

Correspondence

Long-term memory
in wild falcons

Katie J. Harrington^{1,3,*},
Alice M.I. Auersperg¹, Laura Biondi²,
and Megan L. Lambert¹

Long-term memory — information retention over long timescales — can allow animals to retain foraging skills and efficiently respond to seasonally available resources and changing environments¹. Most long-term memory research is with captive species, focusing on spatial, individual or object recognition, with less known about wild species and the retention of motor task abilities, as in the case of complex foraging skills^{2,3}. We have examined whether wild striated caracaras (*Phalacrocorax australis*), recently shown to rapidly and flexibly innovate with an eight-task puzzle box⁴, retain task memories one year later. We found that, despite no reinforcement, caracaras repeated motor techniques that led to their most recent success on tasks the year prior, solving nearly twice as fast as a naïve control group and four times faster than when naïve. Our results suggest long-term memory may be important for non-migratory opportunistic generalists, particularly in remote island environments with seasonally available resources, and further highlight how striated caracaras are promising candidates for avian cognitive studies.

Falconiformes are a sister taxon to cognitively well-studied parrots and passerines⁵. Within Falconiformes, the socially complex, neophilic and innovative striated caracara is an emerging model in avian cognitive ecology⁴. We originally tested 15 individually marked wild striated caracaras using an eight-task comparative problem-solving paradigm to assess behavior, rate, and flexibility over repeated exposure in a natural setting⁴. We retested five caracaras — three females, two adult and one juvenile (i.e., second year), and two males (both juveniles) — still present 384–392 days after their most recent trial using the same apparatus

and protocol. As a control, we tested seven caracaras — three females and four males in their hatch-years, equivalent in age to three of the experienced subjects during their original testing — that were naïve to the tasks, although in contrast to the experienced group when they were naïve, familiar with the apparatus' general structure and protocol.

Individuals were sampled from the same population and location, under similar conditions as in the original study. We recorded contact latency, performance rate (solutions per minute), task solution latency, and task-directed motor techniques (ethogram, Figure S1) for motor diversity scores⁶ and to determine whether task solutions matched those used most recently the year prior. We did not compare total solutions, since previously subjects reached ceiling or near-ceiling levels or were precluded by natural interruptions. If experienced individuals repeated

their most recent task solutions, with solution techniques varying between tasks, this would imply task-specific memory. Moreover, in line with recent long-term task memory research^{7,8}, if caracaras remember tasks, we expect faster solutions compared to when they were naïve and the naïve control group.

We found no group differences in latency to first contact the puzzle box (mean $\pm$ SD: experienced, 21 $\pm$ 23 seconds; naïve control, 49 $\pm$ 87 seconds; t-test: $p = 0.45$; Table S1), suggesting no motivational differences between the two groups, likely due in general to caracaras' neophilic and explorative tendencies and more specifically to the naïve control's familiarity with the apparatus' general structure.

As a group, experienced caracaras used their same most recently used solution technique as the year prior for 69% of tasks (20/29 solution techniques matched; mixed model

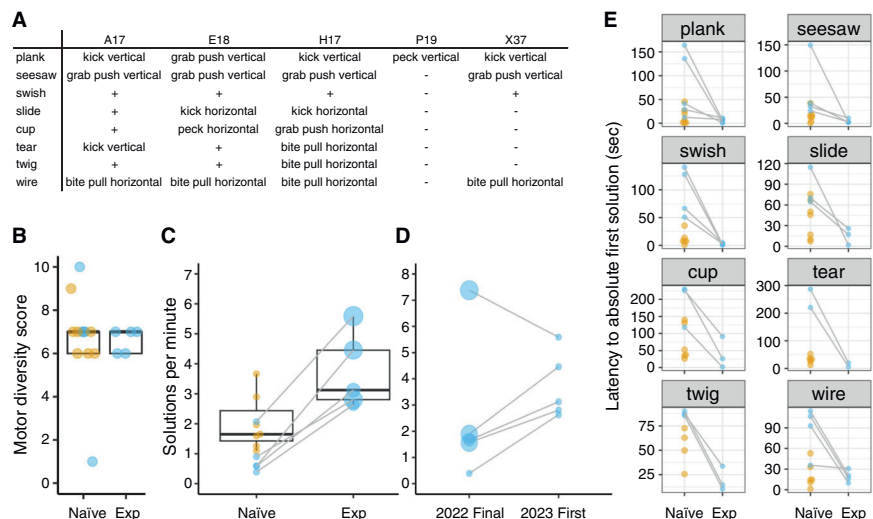


Figure 1. Experienced caracaras repeated the solution technique that led to their most recent success on tasks the year prior, solving twice as fast as a naïve control group.

(A) Individuals' (identified across the top row) task specific motor techniques applied in both years. Crosses denote the task was solved using a different technique. Horizontal dashes indicate the task was not solved in both years. (B) Caracaras showed no group differences in motor diversity scores: experienced (exp) group, blue circles, left and right are during original study and retesting, respectively; naïve control, orange circles. (C) Caracaras' performance rate (solutions per minute) when naïve and retested (blue circles), paired samples indicated by gray lines, compared to the naïve control (orange circle). (D) Experienced birds (blue circles) solved faster than during their final trial the year prior (circle area scales with the number of trials the year prior). (E) Experienced caracaras solved individual tasks faster than when naïve a year prior (blue circles paired by gray lines) and faster than the naïve control group (orange circles). Unpaired tasks in 2023 were due to the task remaining unsolved in 2022 (for example because of an interrupted trial). For panels (B) and (C), boxplots represent experienced and naïve groups in the present study, with horizontal bars showing median and first and third quartiles and whiskers extending to largest and smallest values (at most 1.5 * inter-quartile range). See also Figure S1 and Table S1.



with binomial error structure, intercept estimate: 0.7985, s.e. 0.4014, $z = 1.9894$, $p = 0.0467$; Figure 1A). Except for the wire and seesaw tasks, solution techniques varied across tasks and among individuals, suggesting individuals remembered task specific behaviors.

Experienced caracaras solved nearly twice as fast as the naïve control group (performance rates: experienced, 3.72 ± 1.27 solutions per minute; naïve, 2.01 ± 0.93 ; t-test: $p = 0.038$) and four times faster than when naïve (2022 first trial, 0.91 ± 0.67 ; 2023 trial, 3.72 ± 1.27 ; t-test: $p = 0.0017$; Figure 1C and Table S1). Moreover, experienced birds solved faster than their final trial the year prior, except one notable bird who only solved faster than his third trial yet outperformed other tested birds (2022 final, 1.38 ± 0.67 ; 2023 trial, 3.25 ± 0.83 ; t-test: $p = 0.0095$; Figure 1D). Interestingly, the naïve control group were faster innovators than the experienced had been when naïve (experienced when naïve, 0.91 ± 0.68 ; naïve control, 2.01 ± 0.93 ; t-test: $p = 0.0379$). At the task level, experienced birds solved faster than the naïve control, and faster than when naïve (Figure 1E).

We found no difference in motor diversity scores between experienced birds when naïve and at present, suggesting increased speed was not due to refined behavioral repertoires over time (when naïve, 6.4 ± 3.29 motor techniques; at present, 6.6 ± 0.55 ; paired t-test: $p = 0.908$; Figure 1B). Furthermore, we found no differences in motor diversity scores between the experienced when naïve and the naïve control (experienced when naïve, 6.4 ± 3.29 ; naïve control, 6.86 ± 1.07 ; t-test: $p = 0.7773$), and none between the experienced during retesting and naïve control (experienced, 6.6 ± 0.55 ; naïve control: 6.86 ± 1.07 ; t-test: $p = 0.5991$).

Our results are unlikely due to group differences in motivation, as naïve and experienced were similarly motivated to contact the apparatus (Table S1), or age-related differences in innovation, exploration or problem-solving ability. In the original study, younger birds tended to solve faster than older during initial exposure,

suggesting higher innovativeness; moreover, at the task level, hatch-years first succeeded faster than juveniles at the seesaw, slide, wire door, and — more notably — the twig task, seemingly the most difficult based on solution latencies⁴. While the naïve control group was unable to solve as quickly as experienced birds, they solved faster than the experienced had when naïve (Figure 1C), perhaps partly due to familiarity with the apparatus' general structure. However, familiarity is unlikely to primarily explain differences in innovation rates as the groups had comparable latencies to first contact with the puzzle box (suggesting both lacked neophobia) and when naïve were equally unfamiliar with test tasks.

Our results demonstrate long-term memory in wild striated caracaras, with individuals retaining memories for multiple solutions to an eight-task puzzle box for over one year without reinforcement, in line with abilities shown by wild North Island robins (*Petroica longipes*) and Mexican jays (*Aphelocoma wollweberi*) when recalling learned novel foraging tasks after long intervals without reinforcement^{3,9}. Caracaras' long-term memory may facilitate responses to seasonally pulsed resources and — for a social species with long adolescence and lifespan — increase chances that novel techniques spread via social learning and promote skill persistence across generations³. Our findings advance our evolutionary understanding of memory in the technical domain and add insight into complex cognitive demands of a wild species.

SUPPLEMENTAL INFORMATION

Supplemental information including one figure, one table and experimental procedures can be found with this article online at <https://doi.org/10.1016/j.cub.2024.07.012>.

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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, K.J.H.; Writing, Original Draft, K.J.H.; Writing, Review and Editing, K.J.H., M.L.L., A.M.I.A., 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.

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¹Comparative Cognition Unit, Messerli Research Institute, University of Veterinary Medicine Vienna, Veterinärplatz 1, 1210 Vienna, Austria. ²Instituto de Investigaciones Marinas y Costeras (IIMyC), UNMDP — CONICET, Juan B. Justo 2550, Mar del Plata B7602GSD, Argentina.

³Lead contact.

⁴E-mail: katherine.harrington@vetmeduni.ac.at