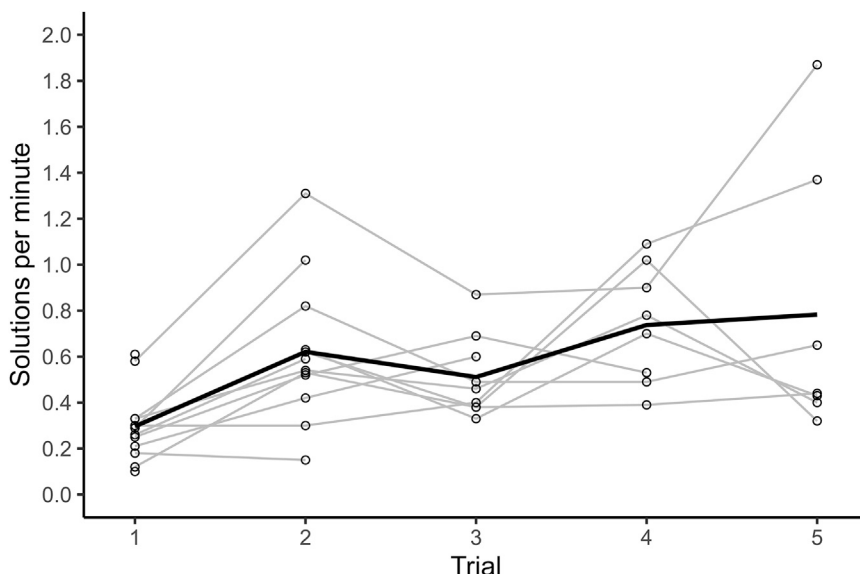


Figure 2. Rate of solutions per minute over trials

Innovation rates during individuals' first trial, when subjects were required to apply for the first-time existing behaviors to a novel situation, and subsequent increasing performance rates (i.e., solutions per minute) across trials 2–5. Gray lines represent individuals and the black line represents the mean.

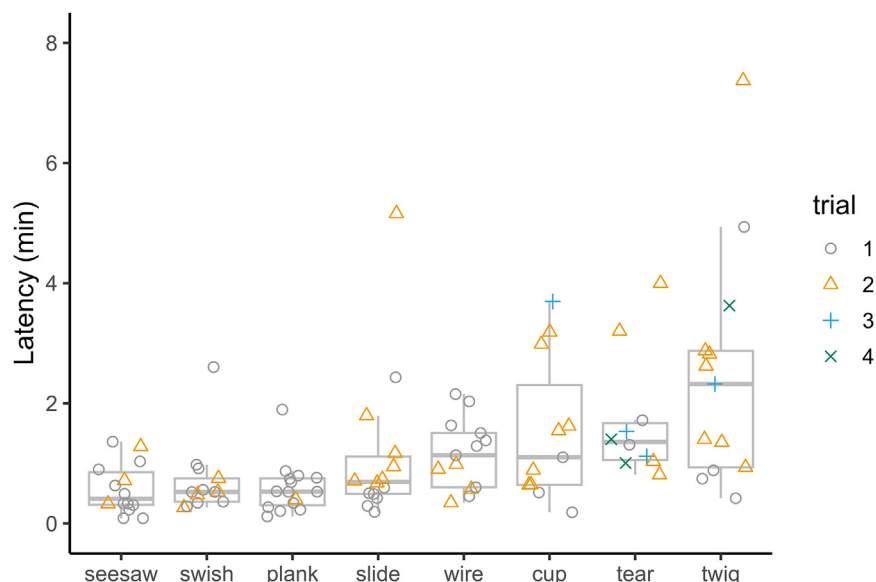


Figure 3. Latency to absolute first success per task (trials pooled, i.e., 51 trials of 15 individuals)

Points represent the latencies (min) to absolute first solution. Point shapes represent the trial in which the solution was first achieved. Boxplot bars show median and first and third quartiles, while whiskers extend to the largest and smallest values (at most 1.5 * IQR [inter-quartile range]).

See also Figures S1, S2, and S3.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2023.10.061>.

A video abstract is available at <https://doi.org/10.1016/j.cub.2023.10.061#mmc3>.

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AUTHOR CONTRIBUTIONS

Conceptualization, K.J.H. and M.L.L.; methodology, K.J.H., M.L.L., and A.M.I.A.; investigation, K.J.H. and M.L.L.; formal analysis, R.F. and K.J.H.;

writing – original draft, K.J.H.; writing – review & editing, K.J.H., M.L.L., A.M.I.A., R.F., and L.B.; supervision, M.L.L.; funding acquisition, M.L.L. and K.J.H.; resources, K.J.H., A.M.I.A., and M.L.L.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental models: Organisms/strains		
Striated caracara (<i>Phalacrocorax australis</i>)	Saunders Island, Falkland Islands	N/A
Software and algorithms		
BORIS v 6.0.574	Friard and Gamba ⁴⁷	https://www.boris.unito.it/
R v.4.2.2	R Development Core Team ⁴⁸	https://www.r-project.org/
Other		
Panasonic HC-V180 Full HD	Panasonic	https://www.panasonic.com/de/consumer/foto-video/camcorder/hc-v180.html

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Katie Harrington (katherine.harrington@vetmeduni.ac.at).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All datasets used for analysis in this study have been deposited at Science DataBank (file: df_box.RData, ContactFreq.RData, PropSolv_CaraGoffin.RData) and are publicly available as of the date of publication (ScienceDB: <https://doi.org/10.57760/sciencedb.13251>).
- All code generated during this study has been deposited at Science DataBank (files: CaracaraInnovation.R, CaracaraFunctions.R) and is publicly available as of the date of publication (ScienceDB: <https://doi.org/10.57760/sciencedb.13251>).
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Subjects and study site

Striated caracaras are opportunistic, generalist, mostly ground-dwelling falcons restricted to harsh coastal areas of southern South America and the Falkland Islands (Malvinas).^{49,50} Relative to many bird species, striated caracaras have a long adolescence,³¹ a suggested physiological correlate to behavioral and cognitive flexibility.⁵¹ The caracara population on the Falklands (Malvinas) is genetically and behaviorally distinct from the mainland (U. Balza and KH, unpublished data). Falklands striated caracaras' ecology and behavior overlaps extensively with an established parrot model for technical innovation: Like kea parrots (*Nestor notabilis*), Falklands striated caracaras face seasonal resource unpredictability and are neophilic, exploratory, and playful.^{16,19,31,52} Moreover, they are behaviorally flexible, e.g., they associate with anthropogenic resources, seasonally alter activity levels, extractively forage, and albeit historically persecuted, remain unwary of humans similar to how they were first described by sailors prior to human settlement in the Falklands.^{31,53–55} Furthermore, Falklands striated caracaras are known for foraging innovations, including predation of an octopus^{56,57} and unearthing invasive invertebrates in invasive grasslands.⁵³

Studies of innovative problem solving in the wild provide invaluable insight from the use of experimental protocols in natural settings (e.g., Jacobson et al.,⁵⁸ Thornton and Samson,⁵⁹ and Johnson-Ulrich et al.⁶⁰ and reviewed in Byrne and Bates⁶¹ and Szabo et al.⁶²). Our study occurred on Saunders Island, Falkland Islands (Malvinas) (51.37°S 60.09°W) approximately 400 km northeast of Cape Horn. Saunders is a designated Important Bird and Biodiversity Area,⁶³ a privately-owned sheep farm (human pop. 6), and the site of long-term monitoring where caracaras have been ringed biannually from 2010 to 2019 (see Harrington et al.⁵⁴ and Harrington et al.⁵⁵). Prior to testing, we ringed 83 potential subjects and inferred age by plumage³¹ and estimated sex by mass (11 adults [5 females, 6 males], 9 sub-adults [4, 5], 28 juveniles [13, 17], and 35 hatch-years [12, 21] (see Harrington et al.⁵⁴ for protocol). Caracaras are conspicuous and attracted to group trapping events that mimic naturally occurring ephemeral feeding events, thus we are confident that our effort represents the population on Saunders during our study.

Ethics statement

All capture and handling methods complied with the Conservation of Wildlife and Nature Ordinance of 1999, Section 9, License to carry out Scientific Research (Permit #R15/2022, Falkland Islands Government) and were approved by the University of Ottawa Animal Ethics Committee (protocol no. BLF-3745).

METHOD DETAILS

Apparatus

We adopted a comparative paradigm that blends the designs by Rössler et al.,²⁰ Rössler et al.,⁶⁴ and Auersperg et al.,²¹ adapting the presentation to meet the requirements for testing in natural conditions and to overcome limitations of motivation, species-specific motor capabilities, and sampling bias.^{65,66} Our custom-built innovation box (see Figure 1, a–h) allows participants to shift among and interact with eight food-rewarded tasks using distinct motor actions to solve and obtain as many rewards as possible during a single trial. Unlike the MAB paradigm (i.e., one solution per session and previously solved tasks blocked in subsequent sessions, e.g., Benson-Amram and Holekamp⁶⁷ and Petelle et al.⁶⁸), task panel positions are randomized and panels are rebaited between trials to allow for specific measures of innovation and performance rates, group specific strategies (e.g., order of approach, solution order, and motor techniques), and problem-solving behavior (e.g., individual differences in approach and handling).²⁰ As sample sizes in cognitive studies are generally small, the increased variation of treatments (i.e., number and diversity of tasks) in place of a single or small set of problem-solving tasks improves replicability and generalizability of results.⁶⁶

Procedure and data collection

Trials were opportunistic from 18 August to 3 September 2022 (i.e., austral winter non-breeding season) between 0800 and 1800. For each trial, the 8-task apparatus was presented fully baited in the same ground location centered in a 3-m radial trial arena. Prior to presentation and out of sight, task panels were baited with a high-quality familiar food (i.e., 1 cm² mutton). Between trials, the box was removed and rebaited out of sight, and remained unavailable. For experimenters to place the box in the trial arena, at least one potential subject needed to be nearby the trial arena (i.e., a ringed bird, identified using the naked eye or binoculars). More than one bird could be present in the vicinity (i.e., within 100 m) when a trial began.

A trial began when a potential subject entered the arena and ended after the subject retrieved all food rewards or 3 min lapsed with no contact. Experimenters tried to prevent conspecific interruptions and mitigate social learning by concurrently providing an attractive food source outside the arena, such that only the active subject was likely to attend to the apparatus. While test subjects were not drawn away from the apparatus by the alternative food source (perhaps as they had a monopoly on it), it is possible that the alternative food source was distracting at an imperceivable level for experimenters, which may have had a conservative effect on subjects' performance levels. Birds were permitted one trial per day. If a bird tried to participate in more than one trial within the same day, an experimenter would intercept their approach before they reached the arena threshold and walk them off to allow another subject to enter and participate. Caracaras most often approached on foot, making it possible for experimenters to prohibit birds from entering the arena during another subject's trial. Due to time constraints, birds were capped at five trials within the study period to facilitate repeated measures across individuals. For each trial, we recorded the subject's identity (i.e., alphanumeric ring) and used a Likert scale to visually assess their crop (i.e., a distensible food storage area at the top of the digestive tract⁶⁹ as a proxy for hunger driven motivation (i.e., crop not visible, partially visible, or fully visible). We videotaped trials 4 m from the apparatus using a handheld Panasonic HC-V180 Full HD Camcorder.

As caracaras self-selected to voluntarily participate in trials, our sample may reflect a STRANGE-related bias,⁷⁰ despite this, to the best of our knowledge, our results are representative of juvenile Falkland Islands striated caracaras during austral winter (i.e., non-breeding season).

QUANTIFICATION AND STATISTICAL ANALYSIS

We used Behavioral Observation Research Interactive Software (BORIS, version 6.0.574⁴⁷) to behaviorally code all videotaped trials. We developed an ethogram to code contact with each task panel modified by motor skill applied. We initially scored four behaviors (bite, peck, kick, and grab), as these were the most discrete and reliable to identify. However, we observed bite and grab less frequently than peck and kick, so we found that level of resolution did not enhance our analysis. We additionally coded when a task was solved (i.e., an action that made the food reward accessible) and when a reward was retrieved. Because this study was conducted in the wild and test birds could be interrupted by naturally occurring events, we also coded all trial interruptions, defined as a subject moving more than three body lengths away from the apparatus seemingly in response to an external factor (e.g., an experimenter's movement while deterring conspecifics from entering the trial arena or a curious farm animal displacing the subject at the apparatus [e.g., domestic goose, horse, cat, or sheep]).

From the coded videos, for each trial, we recorded latency to contact the box (i.e., time from entering arena threshold until first contact), latency to solution per task panel (i.e., total time within one body length of a task panel prior to solving), frequency of motor actions applied to each task panel, duration within one body length at each task panel before and after solving (i.e., as a conservative measure of visual exploration and interest), and total solutions found. We subtracted interruption durations from the individuals' total trial duration; we also noted the total number of interruptions per trial which we later used to control for possible effects on

performance. We calculated innovation rate as an individual's total solutions per unit time during their first trial, when the subject was required to apply for the first time existing behaviors to a novel situation. In subsequent trials, we consider the same measure as the individual's general performance rate.

Twenty percent of videos were pseudo-randomly selected and externally coded to assess inter-rater reliability. Agreement was high for latencies [$ICC_{(1)} = 0.996$, $F_{(6,6.8)} = 440$, $p < 0.000.1$], durations [$ICC_{(1)} = 0.744$, $F_{(93,94)} = 6.81$, $p < 0.0001$], and innovation rates [$ICC_{(1)} = 0.99$, $F_{(8,8.07)} = 187$, $p < 0.0001$] (R package 'irr'⁷¹).

For our response variables in our box-level models, we use performance rate, proportion of solutions found (i.e., number of successes and failures per trial), and latency to contact the box (log transformed to improve fit for linear model assumptions). To investigate performance rate and latency to contact across trials, we fitted linear mixed models (LMM⁷²). To investigate proportion of tasks solved across trials, we fitted a logistic generalized linear mixed model with binomial error structure and a logit link function, using a two-columns matrix with the number of successes and failures per trial for each individual as the response.^{72,73} For each model, we use trial number as our test predictor and total number of interruptions as a control predictor. As random intercept effects, we included subject and date to account for repeated observations of the same individual and day to day effects. We analyzed 51 trials comprising 15 individuals who each participated in a maximum of five trials across a 17-day period.

To investigate whether increased contact with tasks resulted in faster solutions in subsequent trials, we first fitted a LMM including all observations to assess an overall effect. To explore any panel specific effects, we further ran separate LMMs at the panel level. For each model, we included contact frequency as a test predictor and individual as a random intercepts effect. As an alternative, we fitted a model that included contact frequency as a test predictor together with trial number as a control predictor, to control for a general increased exposure to the panels. These models had low sample size and high levels of collinearity between predictors and are therefore presented as alternatives (Table S1).

We fitted the models in R (version 4.2.2; R Core Team 2022⁴⁸) using the functions lmer and glmer, respectively, from the package 'lme4' (version 1.1–31⁷⁴). All covariates were z-transformed to ease model convergence and interpretation of model estimates.⁷⁵ To keep Type I error rate at the nominal level of 5%, we included all possible identifiable random slopes within the random intercepts effects.^{76,77}

After fitting our models, we confirmed that (1) the model assumptions were not violated by visually inspecting QQ-plots (Field⁸³), (2) the 'Best Linear Unbiased Predictors' (BLUPS) were approximately normally distributed,⁷² (3) overdispersion was not an issue for the logistic model (dispersion parameter = 1.07), and (4) the absence of collinearity by calculating the 'Variance Inflation Factor' using the R package 'car' version 3.0–12 (VIF = 1.001, 1.02, and 1.02, respectively for performance rate, proportion of tasks solved, and latency to contact; for VIF values for solution latency models see Table S1; Fox and Weisberg⁷⁸). We confirmed model stability by comparing model estimates of the full model to estimates of models in which levels of random effects were excluded one at a time⁷⁹ using a function written by Roger Mundry (Leibniz ScienceCampus Primate Cognition, Göttingen). We tested the significance of trial number by means of the Satterthwaite approximation⁸⁰ using the function 'lmer' of the package 'lmerTest'⁸¹ and a model fitted with restricted maximum likelihood.

We used a Spearman's rank correlation to assess the relationship between contact frequency after the reward was taken (i.e., post-solution) and latency to solution in subsequent trials averaged for each panel, and to assess the proportion of trials in which a task was solved between the Goffin's cockatoos in Rössler et al.²⁰ and the striated caracaras in this study.

Due to the voluntary participation of caracaras, the unpredictable availability of potential participants, and the limited winter day-length, we were unable to reach a sufficient sample spread of age, sex, or crop status to analyze these factors and these were thus not included. We excluded from the analysis six trials from six individuals (i.e., one trial per individual) that contacted the box and did not engage further (e.g., they were interrupted by a conspecific, heterospecific, farm event, etc., and did not return for the remainder of testing).

We created plots using the R package 'ggplot2'.⁸²