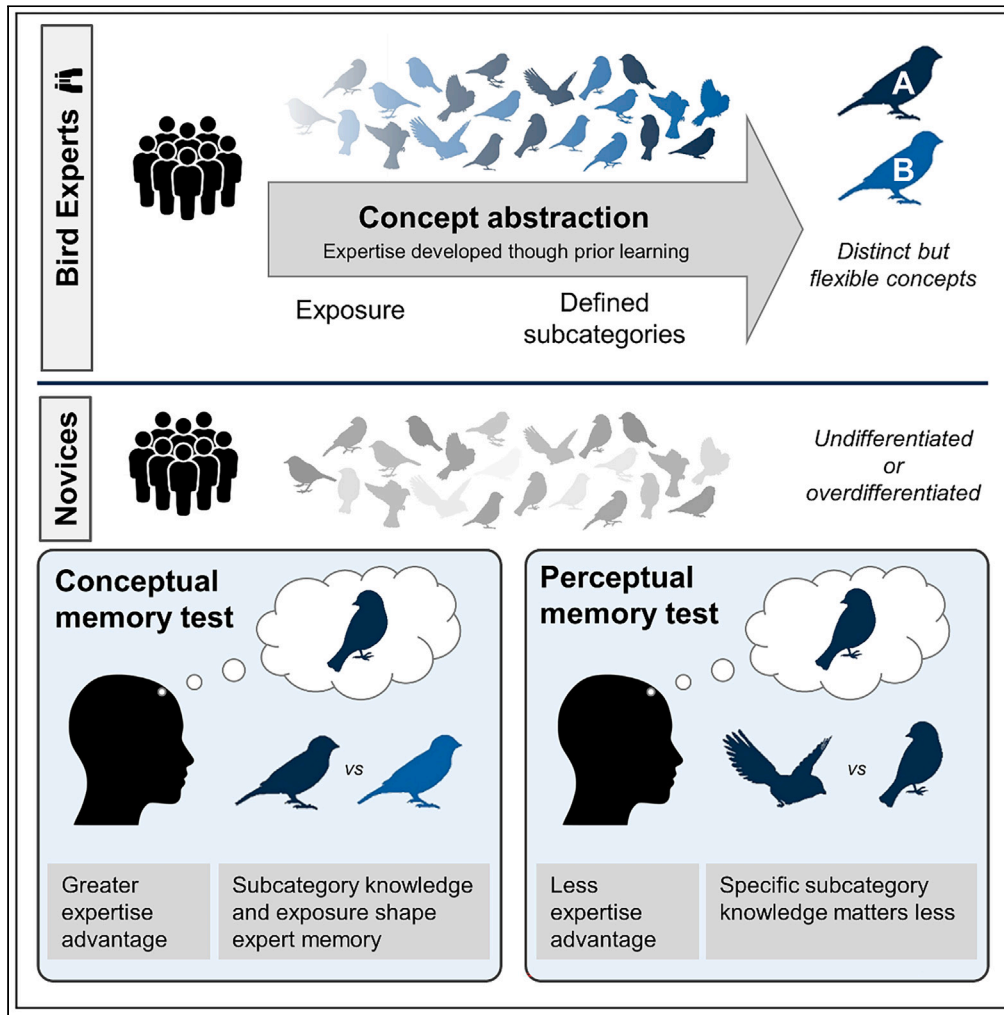


Article

Interactive influences of prior knowledge on episodic memory



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Highlights

Expert memory benefitted most on memory test requiring conceptual abstraction

Memory for incidental perceptual details was less sensitive to prior knowledge

Individual item knowledge and prior exposure (e.g., via environment) both shape memory



Article

Interactive influences of prior knowledge on episodic memory

Erik A. Wing,^{1,4,*} Asaf Gilboa,^{1,2,3} and Jennifer D. Ryan^{1,2}

SUMMARY

Many species adapt to their environments by accruing relevant knowledge and expertise, which in turn shapes memory formation. Human experts remember items in their field better than novices, but different types of knowledge or exposure influence memory in different ways. By examining both expert knowledge for bird species and ecological data on environmental prevalence, we sought to disentangle the contributions of specific knowledge about individual items from those of conceptual familiarity due to prior exposure. Conceptually oriented memory in experts was highest for identifiable species. When lacking this specific knowledge, however, experts tended to mistakenly remember studying environmentally common vs. environmentally uncommon species, with no comparable effect in novices. Perceptually oriented memory showed a smaller expertise advantage and less influence from species-level knowledge. Thus, expert memory benefits more from conceptual abstraction but is shaped by multiple types of experience—specific knowledge and prior exposure—revealing a complex relationship between semantic and episodic memory signals.

INTRODUCTION

Knowledge influences a host of different cognitive operations, perhaps none so dramatically as episodic memory. The interplay between knowledge and memory is particularly apparent in the literature of expertise, with past work finding that experts are able to better remember information from their domain of specialization at much higher rates than novices. This trend has been shown across diverse areas, including chess,¹ wine,² navigation,³ and music.⁴ The ways in which knowledge supports episodic memory may vary across contexts, however, and a variety of related ideas have been offered to account for these effects. Among them include the ability to chunk disparate information into meaningful units, the ability to organize well-known information in mind, and to draw on subtle conceptual distinctions in the service of separating overlapping items and reducing interference.^{1,5–7}

The specific circumstances under which expertise benefits memory can be more revealing than the mere existence of a benefit. Are experts particularly suited to remembering subtle distinctions between overlapping items? Perhaps not in all cases. Memory may excel when tests emphasize dimensions relevant to the organization of specialized knowledge but benefit less when tests involve discriminating along incidental dimensions.^{8–10} For example, a car expert might be able to remember seeing a 2005 Civic (rather than a 2006 model) but be uncertain about the car's color, which is not integral to the conceptual differentiation of car makes and models. Increased mnemonic sensitivity to conceptual features should be particularly evident in expert domains requiring abstraction—the ability to learn and recognize defining features of a concept while downweighting features that are variable or not diagnostic for identification.^{11–13} Using multiple tests to examine different aspects of memory may therefore help explain how the expert memory advantage reflects underlying differences in how domain items are perceived and categorized.

A separate body of literature highlights a seeming paradox about how semantic and episodic memories interact. Although prior knowledge typically benefits memory, some forms of pre-experimental knowledge or exposure might also be mistaken for episodic oldness. This connection has been explored in work linking episodic recognition with conceptual fluency.^{14–17} Conceptual fluency, the ease of processing information due to some meaning-related dimension, can arise through repeated experience with items or concepts. Notably, repeated experience is also necessary for developing expertise. The interactive influence of different forms of prior experience on memory, however, has largely been overlooked. Some evidence points toward distinct influences. For example, recognition memory is unsurprisingly better for celebrity names (discrete knowledge with verbal labels) than for non-famous names, but worse for more common vs. less common non-famous names due to an increase in false alarms for the former^{18,19} (see related literature on word frequency effect²⁰). Therefore, although prior knowledge can increase memory capacity and flexibility, increased exposure to concepts may also interfere with accurate recognition. Particularly during real-world learning, signals from prior knowledge that might either facilitate or hinder memory may be intertwined.

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Disentangling these aspects of prior experience is therefore a difficult but important challenge in understanding how semantic and episodic signals interact.

In the present study, we examined how prior experience shapes memory using measures of expert subcategory knowledge and concept exposure. After studying bird photographs, participants first attempted to distinguish repeated from novel bird illustrations (*illustration memory test*) in a recognition task that required abstraction between picture formats. Prior knowledge varied both across groups—expert birdwatchers and matched novices—and across individual bird stimuli—potentially recognizable local species as well as nonlocal species unknown to participants. Separately, to index potential exposure to bird concepts, we obtained measures of environmental prevalence for each local bird species from a database of ecological species distributions. We examined memory as a function of identification ability (i.e., could participants name the bird) as well as species prevalence. Although more common birds should be easier to identify, high environmental frequency might also be mistaken for oldness in the memory test if semantic and episodic signals are blurred. We therefore explored memory within a potential middle zone of semantic knowledge or exposure by looking at species that could not be identified but which were more or less frequent in the local environment.

As a comparison with the illustration test, participants also completed a separate test for specific perceptual details (*photo memory test; two-alternative forced choice, 2AFC*). On each trial, participants selected which of two photographs of the same bird species was initially studied. This test required little abstraction given that targets and lures depicted the same species. To the extent that expertise supports aspects of memory that are aligned with relevant conceptual distinctions, we expected a smaller group advantage for experts than on the illustration memory test. Along similar lines, the type of abstracted knowledge or verbal labels that might support memory for local versus nonlocal species within experts should be largely irrelevant to the perceptually focused discrimination between exemplar photos. Therefore, we also expected that factors like name knowledge and bird frequency would contribute less to memory decisions for photograph exemplars.

In sum, we sought to clarify which aspects of knowledge support different types of memory across multiple tests. In a test requiring high levels of concept abstraction, we examined two different measures—name knowledge (subcategory labels) and species prevalence (concept exposure/fluency)—to determine how two different forms of prior experience shaped memory. We then examined a test for which little abstraction was necessary to understand how memory in experts hinges upon the conceptual distinctions that are present or absent during different memory judgments.

RESULTS

Species naming test accuracy

The ability of participants to identify species names from illustrations provides a conservative estimate of specific semantic knowledge at the level of individual items. Across all items in the illustration test (i.e., the 48 studied species and 48 new species), mean accuracy in experts was 61.8% (standard error (SE) = 1.1%) for local birds and 3.2% (SE = 0.4%) for nonlocal birds. In novices, mean accuracy was 1.7% (0.3%) for local birds and 0.0% (SE = 0.0%) for nonlocal birds. These results confirm that experts could recognize a majority of birds in the local condition at the level of individual species but were generally unable to recognize nonlocal birds. By contrast, species naming accuracy in novices was extremely low, even for local birds.

Illustration memory test

In addition to illustrations of species whose photographs were shown in the study phase, the illustration memory test included two types of foil items: illustrations of birds from the same families that appeared during the study phase (studied-family foils) and illustrations of birds from novel families (novel-family foils) (Figure 1). Because this categorical dimension was expected to influence detection of new items, recognition accuracy on the illustration memory test was calculated first using only targets and studied-family foils, with performance on novel-family foils addressed separately (novel family recognition section).

Overall memory discriminability

Memory discriminability (*d*-prime) and response rates for the illustration test are shown in Figure 2. *D*-prime values were calculated within participant and bird species region (local vs. nonlocal) using targets and foils of the same bird families (A–D, see Figure 1) as the target birds (i.e., studied-family foils; responses to novel-family foils (families E–G) are discussed in a subsequent section). Subjectwise *d*-prime values were submitted to a 2 × 2 ANOVA with factors of group (experts vs. novices) and bird species region (local vs. nonlocal). This yielded a significant group × region interaction ($F(1,84) = 34.051$; $p < 0.001$, $\eta^2_G = 0.151$) as well as main effects of group ($F(1,84) = 165.807$; $p < 0.001$, $\eta^2_G = 0.526$) and region ($F(1,84) = 45.954$; $p < 0.001$, $\eta^2_G = 0.151$). Within experts, there was a large advantage for the local vs. nonlocal condition ($t(40) = 8.810$, $p < 0.001$, $D = 1.38$), with no analogous difference seen within novices ($t(44) = 0.677$; $p = 0.502$, $D = 0.10$). Although collapsing across region, overall performance in novices was above chance (mean = 0.153, SD = 0.268, $t(44) = 3.816$, $p < 0.001$), the substantial main effect of group underscores the benefit of prior knowledge for memory requiring translation between visual formats. Notably, experts' memory did not entirely depend on the availability of a label, as reflected in their memory performance for nonlocal birds (Figure 2, left), whose names were largely unknown.

To examine how this pattern of results may relate to changes in response criterion, we next calculated criterion values (*c*) within local and nonlocal sets and submitted these values to a 2 × 2 ANOVA with factors of group and region. This analysis revealed a significant group × region interaction ($F(1,84) = 4.638$, $p = 0.034$, $\eta^2_G = 0.013$), a significant effect of region ($F(1,84) = 6.409$, $p = 0.018$, $\eta^2_G = 0.018$) but no effect of group ($F(1,84) = 0.051$, $p = 0.821$, $\eta^2_G = 0.0005$). Notably, although no main effect of group was found for criterion measures, the interaction

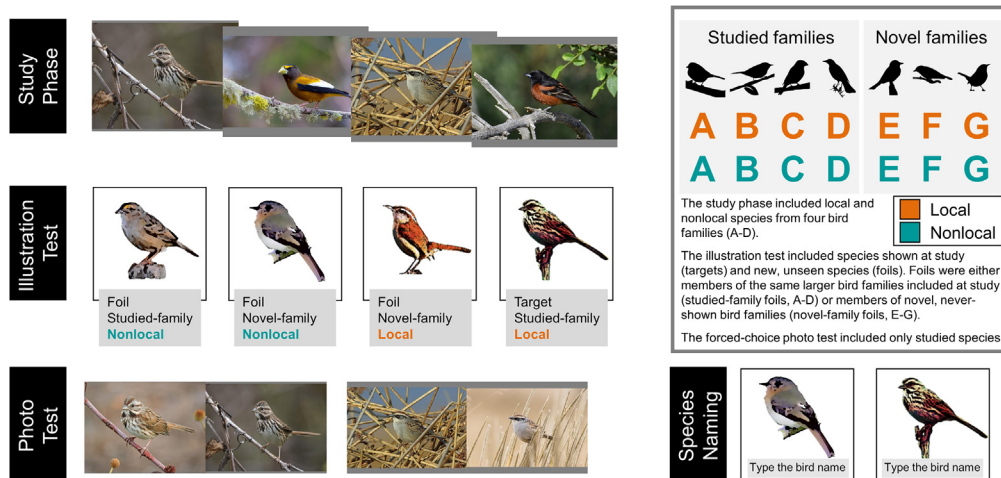


Figure 1. Schematic overview

Study Phase. Participants saw photographs of bird species from four different bird families, each of which contained species that were found in the region where expert participants lived (local) as well as the same number of species from other parts of the world (nonlocal). **Illustration test.** Participants decided whether or not illustrations matched a species shown in the study phase. Illustrations included species shown at study (targets), illustrations of new species belonging to the same bird families shown at encoding (Studied-family foils, families A–D), and illustrations of new species from novel bird families not included during study (Novel-family foils, families E–G). **Photo test.** Participants viewed pairs of photos depicting the same bird species (families A–D) and decided which photo version appeared in the initial study phase. **Species naming test.** All bird species (targets and foils, families A–G) were shown, one at a time, and participants were given a chance to identify the bird by typing its name. Note: In the figure, copyrighted field guide illustrations used in the study have been replaced with open-source photographs modified for artistic effect.

effect was produced by a reduction in criterion for local birds within experts ($t(40) = 2.690, p = 0.01$). Thus, although experts show higher discriminability for local birds, they nonetheless show a more liberal criterion for responding “yes” compared with nonlocal bird responses.

Influence of trial type

We next examined whether the memory benefit for local species in experts arose primarily through increased detection of repeated targets, increased rejection of foils, or both. Although recognition should be greater for well-known species, it is also possible that prior exposure to local birds might lead to an increase in false alarms for semantically familiar items that are new in an episodic context.

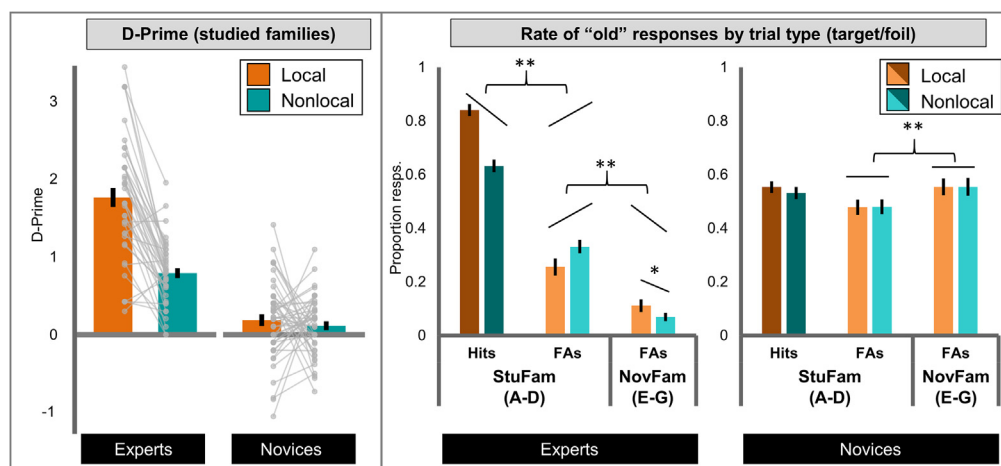


Figure 2. Illustration memory performance

Overall memory discriminability (d-prime) by group and region shows a significant interaction (left). Response rates to targets (hit rate) and foils (false alarm rate, FAs) from studied bird families (StuFam; families A–D) and novel bird families (NovFam; families E–G) (middle/right). Relative to nonlocal species, experts are more accurate for both targets and studied-family foils, although this improvement is more pronounced in the former, producing an interaction. In experts (but not novices), novel-family false alarms are lower than studied-family false alarms overall, but show the opposite pattern with respect to local/nonlocal birds, producing an interaction. Error bars reflect SEM. * = $p < 0.05$; ** = $p < 0.01$.

A mixed-effects regression on trialwise accuracy included factors of group (experts vs. novices), region (local vs. nonlocal), and trial type (target vs. studied-family foil). Findings of a significant three-way interaction (estimate = 0.724, $z = 3.093$; SE = 0.234; $p = 0.002$) were followed by tests of the region \times trial type interaction within each participant group (experts: estimate = 0.773, SE = 0.180, $z = 4.307$, $p_{\text{Holm}} < 0.001$; novices: estimate = 0.049, SE = 0.150, $z = 0.328$, $p_{\text{Holm}} = 0.743$). The significant interaction within experts was the product of disproportionately increased accuracy for target trials in the local relative to nonlocal condition (local > nonlocal target contrast: estimate = 1.143, SE = 0.110, $z = 10.370$, $p_{\text{Holm}} < 0.001$) compared to a smaller (but still significant) increase in studied-family foil accuracy (local > nonlocal foil contrast; estimate = 0.369, SE = 0.142, $z = 2.604$, $p_{\text{Holm}} = 0.0184$) (Figure 2, middle: experts). Prior knowledge of individual species therefore preferentially increased hit rate and also conferred a smaller benefit in correctly rejecting local bird foils.

Trialwise reaction times for correct trials were also examined in a similar fashion to the regression on trialwise accuracy. The three-way interaction was not significant ($p > 0.1$), but a significant group by region interaction (estimate = -0.239 , SE = 0.116, $t = -2.065$, $p = 0.039$) indicated that the effect of region on RTs differed between experts and novices. Contrasts revealed that experts had faster correct responses for local vs. nonlocal trials for both hits (estimate = -0.347 , SE = 0.089, $z = -3.908$, $p_{\text{Holm}} < 0.001$) and correct rejections (estimate = -0.443 , SE = 0.127, $z = -3.485$, $p_{\text{Holm}} = 0.002$), with no difference for either type of trial within novices ($p_{\text{Holm}} > 0.1$). In addition, significant main effects of region (estimate = -0.275 , SE = 0.058, $t = -4.749$, $p < 0.001$) and trial type (estimate = -0.484 , SE = 0.059, $t = -8.236$, $p < 0.001$) were found, but the main effect of group was not significant (estimate = 0.092, SE = 0.162, $t = 0.566$, $p = 0.573$). Even within correct trials therefore, knowledge of local species speeded responses.

Overlapping influence of species name knowledge and species frequency on memory

The preceding analyses suggest that more specific knowledge (i.e., local vs. nonlocal birds) improves memory discriminability but may provide a smaller benefit to lure detection. One potential explanation for this finding is that the semantic familiarity of some local items is conflated with episodic familiarity. To explore this possibility, we analyzed memory for each item with respect to naming accuracy (from species naming test) as well as a continuous value of species prevalence that reflected how common a given species is in the local environment (eBird frequency; see STAR Methods). Naming accuracy served as a conservative estimate for subcategory knowledge and was expected to have a strong relationship with memory. Variation in eBird frequency was examined to test whether increased exposure to or fluency with environmentally prevalent species might influence expert memory.

Within experts, a regression of trialwise local item recognition accuracy was conducted with name knowledge (species naming test: correct vs. incorrect), trial type (target vs. foil), and species prevalence (eBird score) as predictors. A significant three-way interaction was observed (estimate = -4.551 , SE = 1.677, $z = -2.714$, $p = 0.007$), with species prevalence having differing effects on target vs. foil accuracy at different levels of name knowledge. An examination of slopes revealed no relationship between species prevalence and memory accuracy for birds that could be named ($ps > 0.1$). However, a significant relationship was found in the absence of name knowledge. Specifically, higher environmental prevalence was associated with significantly lower accuracy on foils (i.e., increased false alarms) (trend = -2.176 , 95% CI [-4.177 -0.176], $z = -2.132$, $p = 0.033$) and had a positive, non-significant relationship with target accuracy (i.e., hit rate) (trend = 1.623, 95% CI [-0.399 3.645], $z = 1.573$, $p = 0.116$; pairwise contrast: $z = 2.61$; $p_{\text{Holm}} = 0.036$; Figure 3 right). In addition, there was a strong main effect of name knowledge (estimate = 0.954, SE = 0.162, $z = 5.900$, $p < 0.001$; Figure 3 left) and of trial type (estimate = 0.716, SE = 0.154, $z = 4.642$, $p < 0.001$) (all other main effects and interactions non-significant).

Finally, a similar regression examined the influence of species prevalence on memory in novices, collapsing the factor of name knowledge, which was near floor for all participants. No significant interaction or main effects were observed (all $ps > 0.1$; Figure 3 right contains slopes within name unknown trials for comparison with experts).

Overall, these analyses suggest that expert memory is influenced by distinct types of prior exposure. The presence of distinct subcategory representations, reflected in identification of individual species on the species naming test, substantially aided recognition of repeated items and new foils. In the absence of this specific knowledge however, episodic recognition in experts, but not novices, was shaped by the prevalence of concepts in the local environment. Higher environmental frequency increased the perception episodic oldness, driving false recognition of abundant concepts.

Novel family recognition

Having examined recognition for repeated bird families, we next examined whether novel-family foils were categorically more differentiable than studied-family counterparts, and whether novel-family foil detection was contingent upon prior knowledge value (local vs. nonlocal status).

A three-way ANOVA on false alarm rate was conducted, with factors of group (experts vs. novices), region (local vs. nonlocal), and foil type (studied-family vs. novel-family). A significant three-way interaction was observed ($F(1,84) = 4.102$, $p = 0.046$, $\eta^2_G = 0.006$) as well as significant two-way interactions of group \times foil type ($F(1,84) = 74.998$, $p < 0.001$, $\eta^2_G = 0.128$) and region \times foil type ($F(1,84) = 5.620$, $p = 0.020$, $\eta^2_G = 0.008$). Examining the two-way interactions within each group revealed a significant effect of region \times foil type for experts ($F(1,40) = 9.067$, $p = 0.004$, $\eta^2_G = 0.035$) but not for novices ($F(1,44) = 0.064$, $p = 0.802$, $\eta^2_G = 0.0001$). Furthermore, experts showed a simple main effect of foil type ($F(1,40) = 104.794$, $p < 0.001$, $\eta^2_G = 0.299$) whereas novices showed a simple main effect of foil type in the opposite direction ($F(1,40) = 9.175$, $p = 0.004$, $\eta^2_G = 0.033$). These main effects arose because, in contrast to novices, experts could more readily reject foils from overarching bird families that had not been previously studied, while novices showed the reversed pattern (Figure 2).

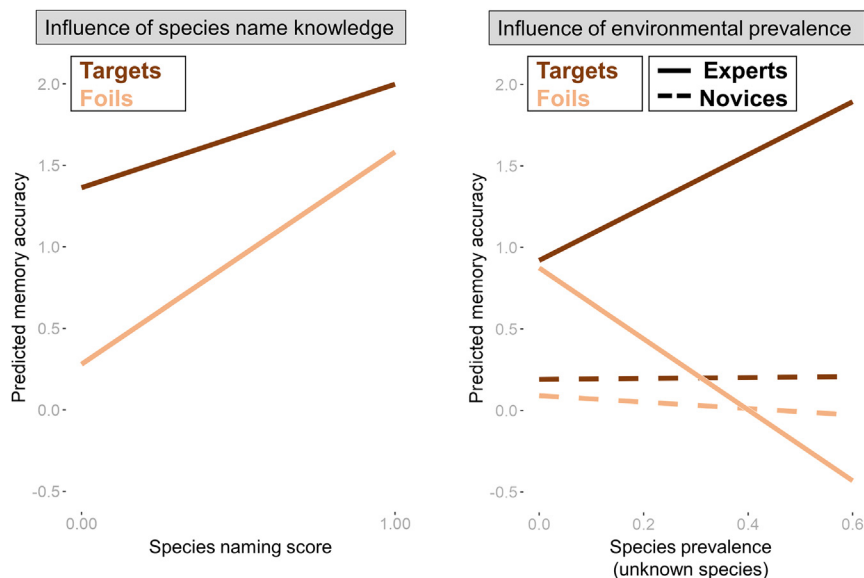


Figure 3. Influence of two forms of pre-experimental exposure on memory

Simple slope plots from regression relating studied-family illustration test memory accuracy to name knowledge (from Species naming test), experts only (left). Species name knowledge is associated with increased illustration test trial accuracy for both targets and foils. Influence of species prevalence (eBird score) within unknown species, experts and novices (right). Within experts, species prevalence is associated with numerically higher memory for targets but significantly lower memory for foils (i.e., increased false alarms). The y axis represents memory outcome accuracy on the logit scale.

Within experts, the interaction of region \times foil type was further examined by testing the difference between local and nonlocal false alarm rate for studied-family and novel-family foils. Notably, although we had previously observed that false alarm rates were lower for local compared to nonlocal studied-family foils (influence of trial type, see previously), the opposite was true for novel-family foils ($t(40) = 2.44, p = 0.019, D = 0.38$). Local species foils were therefore easier to reject than nonlocal foils within studied families but harder to reject within novel families. Because novel family items were generally correctly identified as episodically “new,” the presence of semantically familiar (i.e., local) items in this novel family category may have increased perceived episodic oldness. By contrast, studied-family targets and foils likely required more careful discrimination between intrafamily members. Indeed, an examination of mean RT for correct rejections found that expert responses were substantially slower for studied-family foils (mean = 2.46 s, SE = 0.13 s) than novel-family counterparts (mean = 1.64 s, SE = 0.10 s; difference: $t(40) = 7.856, p_{\text{Bonf}} < 0.001$), whereas no significant differences was found in novices (studied-family mean = 2.34 s, SE = 0.15; novel-family foil mean = 2.53 s, SE = 0.19 s; difference: $t(45) = -1.707, p_{\text{Bonf}} = 0.190$).

As a final step, we examined whether species prevalence of novel-family foils influenced memory accuracy in experts. This regression, run across all novel-family foils, provided converging evidence with findings from the studied-family data: higher environmental frequency was associated with decreased accuracy—i.e., increased false alarms (estimate = $-2.855, SE = 1.0314, z = -2.768, p = 0.006$). A corresponding analysis in novices was not significant (estimate = 0.761, SE = 0.624, $z = 1.219, p = 0.223$). Therefore, even within local novel-family foils, more frequent birds were more likely to elicit false alarms.

These analyses of novel-family foils parallel the increase in false alarms observed for higher frequency studied-family birds. Thus, when prior exposure has not led to specific subcategory labels (name unknown local species), or when all items share the same categorical status (novel families), the use of continuous measures like environmental prevalence suggests that increased prior exposure can be mistaken for episodic familiarity.

Photo memory test

In the photo memory test, trials consisted of a study phase photograph and a similar distracter exemplar photograph of the same bird species. Data from the photo test were first analyzed with respect to participant group and bird region and then related to trialwise measures of prior knowledge.

Overall accuracy and RTs

An initial assessment of the photo memory test was conducted using a logistic regression with fixed effects of group (experts vs. novices) and region (local vs. nonlocal), and trialwise 2AFC accuracy as the outcome variable. The interaction of group and region was not significant ($z = 0.128, p = 0.898$) but there were significant effects of group (estimate = 0.728, SE = 0.101, $z = 7.221, p < 0.001$), produced by higher accuracy with experts, and of region (estimate = 0.189, SE = 0.071, $z = 2.654, p = 0.008$) (Figure 4, left), produced by higher accuracy for local

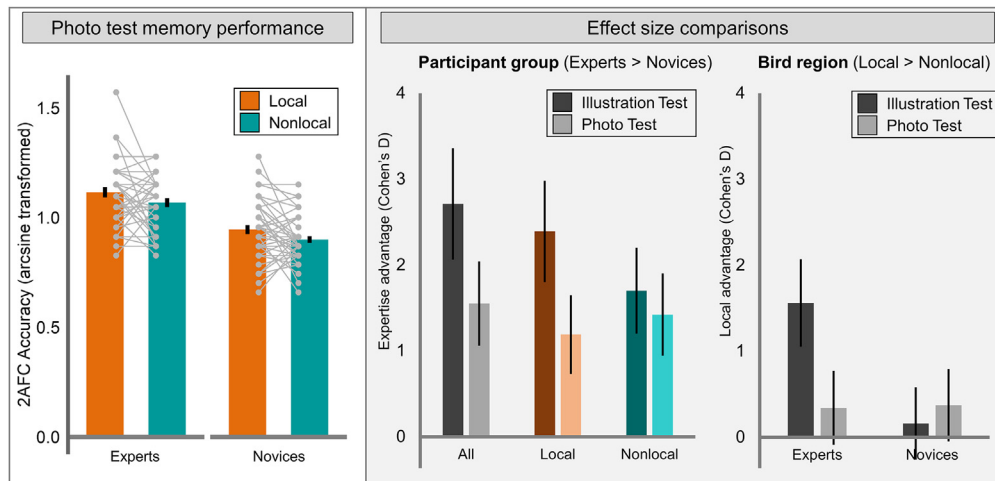


Figure 4. Photo memory and illustration vs. photo memory comparison

Photo test memory performance, error bars reflect SEM (left). Comparison of effect size for the expertise advantage (experts > novices) in the illustration and photo memory tests (center) and for the local species advantage (local > nonlocal) within each test (right). Metrics for the illustration test include studied families only; error bars reflect effect size confidence interval.

birds. This pattern of findings differs markedly from the illustration memory test, where a strong group \times region interaction was produced by greater memory for local vs. nonlocal birds within experts.

Reaction times for correct trials were also examined to determine whether region had a differential effect on speed of responses. The group by region interaction was not significant (estimate = -0.347 , SE = 0.210 , $t = -1.650$, $p = 0.10$), nor were either main effect ($ps > 0.1$).

Photo memory and itemwise measures of knowledge

Given the influence of name knowledge and bird frequency on illustration test accuracy, we also explored whether these factors influenced photo memory accuracy. Similar to the illustration test analysis, a logistic regression on local trial accuracy within experts was conducted, with name knowledge (species naming test: correct vs. incorrect) and species prevalence (eBird score) as fixed effects. The interaction was not significant (estimate = 0.233 , SE = 0.989 , $z = 0.235$, $p = 0.814$). The main effect of name knowledge was significant (estimate = 0.549 , SE = 0.194 , $z = 2.834$, $p = 0.005$) but not the main effect of species prevalence (estimate = -0.102 , SE = 0.492 , $z = -0.207$, $p = 0.836$). This analysis suggests that, although expert photo memory was not better for the local condition overall, it was improved for those species that were best known, as indexed by naming accuracy.

Comparisons between illustration and 2AFC photo memory

Although accuracy on the illustration and photo memory tests cannot be directly compared due to inherent differences in task design, we examined the effect sizes on each test for contrasts between the two participant groups (experts > novices, i.e., the expertise advantage) (Figure 4, center) and contrasts between birds from each region (local > nonlocal, i.e., the local species advantage) (Figure 4, right). Comparisons of illustration test performance were conducted across all studied-family trials using d-prime measures. Comparisons of photo test performance were conducted with arcsine adjusted 2AFC photo accuracy. Plots of effect size emphasize the extent to which the expertise advantage predominates on the illustration test (effect size confidence intervals do not overlap between illustration and photo tests for group contrasts), despite being seen across both local and nonlocal birds on both tests. The within-subject memory advantage for local species over their nonlocal counterparts was only found for experts, where it was exclusive to illustration memory. These comparisons of effect size underscore how prior knowledge at both the group (experts > novices) and item level (local > nonlocal) contribute most strongly to memory judgments on the illustration test, which require flexibility in representational format.

To examine the relationship between the two memory tests at the level of individual trials, a logistic regression was conducted in which factors of group, illustration memory accuracy, and region served as predictors for 2AFC photo memory accuracy. The relationship between memory accuracy between the two tests provides a sense of the interdependencies at a trialwise level—i.e., whether recognition of species in illustration format (illustration test accuracy) bears on later discrimination of studied photograph version (photo memory accuracy). It should be noted however that only target illustration memory can be examined, as there were no 2AFC trials corresponding to species shown as foils on the illustration test. Results from this regression showed no significant three-way interaction, and two-way interactions were also not significant ($ps > 0.1$), except for the effect of group by illustration memory (estimate = 0.324 ; SE = 0.164 ; $z = 2.01$, $p = 0.045$). No other significant effects were observed except for the previously discussed main effect effects of group and region. These results suggest that memory for different formats of the same species concept are largely independent from one another and are consistent with past research probing memory for the same items using different tests as well as the divergent pattern of results for the two tests.

DISCUSSION

Prior knowledge influences memory, but its contributions depend on both the type of knowledge and the type of memory. In the present study, bird species knowledge aided episodic recognition of bird illustrations in experts, but a separate pattern characterized prior exposure in the absence of species name knowledge. In experts but not novices, false alarms increased for local birds with higher environmental prevalence. Prior experience therefore can produce divergent effects on memory depending on what form it takes. In contrast to this illustration test, experts showed a smaller overall advantage (vs. novices) on a photo test for perceptual details and little advantage for local vs. nonlocal species. These results illustrate the contingent influence that experience has on memory. Prior knowledge strongly supports memory judgments that require abstraction (illustration test), particularly when specific subcategory concepts are present. At the same time, in the absence of specific knowledge, conceptual fluency from exposure may also make items seem old in the episodic context. Memory for perceptual details (photo test) benefits less from prior knowledge at the group (experts vs. novices) and individual item (species) level.

The illustration memory test required participants to translate information across picture formats, thereby favoring the ability to abstract information and maintain flexible representations. Unsurprisingly therefore, memory in experts was closely associated with species identification. In comparison with novices, experts also showed better memory for unknown nonlocal species, consistent with an ability to identify meaningful features and organize information in a manner that resists perceptual interference.^{6,21–23} However, knowledge was somewhat less beneficial for discriminating between local foils, potentially because the semantic “oldness” of some local items led to false alarms (for further consideration of prior knowledge in signal detection, see Bird et al.²⁴; Dobbins and Kroll;²⁵ Stenberg et al;¹⁹). This finding highlights the possibility that more subtle effects of prior exposure on recognition may be masked by the strong positive relationship between semantic and episodic memory.

Analysis of species prevalence revealed that, excluding the best-known items, environmentally common species were most likely to elicit false alarms in experts. No comparable effect was found in novices. Along similar lines, experts showed a small but significant increase in novel family false alarms for local (by definition more prevalent) vs. nonlocal species. Despite the subtle influence of species prevalence compared to other dimensions of prior knowledge (e.g., experts vs. novices, name known vs. name unknown), the conflation of episodic and semantic signals during recognition echoes a diverse literature on conceptual fluency. Conceptual fluency in episodic recognition has been studied through a number of manipulations,²⁶ e.g., through semantically related vs. unrelated primes,^{17,27} perceived meaningfulness in abstract shapes,^{28,29} or variations in prior knowledge about facts.³⁰ This work generally finds that conceptual fluency engenders episodic familiarity. Because novices showed no influence of bird frequency on memory, our results indicate that it is prior exposure through birdwatching or learning birds that increases false alarms, even as these activities enhance memory once species are well known. Given that new concepts must be learned, longitudinal work may be helpful to characterize episodic memory for information as it transitions through different stages of acquisition into semantic knowledge. Our results suggest that concepts at the periphery of established knowledge may be particularly susceptible to fluency-based memory distortion, and suggest incipient learning as a setting in which fluency effects may be even more pronounced.

Whereas the illustration test required discriminating between highly similar species illustrations, the photo memory test instead required discriminating between matched photographs of the same species. The lack of conceptual differences between target and lure images required parsing photograph elements such as background content or bird position. Such aspects are generally non-diagnostic for species identification and are likely less resonant with prior knowledge. This alignment between memory outcomes and the goal of an expert domain is illustrated in past work with medical professionals. For example, more experienced radiologists had superior memory for abnormal scans but were actually found to forget typical, non-pathological scans more quickly than their less experienced colleagues³¹ (also see Schill et al.³²; Schmidt and Boshuizen³³). In fields like medicine or object recognition, the practical implication of these findings is that acquiring knowledge may lead to adaptive forgetting of irrelevant information as important details are prioritized in memory. The reduced expert advantage for photo memory (vs. illustration memory) follows this pattern wherein memory advantages reflect changes in how domain-relevant material is initially processed.

In another contrast with illustration memory, experts showed no overall advantage for local vs. nonlocal species during photo discrimination, nor were correct responses faster for local species. Along similar lines, studies of mnemonic separation have found that discriminating state changes in objects (e.g., mailbox open vs. closed) is more challenging than discriminating between different exemplars of the same object (mailbox A vs. mailbox B).^{34,35} For even tighter mnemonic judgments, such as distinguishing repeated and mirror-imaged faces, prior knowledge may confer little benefit or even hinder source memory.³⁶ Despite the lack of a local/nonlocal difference in expert photo memory, we did observe a positive influence of species-level name knowledge on this test. Therefore, although subcategory knowledge appears to contribute less strongly to perceptually driven memory, it may continue to play a subtle role in discriminating between different exemplars.^{37,38}

The nature of memory benefits for other areas of expertise likely depend on a number of factors, including the perceptual modalities involved and the organizational structure of the knowledge domain. Our results suggest bird expertise enabled distinct but flexible representations for distinct bird species, but provided less advantage for discriminating intra-species details (photo test). Research in other expert domains (e.g., wine tasting²; musicians-auditory^{39,40}; musicians-motor⁴¹) highlight the range of sensory processing that can be used to support expert memory, oftentimes in scenarios where categorization of discrete concepts is less central to performance than in the current study. In still other areas of expertise, spatiotemporal sequence is found to play a larger role in organizing memory, such as when remembering the unfolding of various games^{42,43} or recalling routes through an environment.^{44–46} The broad scope of these studies reveals the many ways in which prior knowledge influences memory. Rather than merely providing an encyclopedia of accrued factual

information, experience in an area shapes cognitive processes involved in interpreting and manipulating related information, with downstream consequences for memory.

The present study demonstrates how the mnemonic benefits of prior knowledge turn on the type of information required for memory judgments. When the dimensions of discrimination align with information relevant for conceptual organization, experts can rely on generalized, flexible representations to recognize repeated information across shifts in format. A much smaller prior knowledge benefit is seen in memory for perceptual details that are orthogonal to conceptual organization. Notably, cross format illustration memory shows the simultaneous influence of two types of prior exposure in experts—one related to specific subcategory knowledge and the other related to conceptual fluency. The ability to incorporate data from other fields of research to estimate conceptual priors in certain subpopulations presents a new avenue for understanding how different dimensions of pre-experimental exposure influence memory and other cognitive processes.

Limitations of the study

Controlling for affective and motivational influences on cognition is a challenge for nearly all research comparing expert and non-expert groups on tasks similar to those used in the present study. To address this issue, we took efforts to recruit novice participants with prior interest in the current domain, and more critically, focused on within-participant comparisons. Nonetheless, differences related to general interest in materials the study materials must be considered when interpreting results. Another limitation is that the “local” materials set used in this study come from only a single geographical region. Additional, larger-scale research will be required to ensure that patterns observed in these data are broadly generalizable to variation in conceptual knowledge within other settings.

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to and will be fulfilled by the lead contact, Erik Wing (ewing@research.baycrest.org).

Materials availability

Experimental materials consisted of a set of bird photographs and illustrations. Photographs are publically available from the online database of the Macaulay Library at the Cornell Lab of Ornithology. Copyrighted illustrations are available at www.birdsoftheworld.com.

Data and code availability

- Data. De-identified human data for the study include: (1) Illustration test data (2) Photo test data (3) Species naming test data (4) Multiple-choice bird naming test data. These data have been deposited to an OSF repository and are publicly available as of the date of publication. The DOI is listed in the [key resources table](#).
- Code. All original code has been deposited to an OSF repository and is publicly available as of the date of publication. DOIs are listed in the [key resources table](#).
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

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AUTHOR CONTRIBUTIONS

Conceptualization, E.A.W., A.G., and J.D.R.; methodology, E.A.W.; investigation, E.A.W.; writing – original draft, E.A.W.; writing – review and editing, E.A.W., A.G., and J.D.R.; funding acquisition, A.G. and J.D.R.; resources, E.A.W.; supervision, A.G. and J.D.R.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

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

- [KEY RESOURCES TABLE](#)
- [EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS](#)
- [METHOD DETAILS](#)
 - Experimental procedure
 - Experimental materials
- [QUANTIFICATION AND STATISTICAL ANALYSIS](#)
 - Illustration memory test analyses
 - Photo memory analyses
 - Comparison of memory tasks

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Experimental data and code	This paper	OSF: https://osf.io/5kmg8/
Software and algorithms		
R version 1.4.1717	R Foundation for Statistical computing	https://www.r-project.org/

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Eighty-eight participants took part in the study (42 experts and 46 novices). Experts were recruited through postings to regional bird groups such as the Toronto Ornithological Club, Ontario Field Ornithologists and other birding groups in the Lake Ontario region. Novices were recruited from other groups with nature-related interests (e.g., gardening, hiking, geology). Initial division into the two groups was via self-identification, after which we examined accuracy on a separate bird knowledge test to validate group membership and identify outliers. One expert participant was excluded from the analysis due to outlier performance (>2.5 SD below group mean) and one novice was also excluded (>2.5 SD above group mean). After exclusions, the expert group was 70.7% female with an average age of 46.95 years (SD = 15.79). The novice group was 73.3% female with an average age of 46.84 years (SD = 16.16). Mean years of education was 18.13 (SD = 3.16) for experts and 18.3 (SD = 2.48) for novices. Sample size was based on findings from previous work⁶ showing medium to large effect sizes for both within-group memory contrasts (e.g., local > nonlocal recognition) and between group differences in expertise (experts > novices).

Participants disclosed no history of major neurological or psychiatric disorder and gave informed consent via online survey before beginning the experiment. Participants were compensated via online gift card and the study protocol was approved by the Research Ethics Board at Baycrest Hospital.

METHOD DETAILS

Experimental procedure

The online experiment encompassed several discrete section, completed consecutively in the same experimental session.

Study phase

The study phase consisted of 52 bird photographs divided across two blocks. Participants were instructed to pay attention to the images because they would be relevant for a subsequent section, but were not given further details, and no response was required. Photographs were shown for 4s, followed by a 1s fixation inter-trial interval (ITI). Two filler items were included at the beginning and end of each block. Of the remaining 48 species shown at encoding, half were sometimes present in the region where experts lived (local) and half were not (nonlocal, e.g., species found in South America or Eurasia). Local and nonlocal sets each contained birds from the same families, and both family and local/nonlocal status were distributed evenly across the two study blocks (Figure 1, top right for visualization).

Illustration memory test

The illustration memory test followed immediately after the study phase. For each trial, an “old” or “new” response was required depending on whether participants thought the illustration depicted a species shown in the study phase. Illustrations remained on screen until a response was given. All 48 species shown during the study block appeared in illustration form during this test phase along with 48 foils—illustrations of unstudied species. Targets and foils were distributed evenly across four blocks of 24 items. Of these foil species, 24 were species from the same bird families as those shown at encoding (i.e., studied-family foils) and 24 were species from bird families not represented at study (i.e., novel-family foils, also divided evenly between local and nonlocal species). Species old/new status, family old/new status and bird region were all distributed equally within four test blocks. The order of trials within each block was randomized for each participant.

Photograph memory test

The two-alternative forced-choice (2AFC) photograph test followed immediately after the illustration memory test. On each trial, participants saw two photographs, each depicting the same bird species, and were asked to select the one that had been shown during the study phase. Intra-species variation along observable characteristics like bird age, sex and seasonal plumage was matched across target and lure, and could not be used to support retrieval. Photographs remained on the screen until a response was given. This task was composed of two blocks of 24 trials and included only the bird species that had been shown during the initial study phase (Figure 1). Target location (left/right) was

distributed evenly across bird region and family. The version of the photograph that served as the target (vs. paired foil) was randomized across participants.

Species naming test

On each self-paced trial, participants saw an illustration of a bird and were instructed to type the common name of the species in a box below. Participants were instructed to provide as complete a name as possible. Participants were also told that they could guess if they wished but were not encouraged to guess at random. Stimuli included all 96 bird illustrations shown in the illustration memory test (48 studied species from the study phase/photo memory test; 48 foil species from the illustration test) and an additional 16 bird illustrations associated with a separate task, not discussed here. Binary accuracy was scored from a correct answer key that included common spelling variants (e.g., “gray” vs. “grey”) and aliases (alternate/obsolete names).

Multiple-choice bird name test

The multiple-choice bird name test was adapted from Van Gulick et al.⁴⁷ to assess semantic knowledge of local bird species that were independent from the memory tests or the species naming test. Given that both expert and novice groups were expected to include some variation in bird knowledge across participants, performance on this multiple choice test was used to quantify variance and identify outliers within the self-identified groups.

There were 40 self-paced trials, each of which display three similar bird names. One name option corresponded to a local bird species (species in this section did not overlap with species in any other experiment section) and the other two were distracters that retained the same base form with altered descriptors that are often used in other bird names (e.g., target: White-breasted nuthatch; distractors: Yellow-bellied nuthatch, Black-capped nuthatch). Participants were told to select the option they thought was the name of the real bird species. The order of trials and position of the target item within trials was randomized within participant. One trial was excluded from analysis because two name options were plausibly valid, resulting in average accuracy scores calculated across 39 items with a chance accuracy rate of 33.3%.

Experimental materials

Study set bird photographs included 8 sparrows, 8 warblers, 4 blackbirds and 4 finches found in Ontario (local), and the same number of species never present in that region (nonlocal). An additional 24 species (also split evenly into local and nonlocal groups: 4 sparrows, 4 warblers, 2 blackbirds, 2 finches for each), were reserved for use as studied-family foil items in the illustration memory test. The sampling of birds reserved as studied-family foil items was random across participants, with the constraint that these foil species have equivalent bird prevalence (eBird score) distributions to species selected for the study phase. Foils in the illustration memory test also included 24 species from bird families that were not represented at study (novel-family foils: 4 flycatchers, 4 vireos, 4 wrens local to Ontario and the same number of nonlocal species). Bird region (local/nonlocal) and family were distributed evenly across the two study blocks, and the order of trials within each block was randomized across participants.

Bird photographs were collected from the online repository of the Macaulay Library at the Cornell Lab of Ornithology. Illustrations were collected from Birds of the World database.⁴⁸ For each of the 48 local bird species used in the present study, an environmental prevalence score was obtained from eBird, a worldwide database of bird species observations used extensively in bird ecology research.⁴⁹ For a given period of time, this frequency score reflected the percentage of completed observation checklists containing the given species out of all completed checklists for that period. Because some migratory species are common, but only for brief periods of time, bird frequency scores corresponded to the maximum frequency over any one week period, the smallest time bin available in database records. Frequency statistics were generated from the wider Toronto Region from the period of 2017–2018 and were by definition zero for all nonlocal species. Analyses using this metric therefore include only local birds where frequency is nonzero.

QUANTIFICATION AND STATISTICAL ANALYSIS

Illustration memory test analyses

For a broad picture of memory accuracy on the illustration test, memory discriminability (d') was computed from hit rates and studied-family false alarm rates (foils from families A–D, see [Figure 1](#)), using adjustments for extreme values.⁵⁰ Subjectwise d' values were interested into a 2 (group: experts vs. novices) \times 2 (region: local vs. nonlocal) ANOVA using the *statix* package in R. The same approach was used to test differences in response criterion.

Subsequent analyses of illustration test memory separated performance by trial type, and were conducted using mixed effects regressions with the *lme4* package in R.⁵¹ The first logistic regression included group (experts vs. novices), region (local vs. nonlocal), and trial type (target vs. studied-family foil) as fixed effects, with trialwise accuracy as an outcome variable, and random intercepts for each participant. For logistic regressions, results are reported and plotted on the log odds scale. A corresponding linear regression was used to explore reaction time, with the trialwise RT instead of accuracy as the outcome variable. Unless otherwise noted, correction for multiple comparisons within the same model was conducted using the Holm-Bonferroni procedure.

After exploring how memory varied with a coarse division of prior knowledge value (local vs. nonlocal), a following analysis focused on two metrics relating to prior experience at the level of individual species: name knowledge (from species naming test: known vs. unknown) and species prevalence (from the eBird database on environmental frequency; values mean-centered within the local condition). Along with trial

type (target vs. foil), these factors were included in a logistic regression, with trialwise memory accuracy as the outcome variable, as above. After examining simple slopes for species prevalence, all pairwise slope contrasts involving the significant slope (unknown foils) were tested, along with the test of target vs. foil for name known trials (multiple test correction for 4 comparisons). Although the principal aim was to explore memory variation in experts, the similar regression was repeated in novices, collapsing across name knowledge due to near floor performance.

The final analyses of illustration memory examined responses to novel-family foils (families E-G), which were excluded from prior analyses because their response distributions dramatically differed from studied-family foils. This difference was explored in a three-way ANOVA on foil trial accuracy, with factors of group, region, and foil type (studied-family vs. novel-family). Two separate paired t-tests were also conducted to determine differences in the speed of correct rejections of each foil type, within group. In addition, novel-family foil accuracy was examined in relation to bird frequency in a targeted regression that included only the local condition trials (collapsing across name accuracy) within experts.

Photo memory analyses

Analysis of photo memory accuracy was conducted using the same trialwise regression approach, with 2AFC accuracy as the outcome variable. An initial regression explored group (experts vs. novices) and region (local vs. nonlocal) as fixed effects. A corresponding linear regression tested the influence of these factors on correct trial reaction times.

As with illustration memory, a subsequent model focused on local trials in experts, with factors of name knowledge (from [species naming test](#): known vs. unknown) and species prevalence (from eBird database on environmental frequency; values mean-centered within local condition).

Comparison of memory tasks

Comparison between illustration and photo memory tests was first done by examining the effect size of the group difference (experts vs. controls, i.e., the expertise advantage), calculated separately for local and nonlocal conditions, as well as across all trial. Calculations of effect size were conducted using the *effectsize* package in R⁵² and confidence intervals were estimated using the noncentrality parameter method. For the illustration test, effect size was based on measures of d-prime from studied-family trials, discussed above. For photo memory, effect size was based on arcsine adjusted 2AFC photo accuracy. In addition to group differences, the effect size of the within-subjects advantage for local vs. nonlocal species was also calculated.