

## Episodic-like memory in wild free-living blue tits and great tits

### Highlights

- Wild blue tits and great tits were tested with two episodic-like memory tasks
- Computerized feeders manipulated foraging experiences at an individual level
- Birds recalled what happened, where, and when, as well as incidental information
- Flexible memory systems may enable generalist foragers to exploit patchy resources

### Authors

James R. Davies, Lasse S. Keuneke,  
Nicola S. Clayton,  
Gabrielle L. Davidson

### Correspondence

jd940@cam.ac.uk (J.R.D.),  
gabrielle.davidson@uea.ac.uk (G.L.D.)

### In brief

Davies et al. show evidence for episodic-like memory in wild blue tits and great tits across two different tasks using automated, computerized feeders. These birds can recall what occurred, where, and how long ago. Additionally, they can recall incidentally encoded spatial information, and juveniles, but not adults, can recall incidentally encoded visual information.



## Article

# Episodic-like memory in wild free-living blue tits and great tits

James R. Davies,<sup>1,4,\*</sup> Lasse S. Keuneke,<sup>1,2</sup> Nicola S. Clayton,<sup>1</sup> and Gabrielle L. Davidson<sup>1,3,\*</sup><sup>1</sup>Department of Psychology, University of Cambridge, Cambridge CB2 3EB, UK<sup>2</sup>Institute for Experimental Epileptology and Cognition Research, University of Bonn, Bonn 53127, Germany<sup>3</sup>School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK<sup>4</sup>Lead contact\*Correspondence: [jd940@cam.ac.uk](mailto:jd940@cam.ac.uk) (J.R.D.), [gabrielle.davidson@uea.ac.uk](mailto:gabrielle.davidson@uea.ac.uk) (G.L.D.)<https://doi.org/10.1016/j.cub.2024.06.029>**SUMMARY**

Episodic-like memory in non-human animals represents the behavioral characteristics of human episodic memory—the ability to mentally travel backward in time to “re-live” past experiences. A focus on traditional model species of episodic-like memory may overlook taxa possessing this cognitive ability and consequently its evolution across species. Experiments conducted in the wild have the potential to broaden the scope of episodic-like memory research under the natural conditions in which they evolved. We combine two distinct yet complementary episodic-like memory tasks (the what-where-when memory and incidental encoding paradigms), each targeting a different aspect of human episodic memory, namely the content (what-where-when) and process (incidental encoding), to comprehensively test the memory abilities of wild, free-living, non-caching blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*). Automated feeders with custom-built programs allowed for experimental manipulation of spatiotemporal experiences on an individual-level basis. In the what-where-when memory experiment, after learning individualized temporal feeder rules, the birds demonstrated their ability to recall the “what” (food type), “where” (feeder location), and “when” (time since their initial visit of the day) of previous foraging experiences. In the incidental encoding experiment, the birds showed that they were able to encode and recall incidental spatial information regarding previous foraging experiences (“where” test), and juveniles, but not adults, were also able to recall incidentally encoded visual information (“which” test). Consequently, this study presents multiple lines of converging evidence for episodic-like memory in a wild population of generalist foragers, suggesting that episodic-like memory may be more taxonomically widespread than previously assumed.

**INTRODUCTION**

Mental time travel is the ability to travel through personal subjective time, reliving memories of past experiences, as well as imagining possible future scenarios. Episodic memory, the structural foundation of mental time travel,<sup>1</sup> is the long term-declarative memory system that characteristically involves the conscious recollection of personally experienced events.<sup>2,3</sup> Within declarative memory, episodic memory is considered to be distinct from semantic memory, which concerns the encoding and recall of factual information that critically does not involve a subjective experience during recall.<sup>2</sup>

Episodic memory is thought by many psychologists to be uniquely human<sup>4–9</sup> (but see Corballis<sup>10</sup> and Boeckle et al.<sup>11</sup>). Tulving and Markowitsch<sup>5</sup> argue that although many non-human animals exhibit a sensitive and sophisticated semantic knowledge of their environment, they cannot consciously recall and re-live specific past experiences in the same way as humans. However, because evidence for episodic recall in humans is centered around language-based reports, and with there being no agreed upon non-linguistic behavioral markers of consciousness,<sup>12</sup> it is potentially impossible to ascertain whether non-

human animals have true episodic memory accompanied by its phenomenological components. That said, Tulving’s original definition of episodic memory<sup>2</sup> states that it “receives and stores information about temporally dated episodes or events and temporal-spatial relations among these events” (p. 385). Using this definition, Clayton and colleagues<sup>13</sup> argue that the simultaneous retrieval and integration of information about the “what” and “when” of unique experiences (temporally dated experiences) and “where” they occurred (temporal-spatial relations) can be demonstrated in animals through their behavior in experimental tasks. In the absence of evidence for the associated conscious experiences during recall, this ability is termed “episodic-like memory.”<sup>14</sup>

Over a series of seminal studies, scrub-jays (*Aphelocoma californica*) have fulfilled the criteria for episodic-like memory through the “what-where-when memory” paradigm.<sup>14–19</sup> As jays store non-perishable foods (e.g., nuts) and perishable foods (e.g., insect larvae) for future consumption, these birds remember the contents, location, and timing of their caches and therefore recover foods before they become inedible.<sup>14,20</sup> In utilizing food items that decay at different rates, these experiments demonstrate that the jays, when recovering trial-unique



caches after varying retention intervals, are recalling integrated representations of the what (food type), where (cache location), and when (time of caching relative to retrieval) information associated with each cache site and use these memories flexibly to dictate their search behavior. This what-where-when memory paradigm has since been adapted to investigate episodic-like memory in animals across a variety of taxa. Rodents,<sup>21–32</sup> non-human primates,<sup>33,34</sup> dogs,<sup>35</sup> other corvids,<sup>36</sup> chickadees,<sup>37</sup> and cephalopods,<sup>38,39</sup> but not pigeons,<sup>40,41</sup> have all passed variations of the what-where-when paradigm but in other instances have failed (apes,<sup>42,43</sup> monkeys,<sup>44</sup> corvids,<sup>45</sup> and chickadees<sup>37</sup>).

In addition to holding information about the what, where, and when of events, another characteristic of human episodic memory is that when we recall a particular experience, we are able to retrieve information associated with the event that was inconsequential to our needs, thoughts, or desires at the time of encoding. Although this information held no relevance at the time and was not marked as important enough to explicitly encode into memory, we are able to recall this “incidental” information as it is automatically encoded during the event and subsequently retained as part of the complete memory.<sup>46</sup> Accordingly, the “incidental encoding and unexpected question” paradigm<sup>47</sup> has been developed as an alternative methodology to test episodic-like memory, by unexpectedly asking subjects to recall incidental information about a specific event. Because the memory tests are unexpected to the subjects, they do not have the opportunity to learn that any specific information within an “encoding event” will subsequently become useful when attempting to solve a later memory test (as is the case with other episodic-like memory paradigms<sup>48</sup>). Consequently, if an animal is able to use information that held no significance at the time of encoding to solve a subsequent memory test, this suggests a capacity to encode and recall incidental information and an ability to replay, target, and access this information within the event representation<sup>49–52</sup>; indicative of human episodic memory.<sup>53</sup> Since its emergence,<sup>47</sup> the incidental encoding and unexpected question paradigm has been used to explore episodic-like memory across multiple non-human animal groups, with evidence of incidental encoding in rats,<sup>32,50,54,55</sup> dogs,<sup>56–58</sup> cats,<sup>59</sup> corvids,<sup>49</sup> pigeons,<sup>47,60,61</sup> and dolphins.<sup>53</sup>

Each of these methodologies target a distinct aspect of the human episodic memory system.<sup>48,51,62</sup> The what-where-when memory paradigm tests for the individual components of episodic memory content (i.e., factual, spatial, and temporal details) and assesses whether a subject can recall and use certain information in accordance with the passage of time, whereas the incidental encoding paradigm tests whether subjects are able to recall information that could only have been encoded in certain contexts using processes associated with human episodic memory (i.e., the automatic encoding of incidental information). Any single approach to assess episodic-like memory is arguably limited because evidence is based on the exclusion of alternative non-episodic solutions,<sup>51</sup> rather than proof of episodic-like memory per se. By contrast, if multiple methodological approaches are tested together, probing both the contents and processes of episodic-like memory, it is improbable that these experiments will lead to the false appearance of episodic-like memory through the same methodological failures and will build a more holistic picture of a species’ episodic-like memory

capability (as, for instance, pigeons fail what-where-when tests<sup>40,41</sup> but pass incidental encoding tests,<sup>47,60,61</sup> perhaps suggesting that their episodic-like memory abilities are limited). Here, we provide a multi-faceted assessment of episodic-like memory to accurately model the different traits of human episodic memory, by combining multiple, converging lines of evidence utilizing different paradigms together.<sup>48,63</sup>

Observations of episodic-like memory may be most likely in species where it is predicted to be adaptive.<sup>9,13,20,64,65</sup> Food-hoarding birds (predominantly corvids) are a model for episodic-like memory because they must recall the temporal characteristics of caching locations and do this flexibly in accordance with social interactions.<sup>14–19,36,37,49,66</sup> Other animals, including non-human primates,<sup>33,34</sup> pigeons,<sup>47,60,61</sup> dogs,<sup>35,56–58</sup> rodents,<sup>21–32,50,54,55</sup> cuttlefish,<sup>38,39</sup> and, more recently, dolphins<sup>53</sup> also show evidence for episodic-like memory. Therefore, episodic-like memory is likely more taxonomically widespread than previously assumed, and understanding the evolution of its contents and processes requires modifying experimental paradigms to target additional taxonomic groups. We tested episodic-like memory in two species of Paridae, blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*). These birds form mixed species winter flocks and do not cache food, rather they are opportunistic foragers that feed on a wide range of food types, including insects, beechmast, and provisions from bird feeders.<sup>67</sup> To maximize opportunistic foraging efficiency while minimizing the risk of predation and competition, these birds may benefit from a memory system that allows them to encode ecological information during a single experience (e.g., food availability or recent weather conditions) and recall different details regarding this experience (e.g., what was experienced, where, and how long ago, as well as any associated incidental information). Episodic-like memory would therefore benefit a foraging generalist species because it permits flexible decision making based on rapidly acquired information without the need for prolonged learning. We tested birds in the wild to capture their natural behavior in an environment that reflects the conditions under which cognitive abilities evolved and arguably enables a larger representation of the population,<sup>68</sup> while minimizing welfare concerns because birds can freely engage and disengage from the task. To date, evidence for episodic-like memory in the wild is absent from the literature,<sup>48</sup> in part because of the logistical challenges associated with controlling for non-sequential time-of-day cues and presenting subjects with trial-unique elements necessary to distinguish episodic-like mechanisms from non-episodic alternatives.<sup>69</sup>

To accurately test episodic-like memory in the wild, blue tits and great tits were fitted with passive integrative transponder (PIT) tags, and memory tests were conducted using computerized radiofrequency identification (RFID) feeders to detect PIT tags (Figure 1). Custom-built programs released (or did not release) food through an electronic door, enabling different experimental conditions. This included a time component assigned to different feeders and, crucially, on an individual-basis, thus allowing for experimental manipulations that controlled for potential social and circadian rhythm confounds. Blue tits and great tits form loose fission-fusion, mixed species flocks of variable size and composition during winter<sup>70</sup> and, therefore, visited feeders that were positioned throughout the woodland at different times of day, allowing for participation in trial-unique



**Figure 1. The automated, computerized RFID feeders**

(A) The feeders set up in a triangle array (each 2 m apart) within surrounding cover.

(B) A close up of a feeder, showing the (covered) food container, electronic door, and RFID perch. When a bird lands on the perch, its unique passive integrative transponder (PIT) tag is read, and custom-built programs release (or do not release) food through an electronic door, according to experimental rules assigned to that individual.

tests—a hallmark of episodic-like memory test designs.<sup>14</sup> These features allowed us to adapt two well-established but methodically dissimilar episodic-like memory paradigms<sup>48</sup> (what-where-when memory and incidental encoding) and implement them in the field to comprehensively test wild birds' recall for personal, unique events in their natural environment.

## RESULTS

### Blue tits and great tits pass the what-where-when memory test

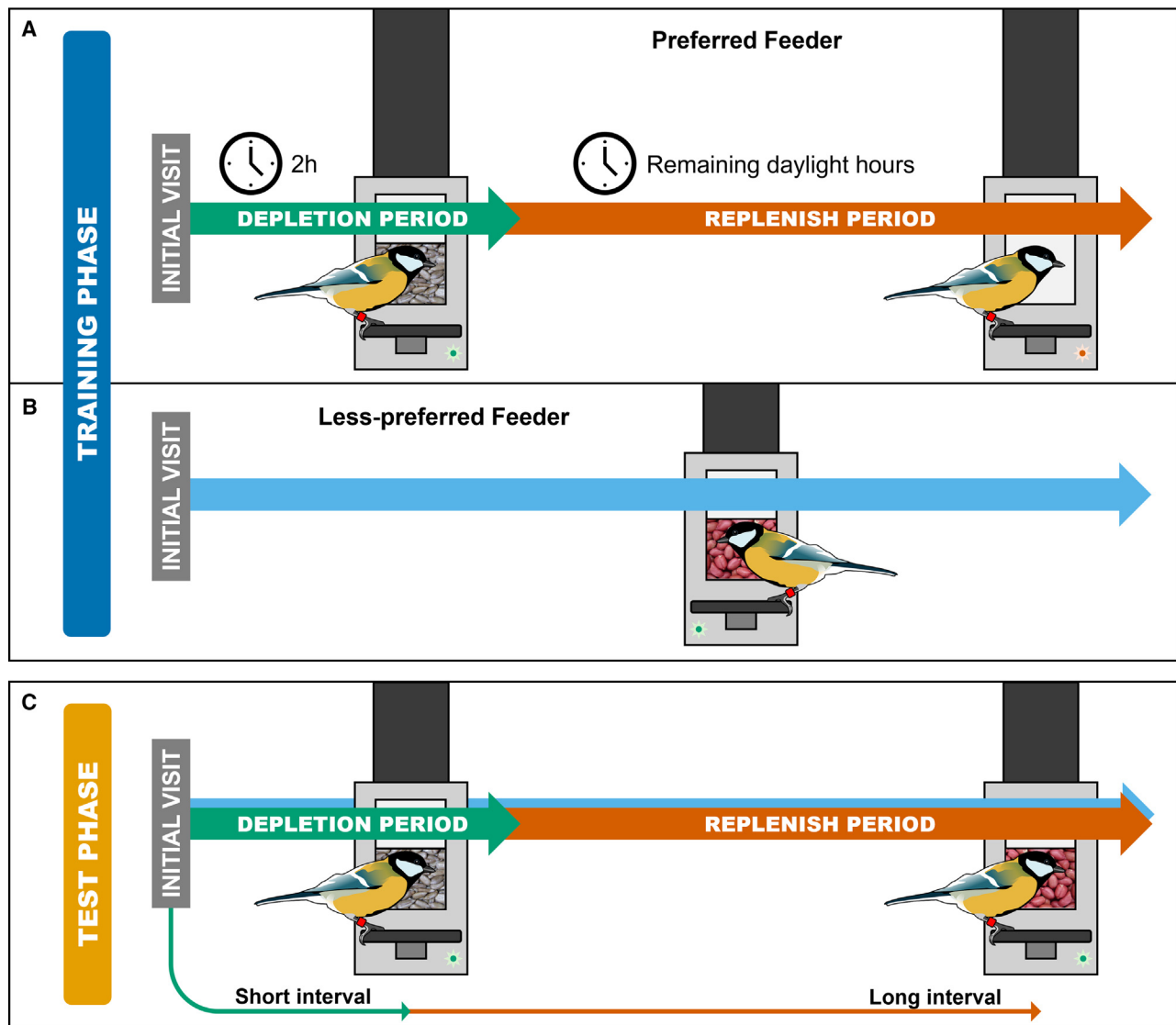
To assess what-where-when memory in these birds, we adapted Clayton and Dickinson's<sup>14</sup> study design for use in the field with non-caching species. In this design, food items of different preferences and degradation rates are used to test whether subjects can keep track of what food is hidden where, in relation to when they had previously interacted with it. We altered the design to simulate a realistic foraging scenario in which two food items, sunflower seeds (preferred) and peanut pieces (less-preferred) (see STAR Methods for food preference test details), had unique depletion and replenishment rates. The birds were first trained to learn the temporal feeder rules in a fixed location. When an individual was first detected on the preferred feeder, the "selective" RFID feeder (NatureCounters.com) triggered a 2-h "depletion period" for that individual. In other words, the feeder was only available to an individual for 2 h, after which point the "replenish period" began and the feeder door remained closed for that individual until the following day (Figure 2A). By contrast, the less-preferred and control feeders (containing no food) always remained accessible to any PIT tagged bird that foraged at them (Figure 2B). Consequently, the birds had access to all feeders during the depletion phase but, crucially, only the less-preferred and control feeders during the replenish phase. All feeder contents were not visible; the items could only be seen through a small door opening if the bird had (successfully) accessed a feeder. Following Clayton and Dickinson,<sup>14</sup> we recorded two types of choices based on the time that had elapsed since a bird's initial visit (triggering their depletion period): "short interval choice," when the preferred food was available (i.e.,

during the depletion period), and "long interval choice": when the preferred food was unavailable (i.e., during the replenish period) (Figure 2C). If birds used what-where-when memory at test (when the feeders were set up in trial-unique locations and compositions), they should choose the less-preferred feeder more after long intervals (during the replenish period) than after short intervals (during the depletion period), thus showing a relative change in preference as observed in comparable episodic-like memory studies.<sup>33,37</sup> Only a bird's first choice after each interval was counted in the analysis, ensuring that their critical choice regarding which feeder to visit was based on a memory of their initial visit of the day, rather than a reaction to a non-rewarding feeder (i.e., a win-stay/lose-shift strategy). Furthermore, to ensure that the birds were informed in their choices (i.e., on food locations across feeder arrays), they had to visit at least one other feeder alongside their visits to the preferred feeder during their initial visit.

In line with passing the what-where-when memory test, the birds' first choices to the less-preferred food were significantly higher after long intervals (i.e., when the preferred food was unavailable), compared with short intervals (i.e., when the preferred food was available) ( $z = -2.55, p = 0.0107$ , estimate =  $-0.914$ , SE = 0.358; Figure 3). There was no effect of species ( $z = -0.877, p = 0.380$ , estimate =  $-0.405$ , SE = 0.462) or age ( $z = -1.10, p = 0.270$ , estimate =  $-0.472$ , SE = 0.428).

### Birds pass incidental encoding tests for "where", and juveniles pass "which"

To assess the ability of the birds to encode, recall, and utilize incidental information in an unexpected memory test, we implemented an incidental encoding test using the same selective feeders in the wild, following an established protocol originally developed in a lab-based context.<sup>53</sup> Because the birds may recall incidentally encoded information regarding both spatial and visual cues in their natural environment, we tested them on their ability to recall incidental details of the feeders in two separate tests: "where" (the spatial position of the feeders) and "which" (the visual characteristics of the feeders). In where tests, the feeders were spatially arranged in a triangle array ("triangle" condition) or linear array ("linear" condition) (Figures 4A and 4B) and thus had distinctive spatial positions. In which tests, each feeder was characterized by a distinctive and unique color ("color" condition) or pattern ("pattern" condition) (Figures 4C

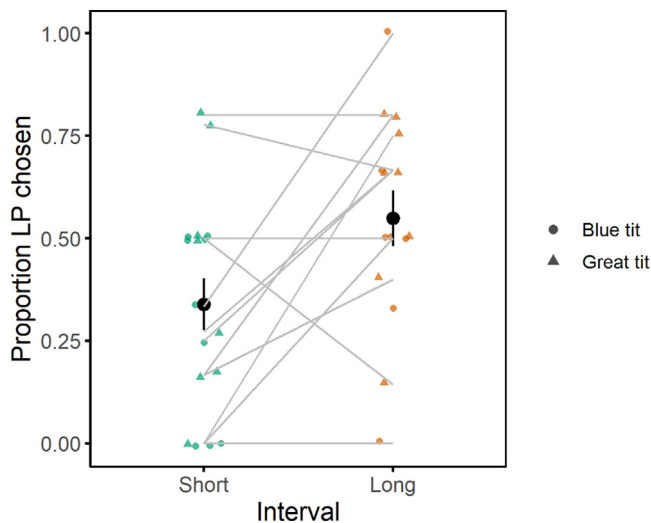


**Figure 2. Schematic representation of the feeder arrays in the training and test phases across the what-where-when memory experiment** (A and B) In the training phase, the birds experienced the “rules” of each feeder type, containing either the preferred food (sunflower seeds) or the less-preferred food (peanuts). Feeder rules: (A) once a bird visited the preferred feeder, this triggered the start of the depletion period, in which they had 2 h to forage until the feeder became inaccessible (the door remained closed) during the replenish period, lasting until the program reset the following morning; (B) birds had free access at any time to the less-preferred feeder. In the test phase, the feeder rules remained the same, but each test period was set up in a trial-unique feeder array composition and location. The contents of the feeders in all phases were not visible until a choice was made.

(C) Depicts “correct” choices in the test phase, i.e., when a bird had returned (after their initial visit) following a short interval (during the depletion period, when the preferred feeder was available) or a long interval (during the replenish period, when the preferred feeder was unavailable). Image sources: Pixabay (bird); Freemages (seeds and peanuts).

and 4D). We ran both color and pattern trials because we may expect a difference in incidental encoding with respect to visual stimulus type.<sup>71</sup> In the “encoding phase,” only one feeder within the array contained food (Figures 4A and 4C). In this phase, the food contents were visible as a salient, unconditioned stimulus to obtain food, and other visual and spatial information were unlikely to be explicitly encoded and thus represented incidental information. After 30 min, the feeders were taken down. Only birds that visited the feeders over a single experience (see STAR Methods for details), were included in the analysis (because

repeated exposure may lead to explicit encoding). 1 h later, the feeders were set up again for the “memory phase” (Figures 4B and 4D). In this phase, the contents of all the feeders were not visible, forcing the use of memory to attempt to locate the food. If birds were able to encode and recall incidental information regarding the spatial position or visual characteristics of the feeders, then they should preferentially visit the feeder that previously contained food (i.e., in the same spatial position or with the same visual characteristic). Only a bird’s first choice to any feeder was counted in the analysis.



**Figure 3. Blue tits and great tits in the what-where-when memory experiment switched their preference from visiting their preferred feeder when the food was available (short interval) to visit the less-preferred feeder when their preferred food was no longer available (long interval)**

Colored dots show the proportion of visits to the peanut feeder across trials for each individual. Gray lines connect each individual's proportion of visits across intervals. Large black dots show the mean proportion  $\pm$  standard error (bars). See also [Figure S3](#) and [Table S1](#).

Birds performed significantly above chance levels (1/3) in the where test ( $z = 2.21, p = 0.027, \text{estimate} = 1.76, \text{SE} = 0.796$ ; [Figure 5A](#)), and there was no effect of condition (linear or triangle) ( $z = -0.373, p = 0.709, \text{estimate} = -0.224, \text{SE} = 0.602$ ), trial order (1–4, i.e., 1 trial per condition) ( $z = 0.523, p = 0.601, \text{estimate} = 0.281, \text{SE} = 0.537$ ), species (blue tit or great tit) ( $z = -0.992, p = 0.321, \text{estimate} = -0.774, \text{SE} = 0.780$ ), or age (adult or juvenile) ( $z = 0.940, p = 0.347, \text{estimate} = 0.531, \text{SE} = 0.565$ ). In the which test, there was a significant effect of age ( $z = 3.21, p = 0.00135, \text{estimate} = 3.041, \text{SE} = 0.949$ ; [Figure 5B](#)). Juvenile birds performed significantly above chance levels ( $p < 0.001$ ), but adults did not ( $p = 0.973$ ). There was no effect of condition (color or pattern) ( $z = -0.809, p = 0.419, \text{estimate} = -0.723, \text{SE} = 0.895$ ), trial order ( $z = 0.292, p = 0.770, \text{estimate} = 0.135, \text{SE} = 0.462$ ), or species ( $z = -1.19, p = 0.233, \text{estimate} = -1.41, \text{SE} = 1.18$ ).

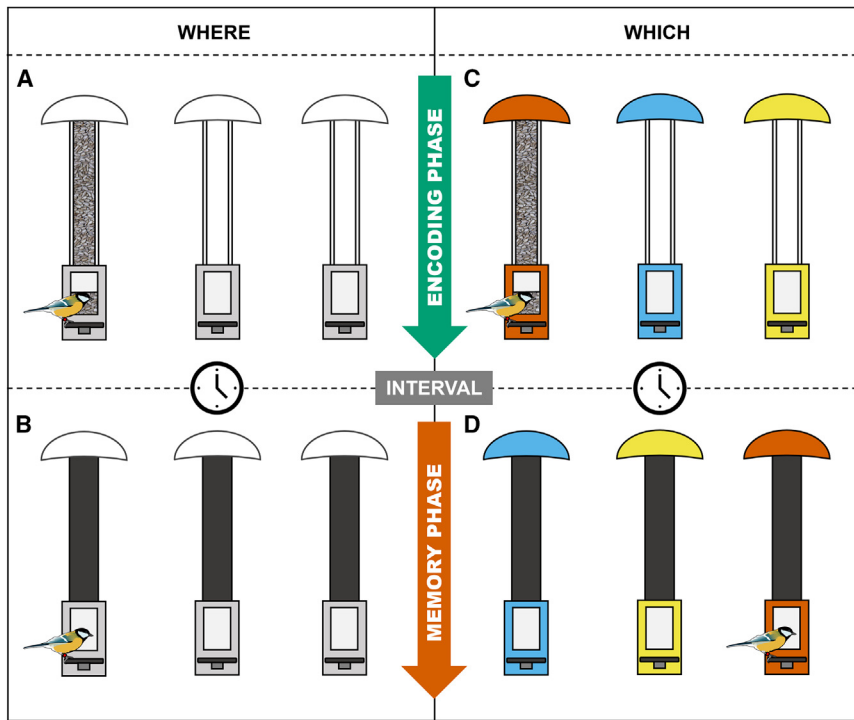
## DISCUSSION

Because our results across both experiments suggest the use of episodic-like memory, we provide two lines of converging evidence for this ability in non-caching, wild, Paridae species. In trial-unique tests, the birds inhibited their food preferences and visited the less-preferred feeder once the individually triggered 2-h depletion period had ended (after which their preferred food was expected to no longer be available), showing that blue tits and great tits encode and recall information relating to what occurred, where, and how long ago in reference to their previous foraging behavior. Furthermore, as they preferentially revisited the feeders with the same (incidental) characteristics across the experimental phases, the birds also demonstrated their ability to encode and recall incidental spatial information associated with

their earlier foraging experiences, and juveniles, but not adults, demonstrated their ability to encode and recall incidental visual information. These abilities were demonstrated in wild subjects within their natural habitats through the use of simulated ecological contexts and thus suggest a situation in which episodic-like memory appears to have evolved in generalist, non-caching species. Although these species are widely used in studies of (social) learning and problem solving in the wild,<sup>72–75</sup> as well as tests of spatial memory in the lab,<sup>76–78</sup> they are not traditionally considered to be among the most “cognitively complex” non-human taxa<sup>79</sup>; yet, our findings point to these species as novel models for studies in episodic-like memory.

To convincingly propose that the witnessed behaviors here can be explained using an episodic-like memory account, other non-episodic memory-related processes must first be discounted.<sup>51</sup> The first main alternative solution is the use of familiarity judgments. When presented with a choice of stimuli that differ in their relative familiarity, because the subject has encountered one of the stimuli more recently than the other(s), the subject may simply choose the stimuli that seems more (or less) familiar.<sup>14</sup> Because relative familiarity is considered distinct from episodic-like memory,<sup>80</sup> experiments must rule out this possibility.<sup>13,14</sup> In the current experiments, the stimuli (feeders) were always presented to the birds simultaneously, meaning that they all shared the same relative familiarity. Because familiarity with all stimuli is consistent in our study, differential familiarity cues were not available to provide a non-episodic familiarity based method to solve the task.<sup>51</sup> Although in the what-where-when task, the preferred food likely held a higher relative familiarity to the less-preferred food, the feeder contents were not visible until a choice was made; therefore, relative familiarity differences in respect to food items could not have been used here.

In theory, a what-where-when test could be solved using circadian rhythm or daylight cues,<sup>13,27,36,69</sup> rather than personal recollection of a previous, temporally distinct event. We controlled for these confounding cues by setting up feeders in each experimental period (during both training and test phases) at a randomized time between 8 am and 12 pm (in approximately 1-h intervals), ensuring that the birds chose in reference to their initial visit and the subsequent depletion period. Furthermore, because we only counted a bird's first choice for each interval (and thus each individual effectively had a single trial per interval, per session), this excludes the possibility of win-stay/lose-shift solutions (i.e., if they visited the preferred feeder in the replenish period first, found the door to remain closed, then subsequently visited the less-preferred feeder). In addition, we discounted the possibility that social information influenced decisions on which feeder to re-visit. If birds flocking together triggered the depletion period at similar times, they could potentially use social information over personal information when revisiting during the long interval choice period, but this was not observed. Individuals assigned to the test phase arrived in distinct flocks, and consequently, the timings of the depletion and replenish periods for each individual precluded social information as a viable explanation for their choices ([Figure S3](#)). Similarly, as in the incidental encoding tests, all birds were prevented access to the feeders in the memory (test) phase, the only social information available would be that a feeder was unrewarded, in which



**Figure 4. Schematic representation of the feeders across the incidental encoding experiment phases in both the “where” test and the “which” test**

In the encoding phase (A and C), the contents of all feeders were visible, but only one feeder contained food. In the memory phase (B and D), set up after an interval of 1 h, the feeder contents in all feeders were no longer visible (occluded by plastic covers). The position of the feeders (either linear or triangular array) remained consistent between the encoding phase and the memory phase in the where trials (A and B) but were altered (i.e., triangle to linear or vice versa) in which trials (C and D). The position of the birds signifies the “correct” choices in the memory phase, i.e., the location or color of the feeder that contained food in the encoding phase. See also Figure S5. Image sources: Pixabay (bird); Freemages (seeds).

case we would expect birds to attempt to feed at alternative feeders and make erroneous choices, which we did not observe.

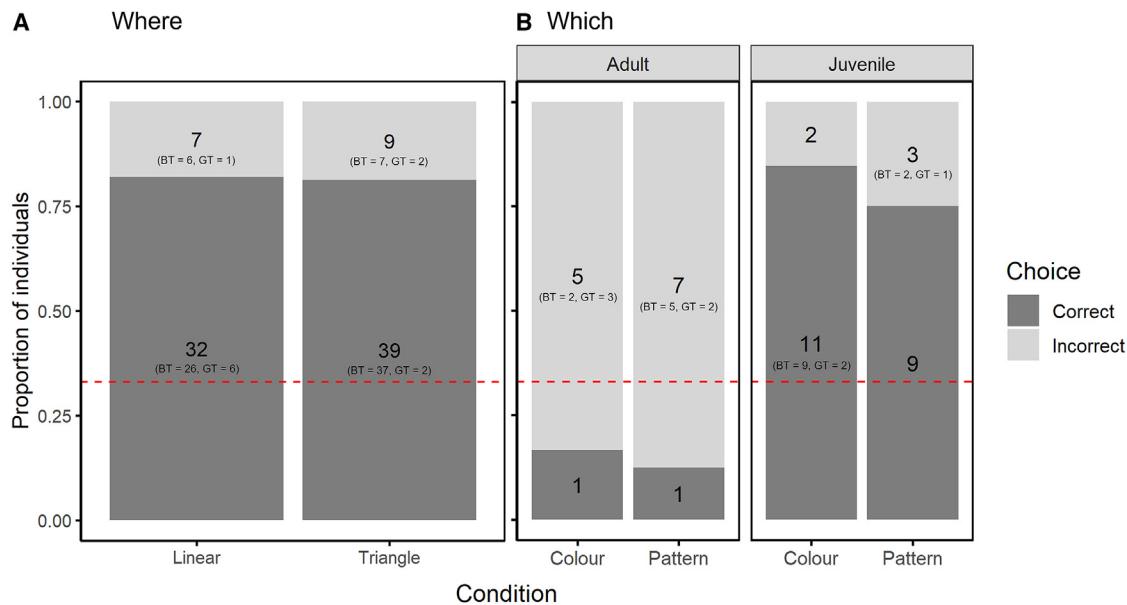
Another possible non-episodic solution is that the subject, at encoding, has retained the relevant information to use it in a subsequent memory test. For instance, rather than remembering back to the original event upon presentation of this memory assessment, as is a defining characteristic of episodic-like memory recall, the subject may be retaining and carrying forward a memory trace representing the required information to use in the subsequent, expected memory test.<sup>51</sup> Although we cannot rule out this mechanism in the what-where-when experiment,<sup>32,47,53,54,60,61</sup> this alternative explanation does not apply to the incidental encoding experiment. When information is encoded incidentally and subsequently assessed in an unexpected test, it is impossible to convert information at encoding into a planned future behavior.<sup>47,51,54,81,82</sup> This is because an animal cannot plan for a future behavior when they do not know that certain information is important and do not know the future presence or nature of a memory test relating to this information.<sup>51</sup>

Taken together, the non-episodic memory processes we describe here do not seem to be sufficient in explaining the performance of the birds in each test, although definitive proof of the use of episodic memory in non-humans through any single paradigm is contestable.<sup>48,51,63</sup> Nevertheless, the contrasting paradigms used here are based on considerably different techniques and assess different aspects of human episodic memory recall<sup>48</sup>; thus, it is unlikely that both these tests together indicate the false appearance of episodic memory.<sup>51</sup> Overall, we interpret these results as evidence that blue tits and great tits can recall the individual components of episodic-like memory content (what, where, and when), while demonstrating that the usage of this recalled information depends on the subjective passage of time. Additionally, we show that these birds can also recall

humans have conscious access to incidentally encoded information during episodic recall,<sup>83–86</sup> we do not claim that the same is true here and therefore continue to use the term episodic-like memory.<sup>14</sup>

Our results generally show no effect of age on episodic-like memory ability, comparable to other studies with non-mammalian species,<sup>39</sup> although in the current study, juveniles, but not adults, used incidentally encoded visual information in the which test. Juvenile blue tits and great tits are more successful at innovating foraging solutions, argued to be a consequence of being outcompeted by adults who monopolize food.<sup>72</sup> We can only speculate as to whether similar mechanisms explain our findings or why adults passed the where test but not the which test. Perhaps with experience, blue tits and great tits rely on spatial information over visual information. We controlled for spatial information in the which test by altering the spatial array between the encoding and memory phases, meaning that spatial and visual cues did not conflict, but future investigations could evaluate whether juveniles still choose the visually relevant information in the memory phase if spatial cues remained fixed. Age-related decay associated with the hippocampus has been reported in mammals,<sup>48</sup> although this is unlikely to be the case here because plumage characteristics indicate a categorical age of 1 year or above; therefore, many adult birds could be relatively young. Equally we were unable to test for sex effects because blue tits cannot be reliably sexed by plumage characteristics.

Although episodic-like memory studies were initially focused on caching corvids,<sup>14–19,36</sup> with later work on a caching Paridae species<sup>37</sup> (black-capped chickadees, *Poecile atricapillus*), recent evidence suggests that this cognitive ability is present across distantly related taxa with wide-ranging socio-ecological challenges.<sup>13,20,48,64,87,88</sup> Caching Paridae species often outperform non-caching species in spatial memory tasks, e.g., Clayton



**Figure 5. Blue tits and great tits in the incidental encoding experiment chose the correct feeder above chance levels (1/3) in the “where” test, and juveniles, but not adults, chose correctly above chance in the “which” test**

(A) Proportion (y axis) and frequency (inside bars) of choices in the where test.

(B) Proportion and frequency of choices in the which test (separated into adults and juveniles). BT, blue tit; GT, great tit. Frequencies without species breakdown are all blue tits. Dashed red line shows performance expected by chance (1/3). See also Table S2.

and Krebs<sup>76</sup> and Clayton<sup>89</sup> but in some instances blue tits and great tits have performed comparably<sup>76,89</sup> or almost equally.<sup>90</sup> Furthermore, great tits show an ability for observational spatial memory<sup>78</sup> (i.e., remembering the observed locations of food items cached by a heterospecific), whereas caching marsh tits (*Poecile palustris*) are unable to do so.<sup>91</sup> Despite being opportunistic foragers, great tits have recently evolved beak adaptations and associated genetic regions in response to increased reliance on garden feeder provisioning.<sup>92</sup> This raises the question as to whether their adaptive morphological specialization may also extend to cognitive specializations. Moreover, their capacity to switch between food resources that deplete and replenish across spatiotemporal scales, whether it be garden feeders, beechmast crops, or insect larvae abundances, may select for episodic-like memory. If so, we would expect episodic-like memory to be widespread across generalist foragers experiencing patchy, dynamic resources<sup>69</sup> or, indeed, in any animals whose natural habitat contains abundant potential sources of useful information<sup>68,88</sup> that can be amenable to flexible memory systems.

Wild studies have the power to elucidate the evolutionary processes underlying the selection of various cognitive traits<sup>93,94</sup> because the information available to an animal in their natural habitat differs from the lab, and in some cases, lab studies can lead to erroneous results when assessing a specie’s cognition. For example, in a what-where-when experiment, wild-caught black-capped chickadees tested in captivity were only able to recall the “when” information when tested in settings that resembled their natural habitat (i.e., with the test involving foraging in trees).<sup>37</sup> Similarly, captive great tits’ learning performance across different spatial scales did not correlate.<sup>95</sup> Therefore, an

animal’s ability to perform in cognitive tests may be influenced by the scale, availability, or sparsity of the naturally occurring information that they are evolutionarily and developmentally attuned to. By utilizing computerized, autonomous experimental apparatuses with dynamic temporal rules assigned on an individual level, we have demonstrated how episodic-like memory can be tested in a natural setting while controlling for extraneous variables. We encourage the further development of this methodology because we believe it has the potential to enhance our understanding of the evolution of cognition and the varying socio-ecological selection pressures shaping it across taxa.

#### STAR★METHODS

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

- KEY RESOURCES TABLE
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## SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2024.06.029>.

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## AUTHOR CONTRIBUTIONS

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## DECLARATION OF INTERESTS

The authors declare no competing interests.

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## STAR★METHODS

### KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data	Open Science Framework	<a href="https://doi.org/10.17605/OSF.IO/QW7GU">https://doi.org/10.17605/OSF.IO/QW7GU</a>
Experimental models: Organisms/strains		
Blue tit ( <i>Cyanistes caeruleus</i> )	Madingley Wood, Cambridgeshire, UK	N/A
Great tit ( <i>Parus major</i> )	Madingley Wood, Cambridgeshire, UK	N/A

### RESOURCE AVAILABILITY

#### Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, James Davies ([jd940@cam.ac.uk](mailto:jd940@cam.ac.uk)).

#### Materials availability

This study did not generate new unique reagents.

#### Data and code availability

- The data and code have been deposited in an Open Science Framework Repository and are 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.

### EXPERIMENTAL MODEL AND SUBJECT DETAILS

#### General

The experiments were reviewed and approved by the University of Cambridge AWERB (Animal Welfare Ethical Review Body) and were conducted under university non-regulated licence (what-where-when, ZOO68/19; incidental encoding, NR2022/92). Experiments took place in Madingley Wood, Cambridgeshire, UK. Birds were ringed as part of longitudinal population monitoring and fitted with a British Trust for Ornithology (BTO) ring, and a passive integrated transponder (PIT) tag. Blue tits and great tits were sexed and aged according to plumage characteristics, although sexing was unreliable for blue tits and therefore not recorded. As interaction with the experimental feeders was voluntary, not all tagged birds could be used in this study.

#### What-where-when memory

Data were collected from January to March 2022. 77 individuals (blue tits,  $n = 50$ ; great tits,  $n = 27$ ) participated in this experiment. A bird was considered to have participated if they took part in at least 16 training trials (the minimum number of trials that an individual passed the training criterion in, see below for definitions). 19 individuals (blue tits,  $n = 11$ ; great tits,  $n = 8$ ) passed the training criterion (reached in 16–42 trials, mean =  $29.16 \pm 1.60$  SE), and of those, 18 (blue tits,  $n = 10$ ; great tits,  $n = 8$ ) participated in at least one test trial. Sample details (individual characteristics, training criterion pass date and number of trials, and test trial participation) can be found in [Table S1](#).

#### Incidental encoding

Data were collected from January to March 2023. 78 individuals (blue tits,  $n = 66$ ; great tits,  $n = 12$ ) participated in this experiment, in that they completed at least one trial across the experiment (in either “which” or “where” tests). 68 individuals (blue tits,  $n = 58$ ; great tits,  $n = 10$ ) completed at least one where test trial (in either “linear” or “triangle” conditions). Of these, 39 birds completed linear condition trials (blue tits,  $n = 32$ ; great tits,  $n = 7$ ) and 48 completed triangle condition trials (blue tits,  $n = 44$ ; great tits,  $n = 4$ ). 30 individuals (blue tits,  $n = 25$ ; great tits,  $n = 5$ ) completed at least one which test trial (in either “colour” or “pattern” conditions). Of these, 19 birds completed colour condition trials (blue tits,  $n = 14$ ; great tits,  $n = 5$ ) and 20 completed pattern condition trials (blue tits,  $n = 17$ ; great tits,  $n = 3$ ). Sample details (individual characteristics and test trial participation) can be found in [Table S2](#).

## METHOD DETAILS

### General

Feeders were hung from metal poles with squirrel baffle-domes placed above and below the feeder, surrounded by a wire cage to shield from rain and squirrels (Figure 1A). The feeder perch (only large enough for a single bird) contained a strain-gauge, which activated the radio-frequency identification reader (thus saving battery power when birds were not visiting). The feeder logged time-stamped visits for each unique PIT tag number, saved to an SD card. Upon detection of a bird, the programmable rules either triggered or did not trigger the servo-operated door to open. Once a bird left (and its PIT tag was no longer detected), the feeder door quickly closed, preventing access to other birds. Whilst another bird may attempt to access the food before the door closed, we never observed successful scrounging attempts (based on video recordings of feeder activity), so these are likely rare or entirely absent.

### What-where-when

#### Food preference test

The what-where-when memory test requires subjects to switch from preferred to unpreferred food choices once the preferred food item is expected to be unavailable. Therefore, we confirmed that birds exhibited a food preference for sunflower seeds over peanuts by providing birds with a choice between pairs of feeders containing either shelled sunflower hearts or peanut pieces matched for size, deployed in January 2021 and again in November and December 2021. Feeder position was swapped every other day to control for positional preferences. We predicted that birds would visit the sunflower seed feeder more than the peanut feeder (based on personal observations).

#### Training phase

Three feeders were placed in a triangular array (Figure 1), as linear arrays can bias learning speed.<sup>73</sup> Feeders were spaced 2m apart, and at equal distance from cover (bramble bushes and elm trees). All feeder doors faced outward toward cover. We assigned three experimental food items (matched for size) to each feeder location: sunflower seeds (preferred), peanuts (less-preferred), and gravel (control) at random. The control feeder was included to ensure that a bird's choice of feeders was not simply due to the avoidance of another feeder (i.e., if they had learned to avoid the preferred feeder after the depletion period had ended). These food locations remained fixed throughout the training phase. All feeders (including doors) were covered with white tape (Figure 1) to obstruct visual access to the food within, forcing the birds to rely on memory, and to increase their visual salience within the woods. When an individual was first detected on the preferred feeder, a 2 hour "depletion period" was triggered for that individual. In other words, the feeder was only available to an individual for 2 hours, after which point the "replenish period" began and the feeder door remained closed for that individual, until the following day (Figure 2A). By contrast, the less-preferred and control feeders always remained accessible to any PIT tagged bird that foraged at them (Figure 2B). Consequently, the birds had access to all feeders during the depletion phase, but crucially, only the less-preferred and control feeders during the replenish phase. If birds used what-where-when memory, they should preferentially visit the preferred feeder during the depletion period, and switch to visiting the less-preferred feeder during the replenish period. To ensure birds learned "when" the preferred feeder was available relative to their daily initial, rather than using circadian rhythm or daylight cues, the feeders were manually set up between 8am and 12pm (randomised in 1-hour intervals each set up date), thus preventing birds from habitually arriving to the feeders at the same time each morning. Feeders were dismantled the following day just before sunset (2:30-5pm according to daylight cycles) and data were downloaded. To ensure the birds used spatial information, rather than local visual cues, the computerised feeders (as well as the poles and cages) were randomised at each set up (with the food type locations remaining consistent). A bird's "initial visit" was their first visit of the day to the preferred feeder, which began the depletion period. When birds visit the array of feeders to forage, they may make multiple visits before leaving the area. These visits are typically within a 5-minute interval (Figure S4). Therefore, to test whether birds remembered where food was available when, we recorded an individual's visit as a "choice" if they had not been detected at a feeder for at least 5 minutes. This conservative threshold ensured the birds' choice was their first visit following a period of inactivity with the feeders, which we define here as a "foraging event". We recorded two types of choices: "short interval choice", when the preferred food was available, and "long interval choice": when the preferred food was unavailable (Figure 2C). To pass the training phase, individuals had to reach a criterion of 8/10 correct training trials, i.e., choosing the less-preferred feeder first during the replenish period, over a period of 10 days (as only one long interval choice could be made per day). We only counted correct long interval choices towards training trials and the criterion as these choices represent the critical inversion of preference and thus demonstrates that they had learned the "when" component of the feeder rules. Once a bird reached the training criterion, the training feeders became inaccessible to them (including the less-preferred and control feeders), and these individuals were provided access to the test feeders. The test feeders and training feeders ran simultaneously in different locations (see below). Therefore, advancing to the test phase was based on individual-level, rather than population-level, progression. This ensured that birds who reached the criterion were not over-reinforced at the training location, and allowed them to immediately advance to the test phase whilst simultaneously allowing others to continue training

#### Test phase

Feeder arrays were set up in trial-unique locations ("sites") throughout the woods. We selected 15 suitable sites (with roughly equal cover and high bird activity) that were at least 20m apart. The order of sites used was pseudo-randomised, in that no single site was selected more than once until the others had been used. If it was not possible to have all three feeders under completely equal cover,

the positions of the feeders (and thus their contents) were counterbalanced across sites, according to their distance from cover. We identified all sites in advance of the experiment, erected support poles in a triangular array, then designated each feeder position according to relative cover within a site (e.g., the closest feeder to cover = 1, furthest away = 3). This then meant that we counterbalanced the relative cover rating of the feeders so that e.g., the less-preferred feeder was not closest to cover more than the preferred or control feeders across sites. If a site was re-used, the positions of the feeders were changed to ensure that each experimental period was trial-unique. The same feeder rules and set up procedures were used for the test phase as the training phase. In order to be considered as participating and included in the analysis, for each site, individuals had to make at least one initial visit to the preferred feeder (triggering the depletion period), at least one visit to one of the other two feeders during the initial foraging event (so they had the opportunity to experience a preferred feeder, a less-preferred feeder and/or a control feeder; thus allowing an informed choice on subsequent visits), and at least one short or long interval choice. Only a bird's first choice (i.e., their first visit to any feeder following a >5-minute period of inactivity) of the day for each interval (short or long) was counted in the analyses. In other words, an individual only had a single trial per interval for each test session (even if they returned in a subsequent foraging event within interval periods). This ensured that their critical choice regarding which feeder to visit after each interval was based on a memory of the initial visit of the day, rather than a reaction to a non-rewarding feeder (i.e., win-stay/lose-shift). 10 blue tits and 8 great tits participated in test trials and made an average of  $4.28 \pm 0.71$  (SE) short interval choices (min = 0, max = 11) and  $3.44 \pm 0.59$  (SE) long interval choices (min = 0, max = 9). 3 birds made short interval choices but no long interval choices and 1 bird made long interval choices but no short interval choices. Results did not differ if they were removed, so we included them in the analysis to increase the sample size.

### Incidental encoding

As the birds readily forage at artificial feeders, no training phase was required. Three sites were selected as testing sites surrounded by roughly equal tree and bush cover with high levels of bird activity. We placed three feeder poles in an array, each 2m apart. Each feeder pole had a pair of feeders to reduce dominance effects on individual choices. As each pair of feeders represents the information cue, we refer to them as “feeder” for simplicity. Although the cover was roughly equal, the feeders were ranked in order of proximity to cover. The rank of the feeder containing food was counterbalanced across testing periods. The feeders were set up in either a linear array (i.e., in a row) or a triangular array (as in the what-where-when test). The position of the feeder with food (e.g., right, middle or left) was also counterbalanced across test periods. Two incidental encoding tests were conducted: the “where” test (incidental encoding of spatial information) and the “which” test (incidental encoding of visual information). Test types were alternated. Both tests were split into two phases: the “encoding phase” and the “memory phase” (Figure 4). In the encoding phase, the feeders were set up from 8:30-10am. In this phase, only one of the 3 feeders contained food (Figures 4A and 4C). The incidental encoding paradigm works on the basis that food contents were visible as a salient, unconditioned stimulus to obtain food and other visual and spatial information were unlikely to be explicitly encoded. These details were not explicitly trained to be associated with food rewards as there were not repeated trials, thus they did not have the opportunity to learn that this information will become a useful cue to obtain rewards in an anticipated memory test. Instead, the additional visual/spatial information represented background, or incidental, information. Moreover, there was no specific motor training required for this experiment (the birds simply landed on a feeder containing visible food and were not required to learn to perform a specific action to receive this food), it is highly unlikely that these details represented useful information to the birds in obtaining current or future rewards. Therefore, if encoded and utilised at test, this information was encoded automatically, mirroring the incidental encoding process of human episodic memory. However, as with what-where-when memory, we do not know if this recall involves conscious experience as it does with humans. The feeders were left up in the encoding phase format for half an hour in order allow time for the birds to discover the food and to make visits, but to minimise the time for them to visit repeatedly. Only birds that visited the feeders over a single foraging event, and thus a single experience, were included in the analysis (as repeated exposure may lead to the explicit encoding of the feeder details). Any bird with a PIT tag could participate in these trials. After this period, the feeders were taken down. After an hour, the feeders were set up again for the memory phase (Figure 4). In this phase, the contents of all the feeders were not visible (the section containing the food was occluded with plastic covers; Figures 4B and 4D), forcing the use of memory to attempt to locate the food. Only a bird's first choice to any feeder was counted in the analysis. None of the feeders contained food (to control for olfactory or subtle visual cues) and were programmed to inhibit access to any bird (to control for social information).

#### Where test

All feeders in where trials were visually identical. In the encoding phase, the feeders were set up in either a linear array (“linear” condition) or in a triangular array (“triangle” condition). Only individuals' first trial for each condition was counted in the analysis, as although food was not accessible in the memory phase thus preventing positive reinforcement, repeated trials may lead to the explicit encoding of feeder details. During the memory phase, the feeders were set back up in the exact same positions (with the actual feeders and feeder poles swapped to prevent the use of accidental visual cues), so that the “correct” feeder was in the exact same spatial position as the feeder containing food in the encoding phase (Figures S5A–S5D). Consequently, if the birds encoded incidental information regarding the spatial position of the feeder that contained food in the encoding phase, then they should re-visit the feeder in the same position in the memory phase. The conditions (linear or triangle) were alternated across test periods.

#### Which test

Each of the feeders in which trials were visually distinct, in that each was topped by a uniquely painted plastic cover (Figures 4C and 4D). In “colour” condition trials, the cover was painted either yellow, red, or blue (visually discriminable to birds<sup>96</sup> and chosen to stand out against the green foliage) (Figures 4C and 4D). In “pattern” condition trials, the covers were painted white with either straight

black stripes, wavy lines, or spots. We ran both colour and pattern trials as we may expect a difference in incidental encoding with respect to visual stimulus type.<sup>71</sup> Again, only an individual's first trial for each condition was counted in the analysis. In the encoding phase, the feeders were set up in either a linear array or in a triangular array, alternated between each test. During the memory phase, the feeders were set back up, but in the alternative array (i.e., if they were set up in a linear array in the encoding phase, then they would be set up in a triangular array in the memory phase), so that the "correct" feeder was now in a distinct spatial location to the feeder containing food in the encoding phase (Figures S5E–S5H). Consequently, if the birds encoded incidental information regarding the visual characteristic of the feeder that contained food in the encoding phase, then they should re-visit the feeder with the same characteristic in the memory phase. The conditions (colour or pattern) were alternated with each test period.

## QUANTIFICATION AND STATISTICAL ANALYSIS

### General

All analysis were conducted using RStudio.<sup>97,98</sup> Visitation data were sorted and filtered using the "dplyr",<sup>99</sup> "lubridate",<sup>100</sup> and "tidyverse"<sup>101</sup> packages. Generalised linear mixed models (GLMMs) were generated with the "lme4" package.<sup>102</sup> Models' assumptions were checked using the "DHARMA" package.<sup>103</sup>

### What-where-when

#### Food preference test

To test whether birds preferred sunflower seeds over peanuts, we performed two GLMMs with the following response variables: 1. Total number of visits to each feeder with a Poisson distribution, and 2. The proportion of visits to one feeder out of total visits to both feeders with a binomial distribution. We included "feeder" (sunflower seeds or peanuts), "species" (great tit or blue tit) and "season" (Jan or Nov/Dec) as fixed effects, including an interaction between feeder and species, and feeder and season. "Individual" and "day" were included as random effects. For model 1, we included observational level random effects to control for overdispersion, and for model 2, we controlled for total number of visits by including the function offset() and the log of total number of visits to both feeders. Birds visited the sunflower heart feeder significantly more than the peanut feeder ( $z = 5.45$ ,  $p < 0.001$ ; Figure S1), and this effect was most pronounced in January compared to November/December (feeder\*season interaction:  $z = -2.77$ ,  $p = 0.006$ ). There was no significant interaction between species and feeder ( $z = 2.22$ ,  $p = 0.27$ ). The proportion of visits to the sunflower heart feeder was significantly greater than the proportion of visits to the peanut feeder ( $z = 6.3$ ,  $p < 0.001$ ; Figure S2), and this effect was more pronounced in January compared to November/December (feeder\*season interaction:  $z = -4.72$ ,  $p < 0.001$ ). There was no significant interaction between species and feeder ( $z = 1.64$ ,  $p = 0.1$ ), and there were significantly less great tit visits compared to blue tit visits ( $z = -2.8$ ,  $p = 0.005$ ).

#### Main test

If blue tits and great tits pass the what-where-when test, they should choose the non-preferred feeder when the preferred feeder is not available. We quantified this as a relative change in food choice, i.e., if the birds chose the less-preferred feeder more during the replenish period compared to during the depletion period. We ran binomial GLMMs with the response variable of "proportion" of choices to the less-preferred feeder. The full model assessed whether the proportion was influenced by the fixed effects "interval" (short - during the depletion period; or long - during the replenish period), "species" (blue tit or great tit), and "age" (juvenile or adult), with number of "trials" modelled with an offset term (offset(log(trials))) to control for variation in the number of trials each individual participated in, and "individual" as a random effect, as well as interactions between interval and species and interval and age. Non-significant interactions were dropped from the final model to avoid over-fitting and Akaike Information Criterion were  $> 4$  units less in the model without interactions.

#### Satiation test

To test whether performance in the what-where-when test could be explained by birds becoming satiated on sunflower seeds and therefore switched to peanuts, rather than recalling when their preferred food was available, we examined the preference test data when both food types were freely available. We performed GLMMs with the proportion of visits to sunflower hearts out of total visits to both feeders with a binomial distribution. We included "hour of the day" as a fixed variable as we expected the proportion of peanuts to increase throughout the day if birds became satiated on sunflower hearts. We also included an interaction with "species" (blue tit or great tit), and included "day" and "individual" as random effects. We ran this analysis twice, once from the preference test data collected in November, and again with the preference test data collected in January. There was no significant main effect for hour of the day (November:  $z = 0.05$ ,  $p = 0.83$ ; January:  $z = 1.04$ ,  $p = 0.30$ ), and the interaction was non-significant (November:  $z = -0.16$ ,  $p = 0.88$ ; January:  $z = 0.54$ ,  $p = 0.60$ ).

### Incidental encoding

#### Main tests

If blue tits and great tits pass the incidental encoding test, they should choose the feeder that previously contained food (i.e., is in the same spatial position or has the same visual characteristics). For each test (where or which) we conducted binomial GLMMs with the binary response variable of "choice" to the correct feeder. Both models assessed whether choice was influenced by the fixed effects "condition" (where = linear or triangle; which = colour or pattern), "species" (blue tit or great tit) and age (adult or juvenile), and "trial order" (1-4, i.e., 1 trial per condition), with "individual" as a random effect. To test against the null value of

0.33, i.e., if choice was above levels expected by chance, we included an offset model (the logit transform of the null value) as an additional fixed effect. Where appropriate, post hoc binomial tests were run to analyse if data within categories (e.g., age:juvenile) were above chance levels.

**Cover test**

Although the relative position of the feeder containing food in relation to cover (i.e., proximity to foliage cover) was pseudorandomised across the experiment, we ran an additional binomial GLMM with the response variable of “proportion of choices” to each feeder in the memory phases (per test session, in both where and which tests) with the fixed effect relative “cover” (rated 1-3) and “session” as a random effect. Cover did not have a significant effect on the proportion of choices to each feeder across the experiment ( $z = -0.688$ ,  $p = 0.491$ ).