

Reward type influences performance and search structure of an omnivorous bird in an open-field maze

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ABSTRACT

Open-field mazes are routinely used to study the spatial cognitive abilities of birds and are often implicitly assumed to be suitable tests of generic spatial memory ability. In recent years there has been extensive research motivated by considerations of an animals' ecology, demonstrating potential examples of specialisations of spatial cognition, as a result of foraging niche. The study reported here demonstrates differences in maze performance as a function of reward type (nectar and invertebrates) that can be predicted from the natural distributions of these rewards. As well as specific implications for the nature of spatial memory specialisation in this species, the results hold more general implications for the use of open-field mazes as tools for measuring and comparing spatial memory ability between species.

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The radial-arm maze (Olton and Samuelson, 1976) was developed to investigate spatial cognition in rodents. It has become "standard protocol" for assessing spatial abilities in the fields of neuroscience, pharmacology and learning (Dubreuil et al., 2003). The open-field maze, a modification of the radial-arm maze where goals are located in open space rather than at the ends of runways, is better suited for testing birds and has been routinely used as a means of assessing spatial memory ability (Balda and Kamil, 1988; Spetch and Honig, 1988; Spetch, 1990; Olson et al., 1993; Healy and Hurlly, 1995) and comparing ability between groups (Wunderle and Martinez, 1987; Stafford et al., 2006) or species (Hilton and Krebs, 1990; Kamil et al., 1994; Olson et al., 1995; Balda et al., 1997) of birds.

The cognitive demands of an open-field maze task map remarkably well onto those required of a nectar forager searching in a patch of flowers. In both cases the locations of the rewards are visible, fixed and depletable (such that revisits reduce efficiency), and both require an ability to use memory of fine-scale spatial location to guide foraging decisions. It is not surprising then, that a number of studies have reported competent performance of nectar foragers using open-field mazes (Cole et al., 1982; Healy and Hurlly, 1995; Wunderle and Martinez, 1987; Burke and Fulham, 2003). The birds in these studies spontaneously attended to and recalled spatial information in order to avoid recently rewarded locations after a retention interval (win-shift). The tendency to win-shift (as opposed to win-stay) was apparent from the begin-

ning of these experiments, even before birds had an opportunity to learn the reinforcement contingency. It has been shown with noisy miners (Aves: Meliphagidae, *Manorina melanoccephala*), generalist Australian honeyeaters, that this effect occurs when foraging for nectar but not when foraging for invertebrates (Sulikowski and Burke, 2007). In that study, win-shift and win-stay performance were similar and both only marginally above chance when birds were rewarded with invertebrates. One explanation for the birds' failure to use fine-scale spatial information when rewarded with invertebrates is that invertebrates, as prey items, have a different and less distinct distribution than nectar. While distribution may correlate with microhabitat type (Dennis et al., 1998) and so larger areas of a territory may reliably contain prey, the specific point location (as opposed to a larger area, somewhere within which prey may be located) of prey items, especially cryptic ones, is neither predictable nor readily observable during search. Further, the mobility of invertebrates means that even once a prey item has been found, its point location is not necessarily depleted for any reliable length of time.

The aim of the current experiment is to test the extent to which the food-type effect reported by Sulikowski and Burke (2007) is a consequence of differential attention to fine-scale spatial information in a free search situation in an open-field maze. Prior studies and the respective distributions of nectar and invertebrates lead to straightforward predictions about performance. We expect to see better performance from nectar foraging birds, subserved by spontaneous attention to point location information and an ability to avoid revisit errors, and worse performance by comparison for invertebrate foragers as they may attend less, or at least not spontaneously, to point location information.

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1. Materials and methods

1.1. Subjects

Subjects were 8 wild-reared noisy miners (*M. melanocephala*), of unknown age and sex. The birds were trapped in February and May of 2007 and data were collected in July and August of 2007. Birds were housed and tested individually in outdoor aviaries measuring approximately 27 m³, at Macquarie University, Sydney. Birds were maintained on Wombaroo[®] Lorikeet and Honeyeater Food. Data were collected in morning and afternoon testing sessions. Morning sessions were conducted prior to the birds being fed and the daily food was removed 2 h before the afternoon session commenced, and replaced thereafter.

These birds previously participated in colour and spatial learning tasks (data not published). This experience and time spent in captivity were counter-balanced between conditions in this study.

1.2. Apparatus

In each trial, an array of 8 feeders was placed on the front wall of the bird's cage.

Each feeder consisted of a metal lid (approximately 1 cm²) and an opaque plastic well (approximately 1 ml capacity) taped together such that the lid fell shut after the bird departed to make visited and non-visited feeders visually indistinguishable. Due to previous experience, all subjects were adept at opening these feeders before this study commenced.

1.3. Procedure

Birds completed 12 trials; 1 per testing session in each of 6 morning (8–11 am) and afternoon (3–6 pm) sessions. Whether a bird began the experiment with a morning or afternoon session was counter-balanced between conditions. A between-subjects design assigned 4 birds to search for 'nectar' rewards (0.3 ml of a 30%, w/v, sucrose solution in each feeder) and 4 birds to search for invertebrate rewards (half a mealworm, *Tenebrio molitor* larva, in each feeder). Half mealworm rewards allowed the fluids of the larva to spill out into the feeder. This encouraged birds to lick the insides of the feeders as they foraged helping to equalise consumption time between the two rewards.

The feeders were hooked onto the front of the cage at the start of each trial and birds were allowed 10 min to explore the array and obtain the food rewards. There were sixteen potential feeder locations in the array, forming a 120 cm-sided, 4 × 4 square grid, with 40 cm separating each feeder location horizontally and vertically (Fig. 1). The locations of the 8 feeders in each trial were randomly selected from these 16 locations. A bird was considered to have visited a feeder if it opened the lid and probed the feeder with its beak or tongue. A trial was aborted if a bird did not make at least 6 visits to feeders within the 10 min time limit. This criterion excluded just 3 trials over the course of the experiment (which were repeated at the end), 1 from each of 3 subjects.

2. Results

2.1. Performance

The number of correct visits (to feeders not previously probed) made before the first revisit error was analysed using a GLM ANOVA with reward (nectar, invertebrates) as a between-subjects factor and time of day (am, pm) and trial (1–6) as within-subjects factors. There was a significant effect of reward ($F_{(1,6)} = 6.755$,

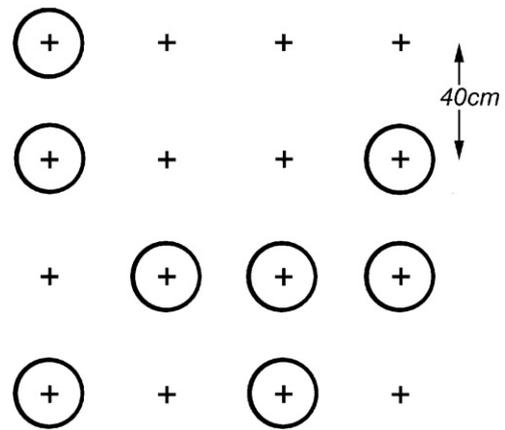


Fig. 1. An example test array. Each cross indicates a potential feeder location. For each trial, 8 of the possible sixteen locations were randomly selected to contain a feeder.

$P = 0.041$) with birds foraging for nectar (hereafter 'nectar birds') making their first revisit error significantly later (after a mean of 6.707 ± 0.164 visits) than 'invertebrate' birds (5.948 ± 0.163 visits; see Fig. 2(A)). There was also a significant time of day × trial linear contrast interaction ($F_{(1,6)} = 6.174$, $P = 0.048$) with performance gradually improving over the pm trials but not over the am trials (see Fig. 2(B)).

Fifty random walk simulations (10 on each of 5 randomly selected test arrays) were conducted to estimate chance performance. In our model the walker stepped from a feeder in any of the 8 possible directions (up, down, left, right, up-right, etc.), with equal likelihood as long as a move in that direction would encounter another feeder (not necessarily adjacently, a single step could move over an empty location to the next feeder). From these simulations we estimated chance performance to be 3.62 ± 0.266 correct visits prior to making an error. One-sample *t*-tests confirmed performance was significantly above chance during both am and pm trials and for both the invertebrate and nectar rewarded groups over all trials (all $t > 7$, all $P < 0.006$).

2.2. Search-bout structure

GLM ANOVAs with factors as described above were used to analyse search-bout structure. While there was no difference between the rewards in the number of visits made per trial ($F_{(1,6)} = 0.006$, $P = 0.939$), there were differences in how these visits were organised into discrete search bouts (a bout ended if the bird left the array and another commenced if the bird returned before the end of the 10 min trial). For both rewards the length of the first bout of a trial was significantly longer than all subsequent bouts (univariate ANOVA, with Bonferroni *post hoc* multiple comparisons; all $P < 0.001$; see Fig. 3(A, ii)), so both the length of the first bout and the average bout length for each trial were analysed.

Analysis of first bout length revealed a significant trial linear contrast ($F_{(1,6)} = 44.944$, $P = 0.001$) and a significant trial × reward linear contrast interaction ($F_{(1,6)} = 13.596$, $P = 0.01$) as invertebrate birds increased the length of their first search bout more dramatically than nectar birds (see Fig. 3(A, i)). The analysis of the average bout length showed a similar pattern, with the trial linear contrast falling just outside significance ($F_{(1,6)} = 5.749$, $P = 0.053$) and a significant trial × reward quadratic contrast interaction ($F_{(1,6)} = 8.185$, $P = 0.029$) with the increase in average bout length in the invertebrate condition occurring only during the final 2 am and pm trials (Fig. 3(A, i)). The increase in average bout length was accom-

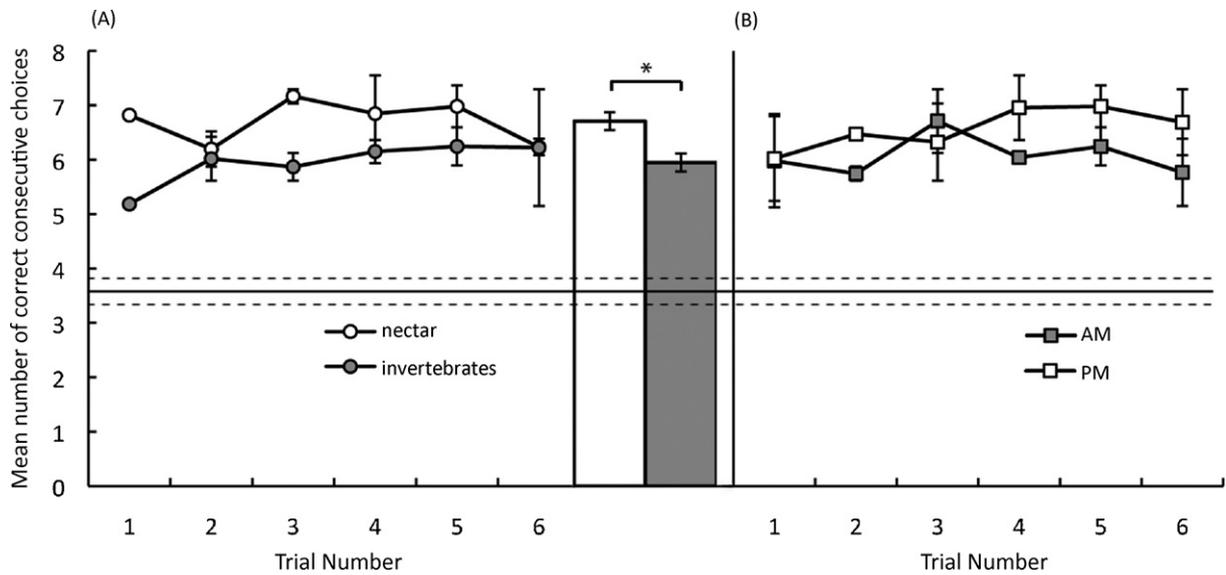


Fig. 2. Performance. (A) Birds searching for nectar rewards made significantly more correct visits to feeders before making their first revisit error, than birds searching for invertebrate rewards. * indicates the significant difference. (B) There was also a significant time of day \times trial linear contrast interaction, with gradual improvement over the pm, but not the am trials. The hard line indicates chance performance (\pm SE) as modelled by a random walk (taken from 50 simulations on five of the test arrays).

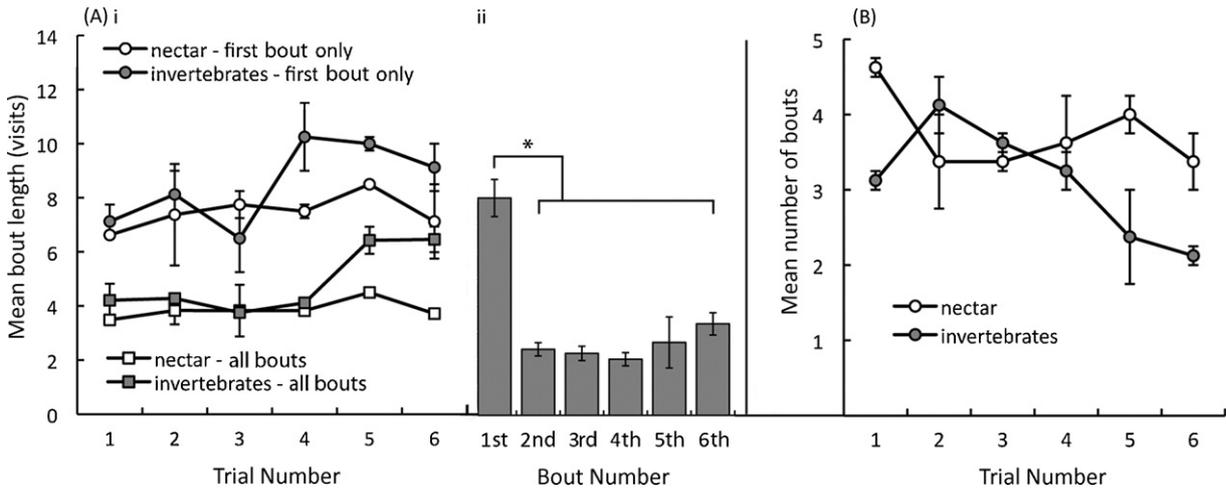


Fig. 3. Search-bout structure. (A, i) A significant trial \times reward type linear contrast interaction (first search bout) and quadratic contrast interaction (all bouts), with only birds searching for invertebrate rewards increasing search bout length towards the end of the experiment. (A, ii) Shows the mean length, of the 1st to the 6th bout of each trial. These means were calculated first for each bird (using only those trials in which that bird had an nth bout) and then averaged across all birds. Both the first bout and mean of all bouts were analysed as the first bout was significantly longer than all subsequent bouts for both reward types combined. (B) Trial \times reward type quadratic contrast interaction (approaching significance), as only birds searching for invertebrate rewards decline in the number of search bouts per trial toward the end of the experiment.

panied by a decrease in the number of bouts per trial with an analysis of number of bouts revealing a significant trial linear contrast ($F_{(1,6)} = 8.750, P = 0.025$) and a near significant trial \times reward quadratic contrast interaction ($F_{(1,6)} = 7.292, P = 0.052$) as nectar birds maintained a steady number of bouts for the last five trials and invertebrate birds decreased their number of bouts over this period (see Fig. 3(B)).

2.3. Motivation

As well as noting the equality of total visits to the array, to further test for possible differences in motivation for the different rewards we measured latency to approach the array after the feeders were placed and time spent foraging in the array during each 10 min trial. Neither latency to approach the array (invertebrate: 6.09 ± 1.52 s, nectar: 5.68 ± 0.95 s, $t_{(6)} = 0.228, P = 0.827$), nor time spent in the array (invertebrate: 2 min 6 s ± 20.4 s, nectar:

2 min 43 s ± 10.4 s; $t_{(6)} = 1.621, P = 0.156$) were significantly different between the groups.

3. Discussion

As predicted, birds foraging for nectar performed better than birds foraging for invertebrates, suggesting that noisy miners may be more likely to attend to small-scale spatial information spontaneously when foraging for nectar than when foraging for invertebrates. The difference is apparent from the first trial, suggesting it does not result from learning during the experiment, but rather an immediate differential response to the two rewards. Whether this is underpinned by an evolved mechanism, or is the result of a general learning mechanism responding to prior life experience is unclear.

Interestingly, there was improvement in performance over the course of the experiment during pm trials only. This may have

resulted from differential motivation or may be evidence of circadian modulation of learning. The latter interpretation is not unprecedented (Chaudhury and Colwell, 2002; Prabhu and Cheng, 2008), but further testing is needed before drawing firm conclusions.

The tendency of invertebrate-foraging birds to combine their search effort into fewer bouts by increasing bout length and decreasing bout number over the experiment is an interesting observation not predicted *a priori*. If invertebrate-foraging birds are not attending to point location information, they may be using a different strategy, one aided by longer bout lengths. There is evidence that insectivorous birds use movement rules during foraging, such as sequentially turning in the same direction after prey capture to achieve area-restricted search (Smith, 1974). Perhaps bout lengths increased in order to minimise disruption to a movement-based strategy. The increase in bout length, however, is unlikely to be tied to the gradual increase in performance in the invertebrate foraging group as the change in bout structure occurs abruptly in the last third of the experiment. The reported differences in bout structure are also unlikely to be due to time constraints. Differences in consumption time per feeder were small between the reward types and each bird spent less than an average of 3 min per 10 min trial foraging in the array, irrespective of reward type. Birds were not, therefore, restricted by time limits in the way they organised their visits into search bouts.

To help rule-out motivational explanations of the performance differences we report, we used three measures (approach latency, mean time spent in the array and mean number of visits to the array). None of these measures showed a significant difference between the reward groups. A related concern that may impact on performance and search-bout structure is differential satiation potential of the rewards. The respective amounts of each reward used in each trial (4 mealworms and 2.4 ml of nectar) are sufficiently below what noisy miners will readily consume within a few minutes (upwards of 20 mealworms and 5 ml of nectar, observed in our lab), and so are likely well within satiation thresholds. While we cannot completely rule out the possibility of subtle undetected motivational differences, or differential satiation potential we conclude that these factors would be unlikely to be major contributors to the differences in performance and search-bout structure we report.

The most famous ecologically inspired applications of open-field mazes compared food-storing and nonstoring species (Hilton and Krebs, 1990; Kamil et al., 1994; Balda et al., 1997). Although not unanimously, these experiments, along with data from other spatial and non-spatial tasks (Balda and Kamil, 1989; Brodbeck, 1994; Krebs et al., 1990; Olson, 1991; Clayton and Krebs, 1994; Brodbeck and Shettleworth, 1995; Healy, 1995; Olson et al., 1995; Bednekoff et al., 1997; McGregor and Healy, 1999; Jones et al., 2002), tended to indicate that food storing birds perform better on (some, though not all) spatial tasks, are more likely to attend to spatial rather than colour cues and may have a longer lasting memory that is less prone to interference, when compared to similar non-storing species. As identified by Kamil (1988) and echoed in Gibson and Kamil (2009) (with similar views expressed by Hampton and Shettleworth, 1996) no one laboratory task can fully illuminate the extent or nature of species differences in cognitive ability. In several instances (Hilton and Krebs, 1990; Healy, 1995; Hampton and Shettleworth, 1996) food-storers did not outperform non-storers on spatial tasks, suggesting that a more detailed consideration of task demands and ecological pressures is appropriate.

An extensive literature exploring birds' use of geometric (Kelly and Spetch, 2001; Gray et al., 2004, 2005), featural (Kelly et al., 1998) and landmark (Sutton, 2002; Sutton and Shettleworth, 2005; Gray and Spetch, 2006) information to solve spatial problems illustrates the value of such considerations. Most recently, Sturz and

Katz (2009) have championed the importance of systematically manipulating task demands and procedures in revealing the mechanisms underlying spatial cognition and in properly identifying meaningful species differences in how these mechanisms operate.

In the current study performance and perhaps search strategy in an open-field maze were influenced by reward type. Birds rewarded with nectar outperformed those rewarded with invertebrates in a way predicted by considerations of the natural distribution of these resources. Further experiments are required to explore the proximate mechanisms by which this occurs. One obvious route is via taste, but differential behavioural responses based on differences in nutrient content and/or gut physiology are also possibilities.

The radial-arm and open-field mazes, rather than tapping into 'general' spatial ability, require a sub-set of specific spatial skills, which will not necessarily be enhanced in all species facing some kind of spatial challenge or, in the case of our study, employed equally in all contexts. Observed differences in these, and other, cognitive paradigms should provide the impetus to ask what it is about the particular species and task involved that is responsible for the differences.

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References

- Balda, R.P., Kamil, A.C., 1988. The spatial memory of Clark's nutcrackers (*Nucifraga columbiana*) in an analogue of the radial arm maze. *Anim. Learn. Behav.* 16, 116–132.
- Balda, R.P., Kamil, A.C., 1989. A comparative study of cache recovery by three corvid species. *Anim. Behav.* 38, 486–495.
- Balda, R.P., Kamil, A.C., Bednekoff, P.A., Hile, A.G., 1997. Species differences in spatial memory performance on a three-dimensional task. *Ethology* 103, 47–55.
- Bednekoff, P.A., Balda, R.P., Kamil, A.C., Hile, A.G., 1997. Long-term spatial memory in four seed-caching corvid species. *Anim. Behav.* 53, 335–341.
- Brodbeck, D.R., 1994. Memory for spatial and local cues—a comparison of a storing and a nonstoring species. *Anim. Learn. Behav.* 22, 119–133.
- Brodbeck, D.R., Shettleworth, S.J., 1995. Matching location and color of a compound stimulus: comparison of a food-storing and nonstoring bird species. *J. Exp. Psychol.: Anim. Behav. Process.* 21, 64–77.
- Burke, D., Fulham, B.J., 2003. An evolved spatial memory bias in a nectar-feeding bird? *Anim. Behav.* 66, 695–701.
- Chaudhury, D., Colwell, C.S., 2002. Circadian modulation of learning and memory in fear-conditioned mice. *Behav. Brain Res.* 133, 95–108.
- Clayton, N.S., Krebs, J.R., 1994. Memory for spatial and object-specific cues in food-storing and non-storing birds. *J. Comp. Physiol. A* 174, 371–379.
- Cole, S., Hainsworth, F.R., Kamil, A.C., Mercier, T., Wolf, L.L., 1982. Spatial-learning as an adaptation in hummingbirds. *Science* 217, 655–657.
- Dennis, P., Young, M.R., Gordon, I.J., 1998. Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. *Ecol. Entomol.* 23, 253–264.
- Dubreuil, D., Tixier, C., Dutrieux, G., Edeline, J.M., 2003. Does the radial arm maze necessarily test spatial memory? *Neurobiol. Learn. Mem.* 79, 109–117.
- Gibson, B., Kamil, A.C., 2009. The synthetic approach to the study of spatial memory: have we properly addressed Tinbergen's "four questions"? *Behav. Process.* 80, 278–287.
- Gray, E.R., Bloomfield, L.L., Ferrey, A., Spetch, M.L., Sturdy, C.B., 2005. Spatial encoding in mountain chickadees: features overshadow geometry. *Biol. Lett.* 1, 314–317.
- Gray, E.R., Spetch, M.L., 2006. Pigeons encode absolute distance but relational direction from landmarks and walls. *J. Exp. Psychol.: Anim. Behav. Process.* 32, 474–480.
- Gray, E.R., Spetch, M.L., Kelly, D.M., Nguyen, A., 2004. Searching in the center: pigeons (*Columba livia*) encode relative distance from walls of an enclosure. *J. Comp. Psychol.* 118, 113–117.
- Hampton, R.R., Shettleworth, S.J., 1996. Hippocampus and memory in a food-storing and in a nonstoring bird species. *Behav. Neurosci.* 110, 946–964.
- Healy, S.D., 1995. Memory for objects and positions: delayed non-matching-to-sample in storing and non-storing tits. *Q. J. Exp. Psychol. B* 48, 179–191.
- Healy, S.D., Hurly, T.A., 1995. Spatial memory in Rufous hummingbirds (*Selasphorus rufus*)—a field test. *Anim. Learn. Behav.* 23, 63–68.

- Hilton, S.C., Krebs, J.K., 1990. Spatial memory of four species of *Parus*: performance in an open-field analogue of a radial maze. *Q. J. Exp. Psychol.* 42B, 345–368.
- Jones, J.E., Antoniadis, E., Shettleworth, S.J., Kamil, A.C., 2002. A comparative study of geometric rule learning by nutcrackers (*Nucifraga columbiana*), pigeons (*Columba livia*), and jackdaws (*Corvus monedula*). *J. Comp. Psychol.* 116, 350–356.
- Kamil, A.C., 1988. A synthetic approach to the study of animal intelligence. In: Leger, D.W. (Ed.), *Comparative Perspectives in Modern Psychology: Nebraska Symposium on Motivation*, vol. 35. University of Nebraska Press, Lincoln, pp. 257–308.
- Kamil, A.C., Balda, R.P., Olson, D.J., 1994. Performance of 4 seed-caching Corvid species in the radial-arm-maze analog. *J. Comp. Psychol.* 108, 385–393.
- Kelly, D.M., Spetch, M.L., 2001. Pigeons encode relative geometry. *J. Exp. Psychol.: Anim. Behav. Process.* 27, 417–422.
- Kelly, D.M., Spetch, M.L., Heth, D.C., 1998. Pigeons' (*Columba livia*) encoding of geometric and featural properties of a spatial environment. *J. Comp. Psychol.* 112, 259–269.
- Krebs, J.R., Healy, S.D., Shettleworth, S.J., 1990. Spatial memory of Paridae: comparison of a storing and a non-storing species, the coal tit, *Parus ater*, and the great tit, *P. major*. *Anim. Behav.* 39, 1127–1137.
- McGregor, A., Healy, S.D., 1999. Spatial accuracy in food-storing and nonstoring birds. *Anim. Behav.* 58, 727–734.
- Olson, D.J., 1991. Species differences in spatial memory among Clark's nutcrackers, scrub jays, and pigeons. *J. Exp. Psychol. Anim. B* 17, 363–376.
- Olson, D.J., Kamil, A.C., Balda, R.P., 1993. Effects of response strategy and retention interval on performance of Clark's nutcrackers in a radial maze analogue. *J. Exp. Psychol.: Anim. Behav. Process.* 19, 138–148.
- Olson, D.J., Kamil, A.C., Balda, R.P., Nims, P.J., 1995. Performance of four seed-caching corvid species in operant tests of nonspatial and spatial memory. *J. Comp. Psychol.* 109, 173–181.
- Olton, D.S., Samuelson, R.J., 1976. Remembrance of places passed: spatial memory in rats. *J. Exp. Psychol.: Anim. Behav. Process.* 2, 97–116.
- Prabhu, C., Cheng, K., 2008. One day is all it takes: circadian modulation of the retrieval of colour memories in honeybees. *Behav. Ecol. Sociobiol.* 63, 11–22.
- Smith, J.N.M., 1974. The food searching behaviour of two European thrushes, II: the adaptiveness of the search patterns. *Behaviour* 49, 1–61.
- Spetch, M.L., Honig, W.K., 1988. Characteristics of pigeons' spatial working memory in an open-field task. *Anim. Learn. Behav.* 16, 123–131.
- Spetch, M.L., 1990. Further studies of pigeons' spatial working memory in the open-field task. *Anim. Learn. Behav.* 18, 332–340.
- Stafford, B.L., Balda, R.P., Kamil, A.C., 2006. Does seed-caching experience affect spatial memory performance by pinyon jays? *Ethology* 112, 1202–1208.
- Sturz, B.R., Katz, J.S., 2009. Learning of absolute and relative distance and direction from discrete visual landmarks by pigeons (*Columba livia*). *J. Comp. Psychol.* 123, 90–113.
- Sulikowski, D., Burke, D., 2007. Food-specific spatial memory biases in an omnivorous bird. *Biol. Lett.* 3, 24–248.
- Sutton, J.E., 2002. Multiple-landmark piloting in pigeons (*Columba livia*): landmark configuration as a discriminative cue. *J. Comp. Psychol.* 116, 391–403.
- Sutton, J.E., Shettleworth, S.J., 2005. Internal sense of direction and landmark use in pigeons (*Columba livia*). *J. Comp. Psychol.* 119, 273–284.
- Wunderle, J.M., Martinez, J.S., 1987. Spatial-learning in the nectarivorous bananaquit—juveniles vs adults. *Anim. Behav.* 35, 652–658.